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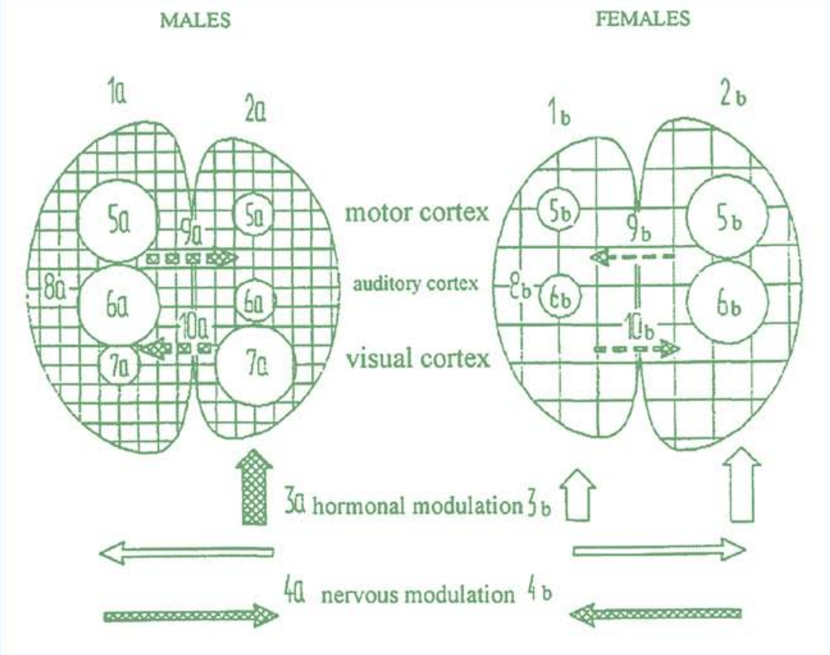
Sex Differences in Lateralization in the Animal Brain

V.L. Bianki and E.B. Filippova

Translated from the Russian by Tatiana A. Ganf



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Sex Differences in Lateralization in the Animal Brain

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CONTENTS

SERIES PREFACE

The workings of the brain, including the human brain are a source of endless fascination. In the last generation, experimental approaches to brain research have expanded massively, partly as a result of the development of powerful new techniques. However, the development of concepts which integrate and make sense of the wealth of available empirical data has lagged far behind the experimental investigation of the brain. This series of books entitled Conceptual Advances in Brain Research (CABR) is intended to provide a forum in which new and interesting conceptual advances can be presented to a wide readership in a coherent and lucid way.

The series will encompass all aspects of the sciences of brain and behaviour, including anatomy, physiology, biochemistry and pharmacology, together with psychological approaches to defining the function of the intact brain. In particular, the series will emphasise modern attempts to forge links between the biological and the psychological levels of describing brain function. It will explore new cybernetic interpretations of the structure of nervous tissue; and it will consider the dynamics of brain activity, integrated across wide areas of the brain and involving vast numbers of nerve cells. These are all subjects which are expanding rapidly at present. Subjects relating to the human nervous system as well as clinical topics related to neurological or psychiatric illnesses will also make important contributions to the series.

These volumes will be aimed at a wide readership within the neurosciences. However, brain research impinges on many other areas of knowledge. Therefore, some volumes may appeal to a readership, extending beyond the neurosciences. Books suitable for the series are monographs, edited multiauthor collections or books deriving from conferences, provided they have a clear underlying conceptual theme. In order to make these books widely accessible within the neurosciences and beyond, the style will emphasise broad scholarship comprehensible by readers in many fields, rather than descriptions in which technical detail of a particular speciality is dominant.

The next decades promise to provide major new revelations about brain function, with far-reaching impact on the way we view ourselves. These great breakthroughs will require a broad interchange of ideas across many fields. We hope that the CABR series plays a significant part in the exploration of this important frontier of knowledge.

Portrait photograph of V.L.Bianki

TRIBUTE TO VSEVOLOD L.BIANKI

Vsevolod L.Bianki was one of the greatest specialists in the field of physiology of higher nervous activity, comparative and developmental physiology, and neurophysiology. All his creative activity was inseparably connected with Saint-Petersburg State University, where he was the creator and head of the laboratory of behavioural neurobiology, attached to the University Institute for Biology. Dr Bianki was the author of more than 250 scientific publications, including six monographs, two of which were published abroad: *The Right and the Left Hemispheres of the Animal Brain,* Gordon and Breach Science Publishers (1988), and *The Mechanisms of Brain Lateralisation,* Ibid (1993). Dr Bianki died in July 1998.

Dr Bianki was mainly concerned with the study of the developmental foundations of the paired functioning of the brain. He discovered the phenomenon of lateral specialization of the animal brain, at the same time as V.Denenberg and F.Nottebohm. The studies of Dr Bianki, and the laboratory headed by him, resulted in establishing that the left and the right animal hemispheres were differentiated for control of a wide range of functions: motor activity, communication, emotional reactions, elaboration of conditioned reflexes, probabilistic learning, noise resistance etc. It was also shown that the main principles of information processing (such as analysis and synthesis, perception of concrete and abstract stimulus characteristics, simultaneous and successive processing) were also lateralized in the animal cortex. These data obtained led Dr Bianki to the conclusion that the emergence of speech in man was the result of the evolution of specialization of the animal brain for analysis of abstract information, and its successive processing.

A number of the investigations of Dr Bianki and his collaborators were devoted to the neurophysiology of interhemispheric relations, and also the grounding of the principle of physiological dominanta as the mechanism of interhemispheric asymmetry. Great attention was also devoted to the study of sexual dimorphism in functional brain asymmetry in animals, the main results of which are described in the present book.

INTRODUCTION

Experimental facts and theoretical tenets accumulated so far make it possible to suggest the appearance of a new trend in those aspects of brain science devoted to functional asymmetry (lateralization) of the brain. The present monograph *Sex Differences in Lateralization in the Animal Brain* is the concluding part of a trilogy devoted to the study of one of the most important properties of the brain–its functional interhemispheric asymmetry. In the first part of the trilogy, *The Asymmetry of the Animal Brain* (Bianki, 1985), the general problems of brain asymmetry were considered. Principles of the general biological significance of functional cerebral asymmetry were advanced and established in that work. The inductive-deductive factor in the manifestation of asymmetry was also considered. In the second and the third parts of the trilogy, particular problems of brain asymmetry are discussed, i.e. the physiological mechanisms of interhemispheric relations (Bianki, 1989) and the correlation between functional brain asymmetry and sex. On the basis of study of the mechanisms of interhemispheric relations the predominant mode of interhemispheric relations was advanced. The monograph on the general problems of brain asymmetry and that on the mechanisms of interhemispheric relations were translated into English (Bianki, 1988; Bianki, 1993).

Not so long ago, little (if any) account was taken of sex differences in many psychiatric, medical and physiological studies. The subjects of study were mainly men. In particular such was the case in American psychology: The number of male subjects was approximately twice as many as female ones in investigations (Holmes and Jorgenson, 1971). A similar situation could also be observed in English studies on the same subject (Borrel and Reid, 1986). Clinical investigations by different defectologists were also mainly performed on men (McGlone, 1980). A real threat was arising of forming 'male' or 'sexless' versions of medicine, psychology and behavioural physiology. A number of declarations were made on the necessity of a sexually differentiated approach to such investigations in text-books and manuals on medicine and education.

There are several reasons for this situation. Many investigations were carried out in male hospitals. In animal studies, males were selected, sometimes deliberately, sometimes accidentally: Their functioning is more stable, and in addition, they are more often trapped by hunters owing to the comparative carelessness of males. It was deemed difficult (and not always necessary) to equalize the sample under investigation for numbers of males and females, or to use mixed samples. Meanwhile a growing number of facts testifying to the possibility of specialised reactions in males and females were being accumulated.

The starting points for the present investigation were facts suggesting the existence of some correlations between the lateral specialization of the human brain and sex.

Functional asymmetry was shown to be more strongly expressed in men than in women (McGlone, 1980). Similar data were described in our preceding monographs based on data obtained from animals. Of great importance were observations made by one member of our laboratory, V.A.Shramm, who worked out a method of determining an animal's sex from the topography of its evoked potential. Nevertheless, as our work progressed, we had to step beyond the theory of brain lateralization and to consider specialization within the brain as a reflection of its more fundamental properties.

Some words should be written about the peculiarities of our approach to the study of the problem under discussion. First of all, we used the inductive method, the techniques of inductive investigation seeming preferable to the deductive method, because of the paucity of the factual material. To some extent we used an unplanned sequence of experimental models, not selecting them beforehand, although we proceeded from a definite hypothesis. Those models could be behavioural, electrophysiological or hormonal, and they concerned different problems of animal physiology. Therefore the monograph may seem somewhat fragmentary. We were always trying to follow the facts and draw conclusions based mainly on experimental results obtained under quite different conditions, conforming, as it were, to the complementarity theory of N.Bohr. It seemed surprising (and reassuring) that (in principle) in a number of cases, the results of behavioural and electrophysiological studies coincided. It should also be emphasized that we sometimes used the neurohormonal approach, and not only the neurological one as had usually been done before. We also proceeded from the well-established concept of partial dominance, and not only from the concept of total hemispheric dominance in humans and animals.

And finally, there is one more specific characteristic of our work: It was performed on animals. From our earlier investigations, and studies by other authors which followed, it became clear that mammalian animals could be good models for studying the lateral specialization of the human brain. It is essential to emphasize that it is very important to be correct in comparing results obtained from humans and from animals. At the same time, use of animal models provides much greater experimental possibilities. The data obtained from such experiments made repeated contributions to theories based mainly on human studies. It should also be noted that, when studying functional asymmetry, we had an impression that the regularities under investigation were revealed more distinctly in animals than in humans, which allowed us to make more categorical conclusions.

As to the authorship, chapters I and IV were written by E.B.Filippova, all the rest of the chapters in the monograph, and general editing belong to V.L.Bianki.

The authors want to thank Dr R.Miller, Professor D.V.Osipov, Professor L.N.Seravin, candidate of biology G.B.Samorodova, candidate of medicine E.N.Ostroukhova, candidate of philology, T.A.Ganf, candidate of biology I.A.Makarova, candidate of biology S.I.Snarsky, candidates of biology V.A.Shramm, E.V.Kharitonov and G.G.Shurgaia.

EDITORIAL COMMENTS

Editing this work from Tatiana Ganf s translation presented some difficulties, partly because of the complexity of the book’s structure, and partly because Vsevolod Bianki was no longer here to answer editorial questions about the sections for which he was primarily responsible. The problems usually involved apparent inconsistencies between text, figures and tables. In most of these cases, careful scrutiny of the manuscript allowed clear editorial decisions to be made. In a few cases the intended meaning could not be clarified. In such instances it was thought important to remain as faithful as possible to the original manuscript; and therefore it was decided to identify the problem areas as ‘unresolved’ rather than impose an arbitrary decision on the manuscript as submitted. These unresolved matters are as follows:

> Figure 7 (p. 47): There is inconsistency between this figure and the text, which would be resolved if ‘2’ indicated ‘left hemisphere *inactivated*’, and ‘3’ indicated ‘right hemisphere *inactivated*’.
>
> Table 1 (p. 52) Item 1b is related to item 5b in the text, but not in the table.
>
> Figure 27 (p. 128). Part III is not wholly consistent with the text on p. 127.
>
> p. 137 (par. 3): Use of the terms ‘direct’ and ‘inverse’ appears not to be the same as defined on p. 117.
>
> Figure 32 (p. 142): It is difficult to match this figure with description in the text.
>
> In Figure 34 (p. 149) and Figure 35 (p. 151) it is not clear how the values of K_c and G_c were turned into laterality indices.

Resolution of the above points might have been possible if Dr Bianki were still alive; and they may also be resolvable for scholars who have access to the original papers in Russian language journals.

A few other points arose where clarification was obtained after discussions with Elena Filippova and Tatiana Ganf:

The word ‘variance’ occurs many times in chapter 2. In the original translation the word was ‘dispersion’. From the contexts in which this word occurs it appears to refer to variance of a measure between individuals, rather than variance of a measure made repeatedly within an individual.

Other matters, identified in the text by numbered superscripts, are as follows:

1. (p. 19): The term 'dominant' is linked with specific functions, and is not a global property of a hemisphere for all functions.

2. (p. 19): In these measures, asymmetry of function 'during concurrent function of the two hemispheres' is not directly observed, but is inferred from the effects of inactivation of one or other hemisphere. This contrasts with data analysis 'during action of an isolated hemisphere' where the emphasis is on comparison of the function of a single hemisphere between groups.

3. (p. 20): See note 2, page 19.

4. (p. 44): See note 2, page 19.

5. (p. 55): See note 2, page 19.

6. (p. 56): See note 2, page 19.

7. (p. 56): See note 2, page 19.

8. (p. 98): All the TCRs recorded were divided into four ranges, depending on the amplitude. The focus of maximum activity was the zone from which the highest amplitude potentials were recorded from the zone under investigation in one of the hemispheres, the location of the stimulating electrode being successively changed within the limits of the cortical zone under investigation.

9. (p. 100): The coefficient of individual asymmetry was calculated according to the formula: $K_{as} = (A - B)/(A + B)$, where A is the corresponding index in the hemisphere dominant in the individual, and B, that in the nondominant hemisphere

10. (p. 150): The author, E.B.Filippova provides the following amplification of this paragraph: 'According to Ukhtomsky the term 'dominanta' represents the stages of the interaction of the nervous centres, which includes a complex of characteristics: the presence of the focus of increased excitability (the dominant focus or the dominant constellation), the summation in it of excitation incoming from other areas, and also their conjugate inhibition. To conclude, the dominanta is the state of interaction between the nervous centres.'

11. (p. 173): Note that the numbering of behavioural measures is given in the legend to this figure.

As editor I am also aware that the experiments described in one section (3.8.) would not be acceptable for publication in modern international journals, for reasons of animal ethics. However, I believe that the work as a whole is of sufficient scientific interest that it should be available in its entirety as an English translation.

Robert Miller

1. Sexual Dimorphism of Interhemispheric Asymmetry in Humans

The problem of functional specialization of the cerebral hemispheres is one of the most obvious problems in modern neurology. Among foreign scientists, great contributions to the study of this problem were made by G.Bogen, A.Galaburda, M.Gazzaniga, N.Geschwind, C.Glick, W.Denenberg, D.Kimura, R.Collins, J.Levi, R.Sperry and many others. In this country interhemispheric asymmetry was investigated by a number of authors and scientific teams: O.S.Adrianov, V.V.Arshavsky, L.J.Balonov, V.L.Bianki, N.N.Braghina, V.L.Deglin, T.A.Dobrokhotova, B.I.Klimentiev, E.A.Kostandov, G.A.Kuraev, V.P.Leutin, L.I.Leushina, J.A.Meerson, V.M.Mosidze, A.A.Nevskaya, L.P.Pavlova, E.S.Petrov, E.G.Simernitskaya, T.P.Khrizman, A.P.Chuprikov and others.

In the course of studying lateral differences in the structure and function of the cerebral hemispheres data have been accumulated on the different degrees of expression of asymmetry in individuals according to their sex. At present the problem of sexual dimorphism of functional specialization between the hemispheres can be considered as an important part of the general problem of lateralization in the nervous system. Determinants of the sex differences in brain organisation have been thought possible in the following domains: physiological (Lansdell and Davie, 1972; Tucker, 1976; Gur *et al.,* 1982), genetic (Stafford, 1961; Money and Alexander, 1966), hormonal (Beker and Ehrhardt, 1974; Resnick *et al.,* 1986; Hampson and Kimura, 1988), differences in the rate of sexual maturation (Waber, 1976), environmental pressures (Maccoby and Jacklin, 1974), and also differences in hemispheric lateralization (McGlone and Kertesz, 1973; Harris, 1978; McGlone, 1978).

1.1. ANATOMICAL STUDIES OF SEXUAL DIMORPHISM OF THE BRAIN

Before considering functional brain asymmetry in men and women, let us dwell on anatomic investigations. The clinician's interest in sexual specificity of brain structure is as old as the study of brain specialisation in humans. In 1880 Crichton-Brown, a pathoanatomist, found that the difference in weight between right and left hemispheres is smaller in women than in men (Crichton-Browne, 1880). In addition, as a result of visual observations, he noted a greater symmetry of the cerebral gyri in women than in men. A similar observation was made later by B.Rubens (Rubens *et al.,* 1976) who reported that,among right-handers, the Sylvian fissure is symmetricalin a greater percentage of women than of men. According to S.Blinkov's data, in men, the average length of the right hemisphere is greater than that of the left hemisphere, this index diminishing with age, while interhemispheric differences are preserved. In women, no differences in the length of the right and left hemispheres, and also no the age changes of this index are observed (Blinkov, 1940). In disagreement with this, according to the later hypothesis of Buffrey and Gray (1972), the male brain was organized more symmetrically than the female brain. However, this hypothes is has found little support.

The superior surface of the temporal lobe, lying anterior to Heschl's gyrus–the so called planum temporale–is connected with auditory speech functions in humans. In 1968 N.Geschwind and W.Levitsky, studying brain preparations, reported that, in 65–70% of cases, the surface area of the planum temporale in the left hemisphere is greater than that in the right (Geschwind and Levitsky, 1968). The asymmetry appeared to be quite remarkable: The area of the planum temporale in the left hemisphere was several times larger than the corresponding area in the right hemisphere. In 10% of cases, inverse asymmetry was observed, whereas in the remainder of the preparations these areas were symmetrical. Later it was observed that the planum temporale was larger in the left hemisphere in the adults of both sexes (Teszner *et al.,* 1972; Galaburda *et al.,* 1978), in newborns, and even in foetuses (starting with the 31st week of pregnancy) (Wada *et al.,* 1975). Moreover, according to S.Witelson's data (Witelson and Pallie, 1973) this anatomic asymmetry is more pronounced in newborn girls than in boys. It should be noted however that in adult women a more frequent predominance of the planum temporale was noted in the right hemisphere than in men (McGlone, 1980).

Special attention should be paid to the studies of the anatomy of the corpus callosum, since this commissure, connecting the cortical zones of the left and the right hemispheres, is certainly part of the neuroanatomical substrate of functional specialization. At the beginning of this century R.Bean (1906) established correlation between one measure of the corpus callosum and both race and sex. The author reported that the middle part of the commissure is larger in representatives of the white race than in negroids, and, within each race, it is larger in men than in women. Hence a conclusion was drawn that the most important part of the cerebrum, the frontal lobes, differ between whites and blacks, and between men and women. No such regularity was observed for the posterior part of the corpus callosum. Bean's contemporary, F.Mall (1909) did not support the dependence of the corpus callosum parameters on race and sex.

A group of scientists has shown that the splenial part of the corpus callosum is greater and more prominent in the brains of women than in those of men (De-Lacoste-Utamsing and Holloway, 1982; De-Lacoste *et al.,* 1986; Holloway and De-Lacoste, 1986). It should be noted that the authors of these reports emphasized the preliminary character of their investigations, and the inadequate quantity of preparations. Nevertheless, their conclusions became widely known, and found both supporters (Nasrallah *et al.,* 1985; Clarke *et al.,* 1986; Yoshi *et al.,* 1986) and opponents, who did not observe sex differences, either in the overall size of the corpus callosum section, or in the parameters of parts of it (Demeter *et al.,* 1985; Bleier *et al.,* 1986; Kertesz *et al.,* 1987). In addition the opinion of A.Kertesz and his colleagues (1987), that there is no correlation between brain size and cross-section area of the corpus callosum, is based on the analysis of 167 preparations. S.Witelson (1985) did notice such a correlation, having studied fewer preparations. Consideration should be given to the fact, that according to Passingham's data (1979), the average brain weight in men is 1442 g, and the body height is 172.8 cm, while in women these measurements are 1284 g and 162.8 cm respectively. In other words there is a correlation between body height and brain weight in humans. Analysing these data, M.Peters (1988) assumed that the sexual dimorphism of the corpus callosum can be considered as the consequence of sex differences in the number of nerve cells in the brain. However this problem remains unstudied. Peters comes to the conclusion that sex differences of corpus callosum parameters cannot be considered as established.

In further investigations of S.Witelson (1989) the parameters of a median-sagittal section of the corpus callosum were compared with hand preference, established in patients before death. The author considered the absolute size and the relative size of seven parts of the corpus callosum, connecting different cerebral areas. In individuals with incomplete right handedness, the total area of the corpus callosum section was greater than in complete right-handers. The greatest difference was observed in the posterior segments of the corpus callosum which contain fibres connecting functionally-asymmetric cortical zones–the posterior parietal and superior temporal regions. The area of the anterior part of the corpus callosum was found to be greater in men (in its absolute size); in contrast, in women, a reduction of this commissure was observed as they grew older. A crucial fact is that, in men, the parameters of one of the parts of the corpus callosum, the isthmus, correlated with the degree of hand preference: In incomplete right-handers the width of this segment was greater than in right-handers, whereas in women it practically never changed with handedness. A lower variability in the middle part of the corpus callosum in women was also noted in the work of W.Byne and his associates (1988). Discussing the results obtained, S.Witelson suggested that the greater size of the corpus callosum results in a more intensive interhemispheric interaction, and is the basis of the bilateral representation of functions in left-handers and in individuals with incomplete right-handedness (Witelson, 1985, 1989; Witelson and Nowakowski, 1991). One of the mechanisms of development of anatomic and functional asymmetry may be the elimination of axons and neuronal cell bodies during the process of embryonic and early post-natal ontogenesis–which is supported by the fact that left-handedness is increased among children born prematurely. The natural death of cells, and the elimination of axons in early periods of brain development also depends on the influence of sex hormones. Witelson considers that a low level of androgens in men, or a reduced sensitivity to them, slows down the process of cell destruction in some brain areas, especially in the parieto-temporal region, which causes enlargement of the corresponding areas of the corpus callosum and reduction of asymmetry (Witelson, 1991). This suggestion agrees with data according to which, in left-handers (both men and women) the testosterone level in saliva is lower than in right-handers (Moffat and Hampson, 1996). The suggested hypothesis accounts for lateralization of function in men since they, unlike women, possessed a correlation between the corpus callosum parameters and hand preference. Thus, in the author's opinion, different neurobiological factors should determine hand preference in men and women (Witelson, 1989, 1991).

Sexual dimorphism has also been noted for the *massa intermedia*–the commissure connecting the left and the right sides of the thalamus. According to M.LeMay's data (1980), the *massa intermedia* is more developed in women than in men. Agenesis of this commissure is more frequent in men. Gorski (1991) studied the cross-section of the *massa* *intermedia,* and the anterior commissure (which connects together mainly the temporal areas of the cortex). The massa intermedia was greater on average by 76% in the female than the male brain in the sample, and in preparations containing the anterior commissure, by 53%. This difference was established in spite of the fact that the male brain is in general greater in size than the female brain. The cross-section area of the anterior commissure was also greater in the preparations of the female brain, by 12% on average.

To understand the mechanism of appearance of cerebral asymmetry, sexual differences of the structure of the vascular system of the brain should also be taken into account. Studies of functional disruptions due to unilateral vascular lesions are very important for knowledge of lateral brain specialization. On the whole, thrombosis of the vessels carrying blood to the left side of the brain occurs more often than that on the right side. Left-sided vascular lesions seem to prevail in both men and women (Sinderman *et al.,* 1970; Hutchinson and Acheson, 1975; Kaste and Waltimo, 1976). After the first case of vascular thrombosis, left-sided lesions occurred more frequently in men, whereas they were more often on the right side in women. In addition, thrombosis of larger proximal vessels on the left side is more characteristic of men whereas in women thrombosis of smaller proximal vessels is more frequent (Kaste and Waltimo, 1976). In S.R.Butler's opinion (1984) the peculiarities of brain blood supply in men and women may create a false impression of a greater asymmetry in men, mainly for speech functions since zones of cerebral ischemia resulting from vascular thrombosis are usually larger in men.

It should be concluded that few authors have proposed the existence of sexual dimorphism on the basis of anatomical measures of the brain. As a rule, womens' brains are considered to be more symmetrical than those of men, to judge from the structure of the left and the right hemispheres, and the degree of the development of the commissural systems.

1.2. FUNCTIONAL STUDIES OF SEXUAL DIMORPHISM OF THE BRAIN

Let us now consider data testifying to the presence of sexual differences in the functional specialization of the human brain. The first findings of sexual dimorphism in lateralization of functions were made clinically in patients with left and right hemisphere lesions. Men with a lobectomy in the temporal area of the left hemisphere encountered difficulties in performing verbal tests whereas similar defects in the right hemisphere caused difficulties in performing non-verbal ones. In women, no significant differences between the right and the left side were observed in the development of the pathology (Lansdell and Urbach, 1965). Similar results were obtained by J.McGlone (1978) from studies of brain tumours, and also by G.Bogen (Bogen *et al.,* 1972). Aphasia resulting from left hemisphere pathology is several times more frequent in men than in women, yet after right hemisphere lesion the occurrence of aphasia in men and women is approximately the same (Lansdell, 1961; McGlone and Kertesz, 1973). No significant sex differences in expressive speech during pharmacological inactivation of hemispheres by the Wada test were observed (Lansdell, 1961). Testing some speech functions–speech fluency, ability to make verbal comparisons, and also general verbal intellect showed that in men the ratings of these functions were considerably lower after left hemisphere pathology, whereas in women they were lower after right hemisphere lesions. J.Inglis and associates (1982), studying patients with unilateral brain lesions, noted that, in women, pathological processes in the left hemisphere caused a decrease in both verbal and spatial abilities, whereas after right hemisphere lesions the deficit of both functions was smaller. Thus, in men the left hemisphere seems to have a greater control of speech whereas the cerebral representation of speech mechanisms in women is more bilateral. J.McGlone (1980) believes that sexual dimorphism in verbal functions may be regarded as established.

As for perceptual abilities in patients with unilateral pathology, the data are not so clear cut: In some works a greater bilaterality of function has been shown in women (Lansdell, 1968a; McGlone, 1977), in others it has been revealed in men (Lansdell, 1968b); in some studies, sexual differences are not observed at all (McGlone and Kertesz, 1973; Edwards *et al.,* 1976; Mack and Levine, 1978).

Studies on healthy subjects have been mainly carried out by the methods of dichotic listening, and tachistoscopic presentation of visual stimuli. Dichotic testing, in which different auditory stimuli are presented simultaneously to both ears, has usually revealed a steady right ear advantage in right-handers, while listening to verbal material: numbers, words and syllables (Kimura, 1961, 1966; Darwin, 1971). Left ear preference has been observed for recognition of non-verbal sounds (Kimura, 1964; Currey, 1967; Knox and Kimura, 1970). In many studies it has been noted that the sex of the subjects has a negligible effect on the left hemisphere advantage in perception of verbal material (Bryden, 1965; McGlone and Davidson, 1973; Briggs and Nebes, 1975; McKeever and van Deventer, 1977). There are data showing dominance of the right ear in women (Dorman and Porter, 1975). However, in the studies of D.Lake and M.Bryden (Bryden, 1965; Lake and Bryden, 1976) more men than women showed an advantage of the right ear when presented with words and numbers. A right ear effect which is more pronounced (and more frequent across subjects) is also reported in men by A.Thiste (1975) and R.Marshman and R.Remington (1974). However in a later study, it was observed that even fewer sex differences in verbal abilities are found (Hyde and Lynn, 1988). It should be noted that according to the data of P.Kannon and A.Lipscomb (1974) the auditory threshold in men is lower for the right than for the left ear, whereas no significant evidence of a difference in thresholds has been found in women.

Dominance of the right visual field (left hemisphere) is known to have been established for word and letter identification (Bryden, 1965, 1973; Kimura, 1966; and others), whereas the advantage of the left visual field (right hemisphere) is supposed to have been found for perception of non-verbal stimuli, such as dot localization in space (Kimura, 1966; McGlone and Davidson, 1973), perception of line orientation (Kimura and Durnford, 1974) and that of depth (Durnford and Kimura, 1971). In some studies it has been shown that the right visual field effect for perception of verbal material is expressed more strongly in right-handed men than in right-handed women (Ehrlichman, 1971; Hannay and Malone, 1976; Levy and Reid, 1976; Koil and Siegel, 1978). A more persistent advantage of the left visual field in men than in women has been observed in perception of non-verbal stimuli, such as photographs of faces (Berlucchi *et al.,* 1976; Umilta *et al.,* 1976; Rizzolatti and Buchtel, 1977), scattered dots (Kimura, 1969; Levy *et al.,* 1972; Davidoff, 1977), or line orientation (Walter *et al.,* 1976; Sasanuma and Kobayashi, 1978). In perceiving the schematic representation of faces, visual depth, and in distinguishing shades the left visual field advantage seems to show no sex differences (Durnford, 1970; Fromm, 1977).

Hiscock and his associates summarized data obtained from numerous experiments in which interhemispheric activity was studied in male and female subjects. Significant sexual differences in lateralization of auditory stimulation were observed in 11 experiments. In nine of them interhemispheric differences were greater in men than in women. When visual stimuli were used, functional asymmetry was stronger in men than in women in 17 out of 20 experiments (Hiscock *et al.,* 1994, 1995).

Analysing data on sensorimotor asymmetries, one can observe that left hand preference and cases of mixed hand preference are more often observed in adult men, whereas women are characterized by stronger expression of dextrality (Annett, 1972, 1973; Bryden, 1977; Hicks *et al.,* 1978; and others). Nevertheless, a more pronounced use of the right hand in women is not accompanied by a greater speed and accuracy in its use (Kimura and Davidson, 1975). Left hand preference in men, as distinct from women, was observed in performing a unimanual task for line orientation (Benton *et al.,* 1978). A slower manual reaction in men was observed when stimuli were presented to the left visual field, while in women it happened when they were presented to the right visual field. Despite this, in tests of tactile two-point discrimination, sensitivity to pressure, localization of point stimuli on each side of the body, and also for Braille reading, thresholds on the left side of the body are lower than on the right; but no sex differences are observed (Hermelin and O'Connor, 1971; Oscar-Berman *et al.,* 1978). In a sensorimotor test without visual control, the accuracy of reproduction was higher among right-handed women when they used the right hand and in left-handed men when they used the left hand (Hassler, 1990). Similar results were obtained for visual recognition of the shape of previously-handled objects, the women showing right hand preference, the men exhibiting no preference in unimanual abilities, although their left hand performed better as compared to women. The authors came to the conclusion that men possess right hemisphere dominance for the function under investigation, whereas in women the left hemisphere was dominant (Genetta-Wadley and Swirsky-Sacchetti, 1990). In the work of Bracha and his associates (1987) spontaneous rotational movements of men and women were studied during the day. Men with a strong right hand preference turned mostly to the right, the rest (35% of the sample studied) turned to the left. Those women who were complete right-handers preferred to turn to the left, whereas incomplete right-handers or left handers (15%) did not show any significant preference for turning direction.

Oral speech in right-handers is known to be connected with right hand motor activity. J.Lomas and D.Kimura (1976) showed that reduction in right hand use during verbal activity is observed only in right handed men.

D.Kimura (1983) studied the interaction between speech and motor disruptions, arising as the result of unilateral speech lesions. Women appeared to become both aphasic and apraxic more frequently when the lesion was localised in the left hemisphere anterior to the Rolandic fissure than if it was posterior to it, whereas in men separate symptoms were observed regardless of the anterior-posterior location of the lesion. The author concludes that the organisation of the functions under investigation may be more diffuse in the male than in the female brain. Similar observations were made by C.Mateer and associates (1982), who reported that men made mistakes in naming objects after stimulation of the frontal and the parietal area of the left hemisphere, whereas with women it happened only after stimulation of the left frontal area. Vignolo and his associates (1986) also noted that all cases of complete aphasia in men were the result of the lesions of posterior areas in the left hemisphere, whereas completely aphasic women had lesions in the left anterior areas. Studying healthy subjects M.Kinsbourne and M.Hiscock (1983) suggested that a rigid functional connection between the cortical localization of two functions accounts for interference during their simultaneous activation. Such inhibition/suppression was observed during verbal test performance, with concommitant working of the right hand. P.Lewis and L.Christiansen (1989), using Kinsbournes's concept, showed that in women, as compared to men, there was a lesser degree of dependence of speech function on activity of the right hand. A greater difference between performance with the right and the left hand was also observed in women. In the authors' opinion these data indicate a more diffuse representation of speech and motor zones in the men's left hemisphere and a relatively greater motor asymmetry in women.

EEG recording in the state of rest, and also during cognitive tasks, showed that women were characterized by greater power and interhemispheric coherence of the EEG compared to men (Wada *et al.,* 1996). In women, irrespective of their cognitive activity, activation is more strongly expressed within the range of the alpha rhythm and the high-frequency beta rhythm in the left hemisphere (Flor-Henry and Koles, 1982) as compared to men. Left hemisphere activation, during arithmetic calculations, was stronger in men than in women (Trotman and Hammond, 1979; Ray *et al.,* 1981). S.Butler and his associates (1982) showed that, in men, arithmetic calculations cause activation of the left hemisphere, whereas face recognition causes activation of the right. In women in both cases left hemisphere activation was observed. The authors suggest that, in women, verbal processes are less subject to the influence of competing spatial functions. N.A.Otmakhova (1987) also reported that in men, memorizing words and numbers presented to the ear caused left hemisphere activation, whereas memorizing music activated the right one. Similar EEG changes were observed in women, but they were less distinct. It should be emphasized that it was only in men that reciprocal interhemispheric relations were observed in listening to words and music, when activation of one hemisphere was accompanied by reduction of the activity of the other. In women, in both cases inter-hemispheric relations were complementary.

Thus, from the majority of studies on the sexual dimorphism of hemispheric specialization in humans it follows that the brain is organized more asymmetrically in men than in women. Evidence for this includes data from clinical, dichotic, tachistoscopic, electro-physiological, and also, anatomical studies; and the only data that do not fit in this conclusion is that women prefer the right hand more frequently and more completely than men. J.McGlone (1980) notes that there seem to be more similarities than differences in the main patterns of brain asymmetry of men and women. However, when sex differences are revealed, more attention should be paid to them, in order to extend our knowledge of the brain functions.

Now let us dwell on the sex differences in those intellectual abilities and behaviour, which, in the opinion of some authors, are influenced both by biological and social factors. In their review of this problem E.Maccoby and C.Jacklin (1974) come to the conclusion that sex differences in the following can be regarded as proven: verbal and visuo-spatial functions, mathematical abilities and aggression. Most authors who have studied different speech parameters are unanimous in thinking that women surpass men in speech fluency, speed of naming objects and in formation of speech associations, but men have an advantage in verbal thinking (see review of C.Hutt, 1972). However J.Hyde and M.Linn (1988) consider that women's advantage for speech has lately decreased as compared to the data of E.Maccoby and C.Jacklin. Reduction in intellectual differences between men and women in other fields has also been noted, possibly owing to the greater progress made by women (Rosentall and Rubin, 1988; Feingold, 1988).

Some investigators have a tendency to account for men's higher spatial abilities in terms of biological factors: the rate of growth and maturation, genetic differences, and also the peculiarities of lateralization (Waber, 1976; Annett, 1985; Geschwind and Galaburda, 1985). Thus, J.Levy (1969) suggested that evolutionary factors underlie sexual dimorphism. In her opinion, in the course of human evolution visuo-spatial abilities became naturally consolidated in men, being necessary for hunting, agonistic relations etc. Women's mode of life contributed to the development of verbal skills, social sensitivity and ease of nonverbal communication, indispensable for bringing up children.

In Waber's opinion (1976), sex differences are conditioned not by sex as such, but by the rate of the organism's maturation. According to her data, early maturing individuals possess greater verbal than spatial abilities, whereas individuals maturing later excel in spatial tests, the former possessing less lateralized speech than the latter.

The opposite opinion is that sex differences in spatial abilities are determined socially. Several authors find support for their views in the motor activity and specific characteristics of children's games (Benbow and Stanley, 1983; Newcombe *et al.,* 1983; Tracy, 1987) These authors are of the opinion that there is an interaction between biological and social factors. In accordance with this approach, boys, owing to their natural disposition, are involved in occupations connected with spatial activity, and construction, which determines their interests and behaviour. Later, participation in spatial kinds of activities helps develop these abilities and intensifies sex differences (Casey and Brabeck, 1990). Nevertheless, studies have appeared recently which support the opinion of the influence of biological factors on spatial functions in women. Women with implicit left-handedness, and also those having left-handed relatives, appear to have practically the same abilities as men in visual and mathematical tests (Tan, 1991a; Casey and Brabeck, 1990).

Mathematical sciences are traditionally considered to be the prerogative of men. C.Benbow and J.Stanley (1983), and also M.Linn and A.Petersen (1985), who studied correlations between mathematical and spatial abilities in children, did not find any steady pattern of sex differences in these functions. However, in the work of C.Benbow and J.Stanley (1983) performed on students, it is emphasized that sex differences are noticeable especially in subjects performing high-level mathematical tasks, where the proportion of men to women is 13:1. The difference in the solution of algebraic tasks is very large, but it is not significant in solving arithmetic and geometrical tasks (Benbow, 1988). In his review of this problem, Benbow presents data obtained from examining hundreds of thousands of talented adolescents aged 12–13 in different European countries. No sex differences were revealed in verbal abilities, yet the boys were noted for their higher mathematical abilities. The difference was stable, was observed in many countries, and was especially striking when tasks on higher mathematics were being solved. It is important to note that several physiological characteristics correlate with this gift, such as left-handedness, a disposition to allergy and myopia, and also a bilateral distribution of cognitive functions.

Concerning aggressiveness, in forensic situations, men are known to be involved much more frequently than women. R.Johnson and H.Kaplan (1988) did not find any sexual differences in those cases where aggression developed in response to provocation. A more definite opinion was formed on the qualitative differences in aggressiveness: In the opinion of many authors, men prefer direct aggressive interaction, whereas women prefer it to be indirect.

A number of authors try to explain sex differences in functional lateralization not so much on biological grounds but in terms of the subjects using different strategies in performing verbal and spatial tests. Thus, M.Bryden (1980) considers that discrepancies in the results of tests of men and women is determined not only by differences in cerebral organisation, but also by different strategies in the distribution of attention and information processing, women being characterized by a greater variability. From a tachistoscopic study carried out by J.Bradshaw (1980) it follows that right-handed women resemble left-handed men in the degree of right hemisphere participation in the analysis of speech stimuli. The author thinks that the right hemisphere, controlling visuo-spatial functions in right-handed men, may contain secondary speech mechanisms activated in response to complicated and unfamiliar stimuli. This accounts for women's superiority in speech and their lagging in nonverbal abilities. Similar opinions are held by J.Levy (1969), L.Harris (1978), and also N.Otmakhova (1987): Localization of speech mechanisms not only in the left but also in the right hemisphere of the women's brain accounts for their advantage in performing speech tasks. W.Ray and N.Newcomb (1981), having studied lateral eye movements as an index of activation, concluded that men always approached the solution of spatial tasks in the same way, whereas women had varied approaches, using speech devices. Women's tendency to use verbal strategies in non-verbal tests has also been noted by other authors (Schweitzer and Chako, 1980; Ray and Newcomb, 1981). However N.Wolf (1994) points to the fact that women use a visual strategy when memorizing words, which consists in uniting them into an integrated visual image. On the basis of dichotic testing the author suggests that the degree of lateralization of speech processes in men is higher than in women, but in women the more local speech zones in the left hemisphere exert a weaker inhibiting influence on the right hemisphere, which makes it possible for them to use image-related thinking in performing verbal tasks. Evidence for this is provided by women's advantage in memorizing emotional words presented to the left ear. Thus, the viewpoint has been formulated of biological differences between the male and the female brain, which is intensified under the pressure of social factors.

J.McGlone (1980) questions whether differences in the preferred strategies may have a major influence on the lateralization of cognitive processes in men and women. In our opinion this doubt is justified, since differences in cognitive styles arise as a result of differences in cerebral organization of functions, in individuals of both sexes, and this affects the results of performance on unilateral tests. D.Kimura and R.Harshman (1984) consider women's brains to be as asymmetric as those of men, as concerns the majority of functions (not only speech but also spatial functions), although intrahemispheric integration of speech and motor zones in men is different. The authors find support for the latter opinion in the fact that during dichotic presentation a stronger right ear advantage for verbal tasks was observed in men, while for nonverbal tasks it was greater in women. Left hemisphere lesions reduce the scores for verbal and nonverbal intellect only in men, whereas right hemisphere lesions cause the deficit of spatial abilities both in men and women. A.Galaburda and his associates (1990) also suppose that sexual dimorphism in speech abilities is determined not by different lateralization but by the relative prevalence of intrahemispheric and interhemisheric connections. They reach the conclusion that the male brain was anatomically more symmetrical, interhemispheric connections prevailing over intrahemipsheric ones, whereas the female brain is more asymmetric anatomically and depends to a greater degree upon intrahemispheric asymmetry.

1.3. SEX HORMONES AND INTERHEMISPHERIC ASYMMETRY

Let us move on to a review of data testifying to the role of sex hormones in the development and regulation of interhemispheric asymmetry in men and women. Reproductive processes in female mammals, including humans, are known to be characterized by cyclic changes in the state of the sex apparatus and in sex sensitivity, under the action of cyclic secretion of ovarian hormones (Savchenko, 1967). In its turn, maturation of the ovum, and periodic ovulation are regulated by the follicle stimulating and luteinizing hormones of the pituitary gland. Gonadotrophin secretion is influenced by gonadotrophin releasing hormones or other hypothalamic releasing factors. The centre for tonic secretion of gonadotrophin releasing hormones, localized in the arcuate part of the hypothalamus, provides for steady production of a certain level of follicle stimulating and luteinizing hormones; and the centre for cyclic activity, in the preoptic area and the anterior hypothalamus works periodically, under the action of the high level of estrogens in the blood.

In a study of the neuronal activity of mid-brain structures, sensitive to sex hormones, carried out by V.Babichev (1981) on rats, it was shown that hypothalamic neuronal activity in young females intensified until the vagina opened, the sensitivity of neurones in the tonic centre to physiological doses of estradiol and testosterone being twice as great as in the cyclic one. In males neurones of the preoptic area do not respond to the introduction of hormones. In the author’s opinion, loss of sensitivity in the cyclic centre of the hypothalamus in males occurs owing to the receptors being bound by androgen molecules, which inactivates them. It should be taken into account that in male rats, in the same way as in men, the testicles secrete androgens in the prenatal period, whereas the ovaries of the females remain inactive up to the period of puberty. Thus, under the influence of androgens sexual differentiation of the brain takes place during the critical period. A similar action of hormones on the brain is usually considered as “organizing”, as opposed to the later, “activating” action, which is mainly directed at the central nervous system, and determines functional sex differences in sexual and asexual behaviour, observed in adults.

It should be noted that an influence of sex hormones at the level of performance of sensory and cognitive tasks, irrespective of the functional hemispheric asymmetry, was shown in a number of studies (Gordon *et al.,* 1986; Gordon and Lee, 1986). The activating action of estrogens upon the central nervous system is shown by the lower stimulus intensity needed for performing visuo-spatial tasks in the middle of the cycle in women (Hampson and Kimura, 1988). However, this activation seems to be expressed differently in the left and the right hemispheres.

One of the models for studying the influence of sex hormones on lateralization of functions is the testing of women’s abilities at different stages of the menstrual cycle. In the work of Creutzfeldt and associates (1976) EEG scores were studied, as well as performance in solving a spatial and an arithmetical task. Significant differences were obtained only for the luteal phase of the cycle, when intensification of the frequency of alpha rhythm coincided with an increase in progesterone concentration. In the same period the reaction time in the tests presented became longer just before menstruation or during it. It is characteristic that in women who took contraceptives no such changes were observed. E.Hampson and D.Kimura (1988) compared the level of sex hormones in the course of the cycle with subjects' performance of a complex of manual tests in which the advantage of women had been established, and with their performance of a spatial task, in which men prevailed. The temporal changes in the level of sex hormones appeared to result in noticeable shifts in cognitive abilities, i.e. at the beginning of the luteal phase of the cycle, characterized by a high level of estradiol and progesterone, a better performance was observed on tests of speed of motor coordination and speech articulation, while a deterioration was seen in the performance of perceptual-spatial tasks. Consequently, the high level of female sex hormones improves the performance of those tests in which women excel, and worsens the solution of those tasks where men have an advantage. The authors suggest that sexual differences may be determined by the current hormonal level, and support the assumption made by H.Nyborg (1983) that reduced abilities in spatial analysis in women are connected with the estradiol phases in the course of the cycle. A similar opinion on the influence of the menstrual cycle on lateralization of cerebral functions was given by D.Bibawi and colleagues (1995). E.Hampson and D.Kimura (1988) also suggested that the cortical structures of the left hemisphere responsible for speech and praxis, which possess sexual dimorphism (as mentioned above) seem to be characterized by sensitivity to the activating influence of the hormones.

This supposition was supported by the data of M.Altemus and associates (1989) who found that the right ear advantage in a dichotic test diminished at the end of the luteal phase of the cycle, before menstruation, and increased with the onset of the follicular phase. It should be noted, however, that the effect observed should be compared with the follicle stimulating hormone level, and with that of estradiol whose concentration during that period is comparatively low.

Right hemisphere dominance in face recognition is reduced during the premenstrual phase (Heister *et al.,* 1989). The strongest interhemispheric asymmetry, comparable with the "male" pattern of right hemisphere prevalence in the visuo-spatial tests was observed in women during menstruation, when the level of female sex hormones is at its lowest. In another study (Rode *et al.,* 1995), the reaction time for visuo-motor reactions after lateralized presentation of verbal and visuo-spatial stimuli was studied. In the former case (verbal stimuli) a left hemisphere advantage was observed during both the luteal and the menstrual phase of the cycle, whereas when nonverbalizable stimuli were used interhemispheric asymmetry with right hemisphere advantage was noted only during menstruation. The above data are supported by an earlier observation that in women with a normal cycle the ability for arithmetic calculations is increased during the luteal phase of the cycle, while that for object naming is increased during the preovulatory one (Wuttke *et al.,* 1975).

In the study of H.Gordon and P.Lee (1986) performance of visuo-spatial and verbal tests by men and women was correlated with the level of sex hormones and gonadotrophins. The level of follicle stimulating hormones in men correlated negatively with their spatial abilities, whereas the testosterone level correlated positively. As for luteinizing hormones a tendency for a positive correlation with verbal and visuo-spatial abilities was observed. In women, a similar correspondence between the level of gonadotrophins and cognitive abilities was noted but it was less pronounced: A positive correlation was observed between verbal test performance and the level of luteinizing hormone, and a negative one was seen during the solution of visuo-spatial tasks. The authors point out that on the whole, women were more successful on verbal task performance, whereas men showed better results when solving spatial tasks. They account for these results by a greater gonadotrophin content in women. In the work of D.L.Robinson and K.Kertzman (1990) it is also reported that the lowest score on solution of a visuo-spatial task in women is observed on the tenth day of the cycle, which coincides with the maximum content of follicle stimilating hormone and an increased estradiol level.

One more item supporting the influence of sex hormones upon cognitive abilities can be found in clinical data. It has been observed that an abnormally high concentration of gonadotrophins in adolescents, occurring during, puberty increases their abilities in verbal and sequential tasks, whereas when this level is abnormally low, visuo-spatial abilities are intensified (Gordon, 1980). Earlier it was shown (Waber, 1976) that adolescents at later stages of puberty have advantages in performing verbal tasks, whereas children of the same age with delayed sexual development are better at visuo-spatial ones. Patients with an X-chromosome defect and underdeveloped gonads are weak in performing spatial tasks. On the contrary, in patients with an excess of X-chromosomes more disruptions are observed in verbal abilities than in spatial ones (Rovet and Netley, 1979; Wuttke *et al.,* 1975).

Thus, a relatively high level of hormones and gonadotrophins during the postnatal period in men and women facilitates performance on tasks classed as typically female, i.e. verbal tests and sequencing tasks, whereas lack of these hormones contributes to the successful solution of tasks thought of as male, i.e. visuo-spatial and probably mathematical ones.

Now let us turn to data on the genetic basis of lateralization of cerebral functions, and the influence of hormonal factors. As mentioned above, women are characterized by a more frequent (and greater) preference for the right hand than men. According to M.Annett's theory (1985), the tendency to right-handedness is determined by a single *rs* gene. The presence of the *rs* allele in one or both chromosomes, i.e. *rs*+- or *rs*++, determines lateralization of speech in the left hemisphere, and a preference for the right hand. Left handers, ambidexters and a small number of right handers do not inherit this right-handedness factor, and are characterized by genotype *rs*-. Such individuals constitute approximately 19% of the population, their hand advantage and cerebral lateralization being determined by random factors. The majority of people, about 49%, are heterozygous for this characteristic, that is *rs*+-. M.Annett suggested that the occurrence of such a genotype is higher among individuals with left handed relatives. Approximately 32% of people have an *rs*++ genotype, which results in rigid dominance of the left hemisphere for information processing, steady right handedness and preference for verbal strategies in the solution of spatial tasks. In the author's opinion this is more characteristic of women than of men with the *rs*++ genotype, since, in men, the left hemisphere and speech develop slower. Statistical data on functional lateralization in left handers and right handers support Annett's views: about 62% of the left handers, as well as 95% of the right handers are characterized the dominance of the left hemisphere for speech processes, whereas the right hemisphere controls speech functions in 19% of the left handers and 5% of the right handers.

In a later study, summarising data on the frequency of aphasia and speech disruptions after left and right hemisphere lesions in left- and right-handers Annett concludes that the clinical data and theoretical calculations correspond (Annett and Alexander, 1996).

In accordance with M.Annett's theory, N.Geschwind and A.Galaburda (1985) suggested that the standard dominance pattern should be distinguished from anomalous dominance. The standard pattern of dominance is characterized by complete dominance of the left hemisphere for speech processes and movements of the leading hand, and a complete dominance of the right hemisphere for visuo-spatial functions. This kind of functional hemispheric specialization may appear to be the definitive characteristic of humans as a species. At its most complete it is inherent in right-handed men. The authors proposed that all cases of functional asymmetry deviating from the standard pattern of dominance should be regarded as anomalous dominance. The latter is more or less characteristic of women. The individual pattern of functional asymmetry in men depends upon the testosterone level during the prenatal period. N.Geschwind and A.Galaburda (1985) suggested that an abnormally high concentration of androgens, or increased sensitivity of the foetal brain structures to their action, slows down the growth of certain zones in the left hemisphere. This is compensated for by the extension of other cortical zones, in particular the homologous zones of the right hemisphere and also the ipsilateral areas, uninhibited by androgens. These processes may result in a more symmetrical organization of functions, even to the point of inversion of the standard pattern. The authors state that the cases of abnormal dominance, when the cortical areas whose functions are inhibited under the influence of androgens and are relatively small, correlate with the exhibition of talent, especially in the field of music, mathematics and also extraordinary spatial abilities. On the other hand, abnormal hemispheric dominance as far as it concerns depression of left hemisphere functions, underlies difficulties in learning and a different class of speech deficits: stammering, alexia and disarticulation, autism, and autoimmune diseases. Thus, disruption in the formation of intrahemispheric ensembles under the influence of androgens is the mechanism of either "pathology of talent "or "pathology of defect". Studying hand preference, N.Geschwind and A.Galaburda found that 11% of left-handers and only 4% of right-handers suffer from autoimmune diseases. As for difficulties in learning and speech disruptions, these deficits occur 10 times more frequently among left-handers (or individuals with left-handed relatives). As mentioned above, such disruptions occur more often in boys; usually they correlate with left hand preference, and are explained by the inhibiting influence of testosterone upon the left hemisphere (Geschwind and Galaburda, 1985).

Data have recently appeared which support the above theory. Thus, the study of *post mortem* brain preparations of foetuses showed that in male foetuses there are interhemispheric differences arising from faster development of the right hemisphere or slowing down the development of the left one (De Lacoste *et al.,* 1991). According to other data, the testosterone level in the blood plasma was lower in individuals with the "standard pattern" of dominance than in those with "abnormal dominance" (Tan, 1991b). For testing spatial abilities in women a group of individuals was singled out who performed the task of mental rotation better than others. It was they who had left-handed relatives (Casey and Brabeck, 1990). Further, it was shown that the women who had left-handed relatives often possessed spatial abilities and progressed in mathematics as well as men (Casey and Brabeck, 1989). In studying functional lateralization in alexic children and their parents, all the alexics, and 90% of their parents, brothers, and sisters possessed a right hemisphere-type lateralization of most functions. Among alexics, there were twice as many boys as girls, yet no sex differences in the degree of laterality were observed: the advantage of the right hemisphere in fathers and brothers was the same as in sisters and mothers (Gordon, 1980). Despite this, comparison of testosterone content in blood plasma with the degree of hand preference showed that an increase in the androgen level correlated with intensification of right-handedness (Tan, 1990; 1991a,b), which contradicts the hypothesis of N.Geschwind and A.Galaburda.

The suggestion that left-handedness is connected with the masculinizing influence of hormones during the prenatal period is also supported by investigations carried out recently. Thus, a decrease in the number of right-handers and an increased use of the left hand was observed among the progeny (daughters) of women who had taken estrogens during pregnancy (Schachter, 1994) and in women with the androgenital syndrome (Nass *et al.,* 1987). An increased number of left-handers as compared to the controls, was observed in homosexual women (McCormick *et al.,* 1990) and transsexual men (Watson and Coren, 1992), and also in women who play the role of a man (Casey and Nuttall, 1990). The cross-section area of the anterior commissure, whose average size in women is larger than in men, is larger in homosexual men by 18% compared to heterosexual women, and by 34% compared to heterosexual men (Gorski, 1992). It is also reported that in transsexual women, as the result of androgen application, improvements were observed within three months in the parameters of visuo-spatial tests, as well as deterioration in verbal abilities.

V.A.Geodakian (1993) suggested a hypothesis of sexual dimorphism in cerebral lateralization of functions on the basis of evolutionary concepts. In essence this hypothesis consists of the fact that any open system developing in a changing medium must be subdivided into two subsystems for perfecting its adaptation. These subsystems are specialized, respectively, for operational and conservative characteristics. This subdivision results in asynchronous evolution, since the evolution of the operational system starts and finishes quicker than that of the conservative system. The author considers that the female sex and the right hemisphere is a conservative subsystem, whereas the male sex and the left hemisphere is thought to emphasise the operational subsystem. In the process of phylogeny the genes responsible for sexual characteristics appear first in the genotype of the male sex and are then transferred to the female sex, and moreover control of new functions is primarily localized in the left hemisphere and then moves on to the right one. The author considers speech, writing, finger movements, arithmetic calculations, analytical and abstract thinking to be evolutionarily young functions, which are lateralized in the left hemisphere. On the other hand, visuo-spatial analysis, intonational speech components, intuition, crude hand movements and concrete situational thinking are classed as evolutionarily old functions, governed by the right hemisphere. The stronger lateralization of functions in the male brain is interpreted as indicating earlier evolution compared to women. The same explanation is given for a more frequent occurrence of left-handedness among men, since in the author's opinion control of the movements of the leading hand shifts more quickly from the left to the right hemisphere in men than in women.

1.4. PREVIOUS STUDIES OF SEXUAL DIMORPHISM OF CEREBRAL ASYMMETRY IN ANIMALS

Summing up the published literature, it must be concluded that several aspects of the sexual differences concerned with cerebral lateralization of functions in humans have been studied. As a rule, on each of the problems studied, experimental data and opinions of investigators have been rather diverse, and often contradictory. The fundamental problem of sexual differences in cerebral organization seems difficult to resolve if one keeps to anthropocentric concepts. In our opinion a comparative, physiological and evolutionary approach to the regularities of the right and left hemisphere function, and the study of the models of cerebral asymmetry in animals opens up new vistas in understanding of this problem.

The earliest data on sexual differences in neuronal structures of the left and the right half of the brain, referring to the description of morphological asymmetry in the rat's cerebrum, were carried out by M.Diamond and associates (Diamond, 1987; Diamond *et al.,* 1982). They showed that in male rats the thickness of the cortex, in fields 17, 18, 18a, 4 and 34, is greater in the right than in the left hemisphere. These sexual differences can be traced, with slight variations, throughout the life span of the animals, and are supported by studies at the cellular level (Diamond, 1991). The size of the corpus callosum turned out also to be dependent upon sex: The area of a sagittal section of this commissure was larger in male than in female rats, especially in the anterior regions and in the splenium. Handling contributed to increasing the corpus callosum section, but only in males (Berrebi *et al.,* 1988; Fitch *et al.,* 1990). After equalizing body mass, the brain of the females is heavier (Wahlsten and Bulman-Fleming, 1987). The percentage of the non-myelinated fibres in the anterior part of the corpus callosum in females turned out to be greater than in males (Mack *et al.,* 1995). De Voogd and F.Nottebohm (1981) showed that the size of the hyperstriatum ventrale, the nucleus controlling vocalization in some song birds, is greater in males than in females. Asymmetric control of vocalization in the gerbil was described by S.Dolman and J.Hutchinson (1991): The compact zone of the hypothalamus, concerned with ultrasonic vocalization, is greater in males than in females. The level of vocalization was determined by the function of the left (not the right) compact zone. In male rats, a faster rate of learning and better orientation in a maze was observed (Roof and Havens, 1992), whereas females surpassed the males in reversal of a conditioned reflex (Guillamon *et al.,* 1986).

In several studies, a greater hemispheric asymmetry was demonstrated in males than in females. Thus, imitation of litter mates' behaviour in the maze resulted in the elaboration of asymmetrical motor reactions in males, whereas in the females no unidirectional runs were observed (Collins, 1988). Lesions of the right hemisphere, unlike those on the left side, led to the onset of hyperactivity and lower catecholamine content in male rats, while in females a lower catecholamine level, unaccompanied by hyperactivity, was observed after lesions of both left and right hemispheres (Lipsey and Robinson, 1986; Starkstein *et al.,* 1989). Preference for one side in a T-shaped maze was stronger in male rats compared to the females (Alonso *et al.,* 1991). In retrieving food from a narrow opening, individual asymmetry in use of the forelimb was greater in females, yet in an "asymmetrical" environment lateralization of preference turned out to be greater in males (Collins, 1975; Betancur *et al.,* 1991).

However, in a series of studies S.Glick and his colleagues found greater asymmetry in female rats. In newborn females, unlike males, the tail is oriented to the left (Denenberg, 1981; Rosen *et al.,* 1983) or to the right (Ross *et al.,* 1981), depending on the genetic line. In males, no such phenomenon was observed. Rotational behaviour in rats, both spontaneous and induced by amphetamine, was carried out in the direction of the tail bias in newborn animals, and was also more pronounced in females. In the author's opinion this is accounted for by asymmetry in dopamine content or metabolism in the nigrostriatal system, which is more robust in females (Glick, 1985). It is possible that, in females, asymmetry is expressed more strongly in subcortical structures, whereas in males it occurs at the cortical level. Similar results obtained from humans suggest that spontaneous rotations are to a great degree characteristic of women regardless of general motor activity (Bracha *et al.,* 1987).

A number of studies have established the influence of sex hormones upon the sexual dimorphism of some behavioural and structural characteristics, whose lateral differences have not been studied before, and also upon the interhemispheric asymmetry in males and females. It would be reasonable to consider separately the effects of early hormonal action and the influence of sex hormones in adult animals. Removal of sex glands in male rats has been shown to eliminate sex differences in maze-learning (Guillamon *et al.,* 1986) and in the organization of the hypothalamic apparatus (Matsumoto and Arai, 1986). Neonatal ovariectomy in females improved spatial orientation in adult animals (Roof and Havens, 1992) and changed the pattern of interhemispheric asymmetry in cortical thickness (Diamond *et al.,* 1982); the measures obtained in adult gonadectomized females were similar to those of males. The neonatal action of androgens eliminates sex differences in the number of progesterone receptors in the frontal cortex (Maggi and Lucchi, 1987), in the parameters of the rat's corpus callosum (Fitch *et al.,* 1990), and also in the degree of interhemispheric EEG correlation in rats (J.Juarez *et al.,* 1995). In pregnant females testosterone injection led to changes of the tail position in the female progeny (Rosen *et al.,* 1983). Similar changes in newborns were caused by putting pregnant females under stress, intensification of left-sided rotation being observed after amphetamine challenge (Fride and Weinstock, 1989).

Removal of sex glands in mature male rats eliminated sex differences in the frequency of the instrumental reactions (Heinsbrock *et al.,* 1987), and resulted in increased activity in an open field (Slob *et al.,* 1986). In females, circling behaviour was weakened by stimulation of the hypothalamus (Robinson *et al.,* 1980), and by change in the metabolism of corticosterone in the hypothalamus (Turner and Weaver, 1985) or after amphetamine in the nigrostriatal system (Becker and Ramirez, 1980). After injection of testosterone into the females of some song birds enlargement of nuclei controlling vocalization was noted. This was accompanied by the formation of songs resembling that of males (Nottebohm, 1977; Pohl-Apel, 1985; Nordeen and Nordeen, 1988).

1.5. CONCLUSION

The above data testify to the fact that sexual dimorphism characterizes many behavioural, morphological and biochemical parameters, which are not immediately concerned with sexual behaviour seen in animals, similar to that observed in humans. Interhemispheric differences in the control of some functions are expressed more strongly in males, while differences in other functions are stronger in females. Sex hormones exert both an organizing and modulating influence on left and right hemisphere functions. It should be noted that the effect of gonadectomy or hormonotherapy upon expression of the brain parameters and behaviour under investigation has been noted in all studies where these methods have been used. The results of systematic studies of sex differences in functional interhemispheric asymmetry in animals obtained from model experiments will be given below.

Thus, in investigating the sexual dimorphism of lateral brain specialization in humans and animals it has been established that the functional and structural specificity of the left and the right hemisphere is expressed differently in representatives of the male and female sex. The results obtained may be briefly summarized as follows:

Morphological asymmetry of the cerebral hemispheres seems to be more marked in men. The sizes of different areas of the corpus callosum are also characterized by sexual dimorphism, and correlate differently with function lateralization in men and women. The anterior commissure and the massa intermedia seem to be larger in women. Left hemisphere lesions in men cause deterioration of both verbal and nonverbal intellect, and result in greater speech disruptions compared to women. In other words, the functional role of the left hemisphere in men seems to be more important. When verbal stimuli were presented unilaterally no significant sex differences were revealed, or a considerable advantage of the left hemisphere in men was found. Less ambiguous results were obtained from testing the functions of the right hemisphere: The dominance of this hemisphere for visuo-spatial stimuli is more marked in men. However, presenting auditory nonverbal stimuli reveals a greater asymmetry in women. Sex differences were not observed on visual presentation to the right hemisphere of stimuli which are difficult to verbalize. Men are characterized by a lesser manual asymmetry, due to better performance by the left hand. Women are characterized by more variable thinking when solving both speech and spatial tasks.

The prenatal influence of androgens both in men and women results in right hemisphere advantage and masculinization. A similar action is exerted by testosterone in adults. Two main hypotheses for the mechanism of hormonal influence on interhemispheric asymmetry have been suggested. In N.Geschwind's (1984) opinion, intensification of the inhibitory influence of androgens upon the left hemisphere results in the reduction of functional differences even producing inversion, and also non-right-handedness. On the contrary, Witelson (1991) holds that lack of androgens during the perinatal period slows down the process of directed cellular death, necessary for the formation of anatomical and then functional brain asymmetry. This causes intensification of transcomissural interaction and diminishes brain asymmetry. Estrogens and gonadotrophins enhance the activation of left hemisphere functions and reducte right hemisphere dominance. In other words, superiority of women for speech skills, and men's advantage for visuo-spatial and mathematical ones is largely determined by the influence of sex hormones.

The results of some investigations on animals support the data on sexual dimorphism of cerebral organization in humans, and raise the question that the magnitude of hemispheric difference is a developmental characteristic, indicating asynchronous evolution of the male and female sex (Geodakian, 1993). From our point of view, this opinion is pre-mature. First, neonatal ovariectomy, or blocking of estradiol secretion in females increases asymmetry, and creates the same pattern of interhemispheric differences which is characteristic of intact males; second, neonatal androgenization of females or orchideetomy of males diminishes asymmetry and reduces the degree of sexual dimorphism. It is possible that the characteristic under investigation, structural or functional asymmetry, is expressed to equal degree in the genotype of both males and females, and is modulated only secondarily by sex hormones, with the result that interhemispheric differences are increased in the male, and diminished in the female phenotype.

2. Behavioural Indices

2.1. METHODOLOGICAL NOTES

The presentation of experimental evidence should be preceded by some definitions, and a description of the peculiarities of data processing we have used. Two types of asymmetry were distinguished: Species-specific (populational) and individual (Bianki, 1979b). Species-specific asymmetry, or lateral specialization of the cerebral hemispheres is left-or right-sided asymmetry which prevails significantly in a species (population) as a whole. A good example of species-specific asymmetry is right-handedness in humans. Individual asymmetry is left- or right-sided asymmetry occurring in most representatives of a species (population), but in this case the number of right- and left-sided individuals appears to be approximately equal. For example, this picture can often be observed when studying forepaw preference in animals. It should be emphasized that in the present monograph, except for cases otherwise specified, the term "asymmetry" means species-specific asymmetry, or lateralization of functions.

Dominant and the nondominant hemispheres were distinguished. The hemisphere was held to be dominant if its inactivation resulted in the greater change of the function under investigation[1].

Temporary hemisphere inactivation was achieved by means of spreading depression according to the technique worked out by Bureš and Burešova (1962). For this purpose a piece of filter paper with an area of 2 mm^2, saturated in 25% KC1 solution was applied to the occipital region of the cortex. Complete cortical depression set in 5 min later, and lasted for 3–3.5 hours.

The following quantitative and qualitative criteria for assessing sex differences during concurrent and isolated cerebral hemisphere activity were used.

DURING CONCURRENT FUNCTION OF THE TWO HEMISPHERES[2]:

THE LEVEL OF DISCRIMINATION was determined as the significance of differences between groups of animals of different sexes in the levels of correct reactions (%).

VARIANCE OF THE LEVEL OF DISCRIMINATION was determined as the significance of differences in variances between groups of animals of different sexes, calculated according to Fisher's criterion ($F = \sigma_1^2/\sigma_2^2, \sigma_1 > \sigma_2$). In biological terms, variance was held to be an index of changeability, variability, diffusion, that is, a progressive character ensuring the adaptation of the species.

THE MAGNITUDE OF ASYMMETRY (assessed by the DIFFERENCE criterion) was based on the differences (A-B), where A, B are performance measures, expressed as percentages during the function of one (A) or the other (B) hemispheres. The measure used was the significance of differences in (A-B) between animals of different sexes.

VARIANCE OF ASYMMETRY (assessed by the DIFFERENCE criterion) was determined as the significance of differences in variance between groups of animals of different sexes.

THE MAGNITUDE OF ASYMMETRY (assessed by the K_{as} criterion) was based on the formula $K_{as} = (A-B)/(A+B)$, where A, B are performance measures, expressed as percentages, during the function of the right (left) (A) and the left (right) (B) hemispheres. The measure used was the significance of differences in K_{as} between groups of animals of different sexes.

VARIANCE OF ASYMMETRY (assessed by the K_{as} criterion) was determined as the significance of differences in variance in groups of animals of different sexes.

PENETRANCE OF ASYMMETRY is the quantitative degree of changeability, indicating the ability of a gene to manifest itself in the phenotype (Timofeev-Resovsky and Ivanov, 1966). It is measured as the percentage of individuals, out of the general population, in whom the character in question is present (species-specific asymmetry). It was determined as the significance of differences between groups of animals of different sexes.

EXPRESSION OF ASYMMETRY is the quantitative measure of changeability indicating the degree to which the gene expresses itself in the phenotype (Timofeev-Resovsky and Ivanov, 1966). It is measured as the percentage of individuals with the most expressed asymmetry (the IIIrd range) out of the overall number of animals with species-specific asymmetry. It is determined as the significance of differences between groups of animals of different sexes.

INDIVIDUAL ASYMMETRY was determined as the differences between groups of animals of different sexes, in the K_{as} magnitudes, (where $K_{as} = (A-B)/(A+B)$, and A, B signify the level of performance in the dominant (A) and the non-dominant (B) hemisphere *in the individual*).

Thus three characteristics of variability of asymmetry were used: variance was the general characteristic, and penetrance and strength of expression were quantitative characteristics.

DURING ACTION OF AN ISOLATED HEMISPHERE[3]:

THE LEVEL OF PERFORMANCE CARRIED OUT BY THE LEFT HEMISPHERE AFTER RIGHT HEMISPHERE INACTIVATION (or vice versa) was determined as the significance of differences between the level of correct reactions (%) in groups of animals of different sexes, with the right (or left) hemisphere inactivated.

VARIANCE OF THE LEVEL OF PERFORMANCE CARRIED OUT BY THE LEFT HEMISPHERE AFTER RIGHT HEMISPHERE INACTIVATION (or vice versa). This was determined as the significance of differences of variance between groups of animals of different sexes with the right (or left) hemisphere inactivated.

THE INFLUENCE OF LEFT (or RIGHT) HEMISPHERE INACTIVATION UPON THE LEVEL OF PERFORMANCE was based on the difference in levels of correct reactions between animals with an intact brain and those with left (or right) hemisphere inactivated. The measure used was the significance of the difference in this effect in groups of animals of different sexes.

VARIANCE OF THE CONSEQUENCES OF LEFT (or RIGHT) HEMISPHERE INACTIVATION UPON THE LEVEL OF PERFORMANCE was based on the variance of differences between the levels of correct reactions in individuals with the intact brain and with the left (or right) hemisphere inactivated. The measure used was the significance of differences between groups of animals of different sexes.

2.2. VOCALIZATION

In the well known study of F.Nottebohm (1979), left hemisphere dominance for control of vocalization was shown in canaries. In male canaries the usual vocal repertoire was disrupted much more after destruction of the left than of the right hyperstriatum. The results of the investigation of M.Petersen and his colleagues (Petersen *et al.,* 1978, 1984; Beecher *et al.,* 1979) conducted on Japanese macaques with intact brains point to the fact that in those macaques use of the left hemisphere was prevalent for analysis of sounds which are meaningful for communication. Similar results were also obtained in experiments on monkeys of the same species with unilateral lesions of the auditory cortex (Heffner and Heffner, 1986). J.Dewson (1977, 1978, 1979) established the fact that the left temporal cortex is dominant in Japanese macaques during their performance of auditory tasks. Experiments on domestic mice have also demonstrated the advantage of the left hemisphere for performance of a communicative acoustic task (Ehert, 1987). Earlier we found that in white rats the left hemisphere was dominant for invariant perception of some vowels and consonants of human speech (Bianki, 1985; Bianki *et al.,* 1989a).

In the experiments described below, lateralization of hemispheric control of pain vocalizations in white rats was studied specially (Bianki and Snarsky, 1988). The experiments were carried out on 200 adult white Wistar rats of both sexes. The animals were divided into three approximately equal groups: those with intact brains, those with left and those with right hemisphere inactivated. Temporary hemispheric inactivation was achieved by means of slowly-spreading depression. During the experiment the rat was suspended in a semi-rigid hammock. Bipolar electrodes were fixed to the base of the tail. Via them the animal received 12 electrical stimulations. Current strength was approximately five times threshold. Stimulations were administered every 5–10 s. Pain vocalizations were tape-recorded, and then subjected to special analysis.

The rat responded to each electrical stimulation with a sound signal after a short latency.

Vocalization could contain up to 7 acoustic “pulses”, but in 85% of cases their number was only 1–3. Isolated pulses varied considerably in their acoustic parameters, and were characterized by durations ranging from tens to hundreds of milliseconds, usually by a noise-like type of acoustic spectrum, and in a number of cases by deep amplitude modulations. At the same time the initial pulse of a pain vocalization was observed to differ from the succeeding ones by its higher peak amplitude, the relative stability of its acoustic parameters, and its short latency. In 18% of cases, vocalization consisted of one pulse. Later this allowed us to analyse only the initial pulse of pain vocalizations.

Firstly, measurements of the duration of the initial pulses of pain vocalizations were carried out. The distribution curve of the duration index in animals with an intact brain is two-peaked, and its shape differs from that of a normal distribution.

The spectrograms of the initial pulses of pain vocalizations were studied. On the basis of the two-peaked nature of the duration distribution curves, separate assessments of spectral parameters for short (up to 140 ms) and long (more than 140 ms) pulses were made. In their spectral characteristics, short and long pulses appeared to be different. The short pulses were narrow-band, noise-like signals, with a spectral maximum at about 1.8 kHz. The long pulses were less homogeneous; their spectra were mainly noise-like, and they were characterized by a considerably greater variability of both spectral width and the positions of the spectral maxima, which, as a rule, were 1.8, 3.0 and 3.9 kHz. A certain similarity between the spectral structure of the initial part of short and long pulses was also revealed. No spectral differences were revealed in either short or long pulses between intact animals and rats with left or right hemispheres inactivated.

Thus the two-peaked duration distribution curves, and the spectral differences of the initial vocalization pulses, made it necessary to analyse short and long signals separately. Pulses lasting from 40 to 140 ms were referred to as “short”, those lasting from 140 to 420 ms were considered to be “long”. For the short pulses, we could not find a similar form of pain vocalizations in the rats’ vocal repertoire described in the literature (Maltsev, 1975; Watts, 1980 *et al.*). Short pulses, which we designated as “pain cries”, seem to be the immediate reflection of pain stimulation. From the acoustic description of long pulses they appear to correspond to the continuum of “squeals”, which are usually recorded during both pain stimulation and aggressive-defensive interaction of individuals, and mainly characterize the direction and degree of expression of defensive behaviour (Watts, 1980). They can be designated as “pain squeals”.

Investigations were carried out on the effect of pain cries and pain squeals upon the behaviour of rats in an open field situation, as well as the peculiarities of the rats’ differentiation of a conditioned reflex (Snarsky, 1991). When recordings of these vocalizations (especially of pain cries) were presented, they appeared to inhibit the rats’ behavioural activity. It was also shown that the natural signal meaning of each of the vocalizations used could be changed, when they were used for subsequent differentiation of conditioned reflexes, with food as reinforcement. Special tests were conducted, with new samples of pain vocalizations or synthesized models of them. From this, it became clear that both temporal and spectral characteristics are essential for recognition of vocalizations, with the latter playing the leading role. On the whole, the data obtained show that the communication sounds under investigation have similar importance as signals, providing a bioacoustic expression of negative emotions, the vocal manifestation of different gradations of reaction to pain. In this respect, the aversive action of the pain cry is more expressive than the pain squeal.

Let us focus on the problem of the role of functional interhemispheric asymmetry in the control of pain vocalizations. A definite conclusion about the existence of such asymmetry may be made here if (as is our usual practice) it is accepted that inactivation of the dominant hemisphere results in a greater change of the parameters under investigation than does that of the non-dominant hemisphere. The latency and frequency of occurrence of pain cries in rats appear to be subject to influence of inactivation of the left hemisphere more than that of the right. Greater changes in the frequency of occurrence of pain squeals are observed as the result of left hemisphere inactivation. These data demonstrate the dominance of the left hemisphere in controlling short and long pain vocalizations. Some differences should also be noted: The frequency of occurrence of pain cries increased after inactivation of either the right or left hemispheres, whereas the frequency of pain squeals decreased as the result of left hemisphere inactivation only.

Thus it was possible to show, in a sample of rats of both sexes, that there exists left hemisphere control for pain vocalizations. On the one hand, the left hemisphere contributes more than the right to reduction of the frequency of occurrence of pain cries, and to increase of the latency of pain cries. On the other hand, the left hemisphere increases the frequency of pain squeals. Consequently, left hemisphere dominance for control of vocalization is made manifest by its predominant role in inhibiting pain cries and in facilitating pain squeals. The biological significance of this pattern of results is that those sounds which possess a specific meaning are inhibited, and those sound signals which carry more general communicative information (aggressive-defensive) are activated.

Now let us consider the problem of sexual dimorphism in functional interhemispheric asymmetry for control of pain vocalization in rats (Bianki and Snarsky, 1990; Snarsky, 1994). The general structure of rats' vocal response to painful electric stimulation was shown to be mainly similar between males and females, and to remain almost unchanged after inactivation of either hemisphere. At the same time, after a more detailed analysis of pain vocalizations, sex differences were revealed, not only for some parameters in the normal situation, but also for their changes after unilateral functional decortication.

The shape of the curves for the distribution of duration of the initial pulses of pain vocalizations is similar in males and females: In both cases the distribution is polymodal, one of the peaks being attributed to a range of short durations (50–70 ms), the other to that of long durations (190–320 ms) (Figure 1.1). Nevertheless, the relative shape of the distributions in males and females differs between the group of animals with an intact brain and that with the right hemisphere inactivated. In animals with the left hemisphere inactivated no sexual dimorphism for this characteristic was observed. Consequently, sexual dimorphism of cortical control of pain vocalizations of different durations seems to be characterized by greater differences (and greater variability) between male and female white rats, for left hemisphere function.

Sex differences can be also revealed by analysing the influence of unilateral cortical inactivation upon the distribution of duration of the initial pulses of pain vocalizations (Fig. 1.2). A greater degree and wider range of changes in the distributions of vocalization duration were observed in females as compared to males. In addition, after left and right hemisphere inactivation, a significant reduction of the median duration of pain vocalizations

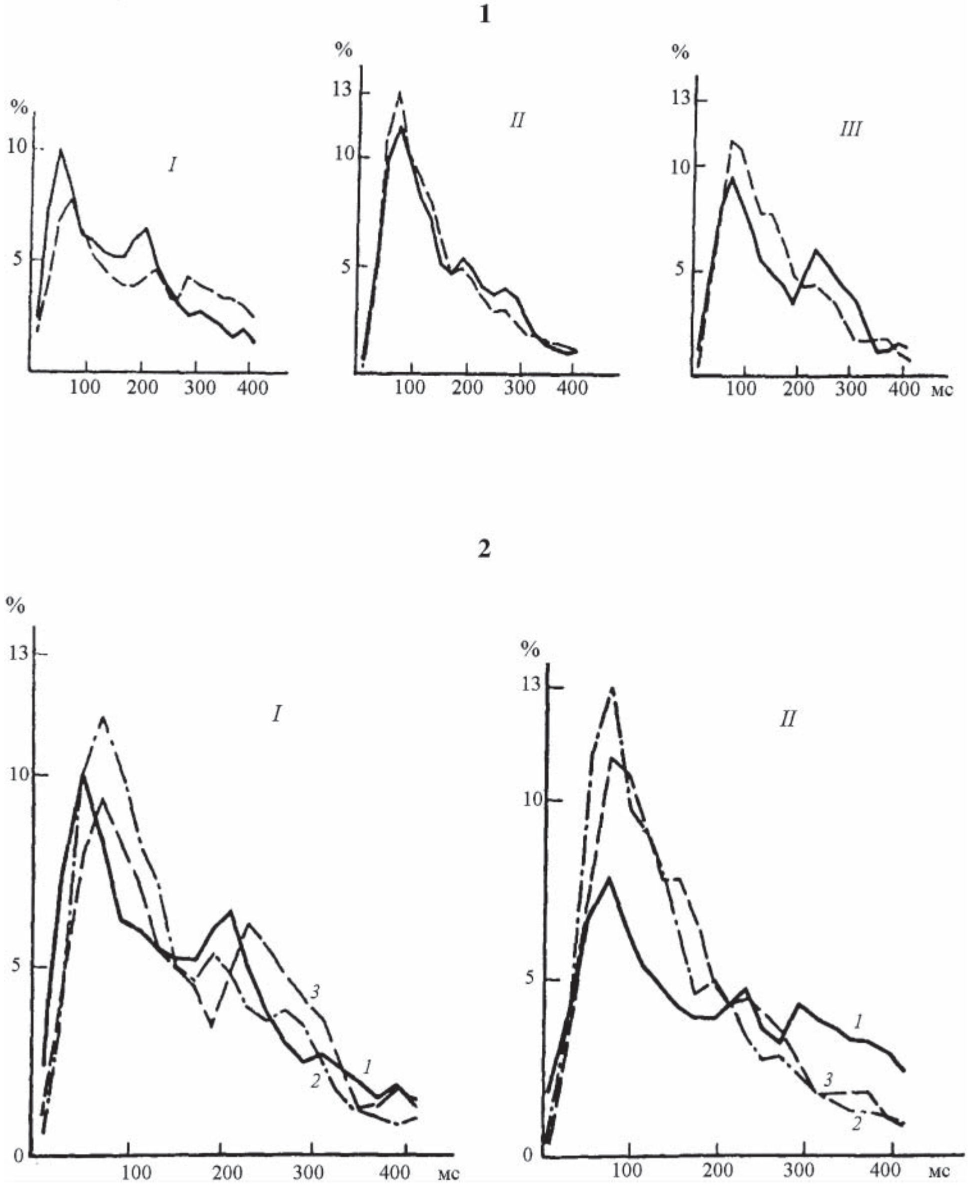


Figure 1: Parameters of the interhemispheric asymmetry of pain vocalizations in males (solid line) and females (broken line). **1:** graphs of the distribution of durations of the initial pulses of pain vocalizations: **I**–intact animals; **II, III**–with left (II) and right (III) hemisphere inactivation. **Abscissa:** duration, ms; **ordinate:** occurrence, %. Bin width: 20 ms. **2**: Distribution of durations of the initial pulses of pain vocalizations before and after hemisphere inactivation: **I**–males, **II**–females; **1**–intact animals, **2**, **3**–those with left (2) and right (3) hemisphere inactivation. **3**: Parameters of pain vocalizations in male and female rats with an intact brain, and with left and right hemisphere inactivation: **I**–cries of pain, **II**–squeals of pain; **a**–latent periods, ms; **b**–probability of occurrence, %; **c**–peak amplitude, conditional units; **1**–intact animals, **2, 3** with left (2) and right (3) hemisphere inactivation. Level of significance **(p)** of differences in vocalization in different animals with left or right hemisphere inactivation from the norm: +-$p<0.05$, +++-$p<0.001$.

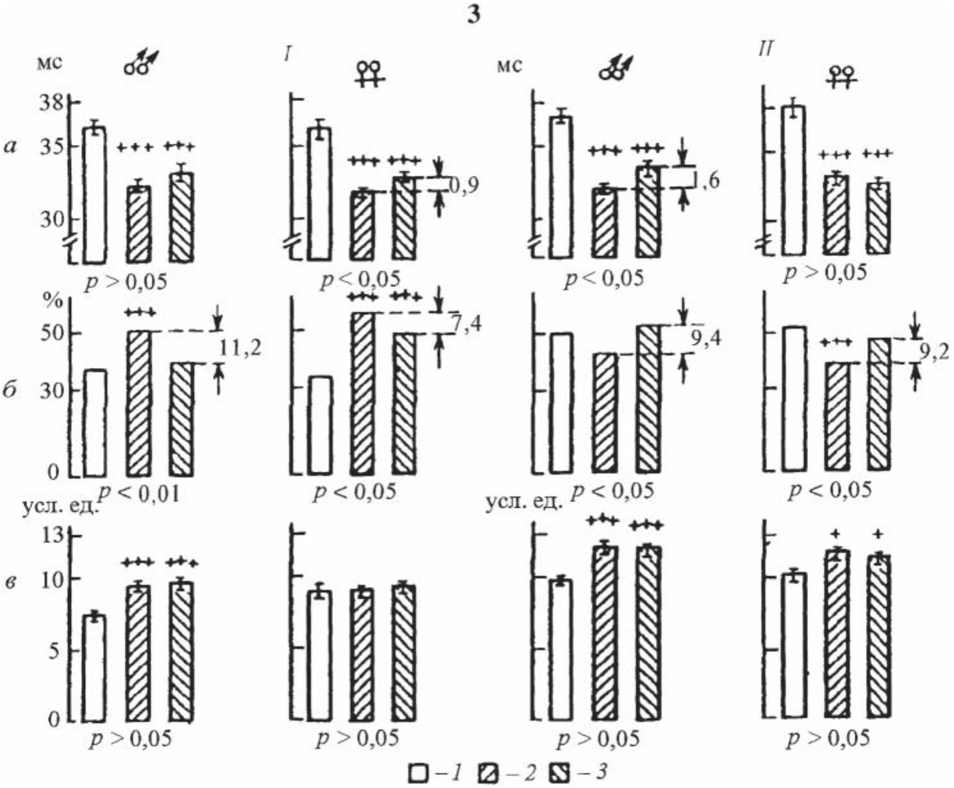


Figure 1: continued

was observed only in females. Thus control of the distribution of vocalization durations is more corticalized in females than in males.

At the same time, lateral differences in control of durations of vocalization, determined by the pattern of distribution during unilateral hemispheric inactivation, were greater in males than in females. Consequently, it can be suggested that, normally, the left and the right hemispheres play different roles in control of the distribution of durations of pain vocalizations, the degree of expression of interhemispheric asymmetry being greater in males than in females.

A further task in the investigation was to attempt to reveal the influence of unilateral inactivation upon different characteristics of pain cries and pain squeals in male and female rats (Fig. 1.3). Cortical inactivation in either hemisphere usually resulted in a reduction of the latency, and growth of the peak amplitude of pain cries and pain squeals in males and females, whereas the frequency of occurrence of pain cries increased, and that of pain squeals diminished. Nevertheless, the range of changes in the latency of pain squeals, and the frequency of pain cries and pain squeals manifestation turned out to be greater in females, whereas the peak amplitude appeared to be greater in males. Sexual dimorphism revealed by changes in the characteristics of pain vocalizations under discussion, took place in different directions depending on the measure used. It also seemed to be conditioned by the peculiarities of the cortical control of mechanisms for initiation and execution of vocalized pain signals in male and female rats.

It is interesting to compare the relative consequences of left and right cortical inactivation in male and female rats, which makes it possible to estimate interhemispheric asymmetry of cortical control, and its sexual dimorphism. In this respect it should be noted that lateral asymmetry is revealed in males and females in an equal number of cases, and is unidirectional. In males, asymmetry was revealed for the latency of pain squeals (Fig. 1.3, II, a) and for the frequency of occurrence of both pain cries and pain squeals (Fig. 1.3, II, b). At the same time, the degree of expression of interhemispheric asymmetry, revealed from the frequency of occurrence of pain cries, was greater in males than in females (Fig. 1.3, I, b).

Now let us attempt to answer the following question: Which hemisphere plays the dominant role in control of pain vocalizations in males and females? For this purpose, when interhemispheric asymmetry was revealed, the size of changes in vocalization characteristics was estimated, having recorded vocalizations after inactivation of left and right hemisphere.

In females, the latency of pain cries decreased more after inactivation of the left hemisphere than after that of the right (Figure 1.3, I, a). In males and females the percentage increase of occurrence of pain cries was greater after left than after right hemisphere inactivation (Figure 1.3, I, b). The left hemisphere dominated in males for the speed of initiation of pain squeals, and the probability of occurrence of pain cries. In males, the latency of pain squeals decreased more after left than after right hemisphere inactivation (Figure 1.3, II, a), whereas in females no lateral differences in latency changes were revealed (Fig. 1.3, II, a). In males there was an insignificant decrease in percentage occurrence of pain squeals after left or right hemisphere inactivation (Figure 1.3, II, b), whereas in females significant changes were observed only after left hemisphere inactivation (Figure 1.3, II, b). Consequently, the left hemisphere dominated for control of initiation of pain squeals in males, and the probability of their occurrence in females.

In summary of these results, it should be noted that both male and female rats preserved the ability for adequate vocal response to painful stimulation after inactivation of either left or right hemispheres. However we managed to find certain sex differences in the changes of some parameters of the vocalizations recorded. It should be observed that this sexual dimorphism was quantitative rather than qualitative. The degree of change, the character of the distribution of changes, and the latency of pain vocalizations were all greater in females after one-sided functional decortication, while that of the peak amplitude was higher in males. Functional interhemispheric asymmetry was significantly stronger in males than in females. Finally, in male rats left hemisphere dominance was revealed for control of the speed of initiation of pain squeals, and in females the left hemisphere was dominant for the rate of initiation of pain cries and the probability of occurrence of both pain squeals and pain cries.

Let us now consider the problem of sex differences in the dynamics of functional interhemispheric asymmetry for control of pain vocalizations (Bianki and Snarsky, 1990). As pointed out, each rat received a series of stimulations consisting of 12 stimuli, with electric currents of 3 mA, and duration of 10 ms, with interstimulus intervals of 5–10 s.

Averaged indices of the influence of unilateral inactivation upon pain cries, as well as of asymmetry, were calculated, at the beginning, in the middle and at the end of the stimulation series (Figure 2, A). Significant differences in the magnitude of interhemispheric asymmetry can be observed only for part of each stimulation series, the males revealing them at the beginning of the series for the latency measure, and at the end of the series for the percentage of occurrence. In females, significant differences in interhemispheric asymmetry were observed only for the percentage of occurrence, and these are found in the middle of the stimulation series. This points to different dynamics of asymmetry in males and females, and also to the dependence of dynamics upon which index is used to calculate asymmetry. The essential point is that, where there was significant asymmetry, the influence of left-sided inactivation was greater than that of right-sided inactivation, which points to left hemisphere dominance both in males and in females.

At the same time, in males, the magnitude of interhemispheric asymmetry, and the influence of left-sided inactivation, calculated from the latency, are decreased after repeated stimulation, in a linear fashion. Use of indices calculated from the percentage of occurrence also show similar coefficients of linear regression. In contrast, the size of the influence of right-sided inactivation is insignificant and does not change noticeably after repeated stimulation. This can be considered as evidence of left hemisphere dominance for control of the dynamics of asymmetry revealed, in males. In females no satisfactory linear approximation of the dependencies under study could be obtained, either for asymmetry, or for the influence of unilateral hemispheric inactivation. In other words there is either no regular connection between them, or there are more complicated relations.

Similar data have also been obtained for pain squeals (Figure 2, B). In males, the magnitude of asymmetry, revealed from latency, is significant throughout the whole series of impulses, although at the beginning it is positive, and at the end negative. The magnitude of asymmetry, revealed from the percentage of occurrence, is maximal at the end of the stimulation period. The crucial point is that in males, at the beginning of the stimulation

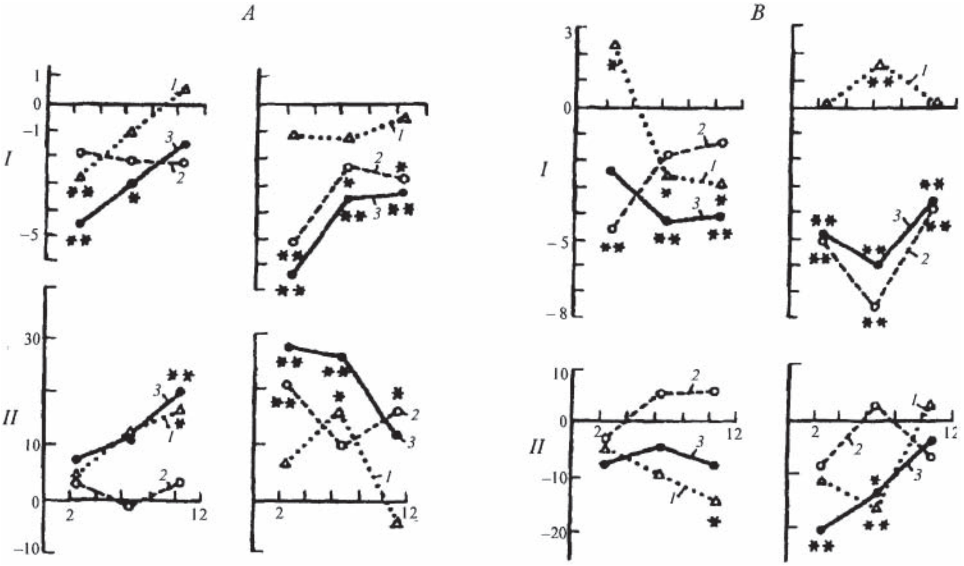


Figure 2: Dynamics of interhemispheric asymmetry in male (on the left) and female (on the right) rats revealed for cries of pain **(A)** and squeals of pain **(B)**. **Abscissa:** stimulation number, **1**–asymmetry; **2, 3**–the influence of right (2) and left (3) hemisphere inactivation. Ordinate: **1** the latent period, ms; **II**–relative number, %. *– $p<0.05$; **– $p<0.01$.

period, right hemisphere dominance was revealed for latency duration, later to be replaced by left hemisphere dominance. In other words, dominance inversion takes place throughout the stimulation series, which corresponds to the rule of the right-left shift (Bianki, 1985). In its turn, in females, asymmetry, revealed both from the latency and from the relative number of squeals, is maximal in the middle of the stimulation series, although, for latency, right hemisphere dominance is observed, whereas for the percentage of occurrence, the left hemisphere is dominant.

In males, the magnitude of asymmetry, and of the influence of left hemisphere inactivation, calculated from the latency and from the percentage of occurrence, depend linearly upon the number of stimulations, and the corresponding coefficients of linear regression do not differ considerably. In contrast, in females the above dependence is not revealed. Consequently, in males the left hemisphere is dominant for the dynamics of interhemispheric asymmetry both for pain squeals and cries, whereas determining the dominant hemisphere for females appeared to be difficult.

The above evidence points to the existence of definite dynamic aspects to the functional interhemispheric asymmetry in series of repeated painful stimulations, the asymmetry increasing, diminishing, and even becoming inverted in its direction during sufficiently short time intervals. The above shifts may to some extent be determined by the extreme nature of the pain applied, and the stress of the experimental situation (immobilization of the individual). This is testified to by data on the influence of stress factors upon lateral asymmetry (Fride and Weinstock, 1989; Zhdanova *et al.,* 1990). The essential point is that the observed dynamics of interhemispheric asymmetry was characterized by sexual dimorphism. Thus, in males the dependence of the degree of asymmetry on the number of painful stimuli is described by a linear law: The degree of expression of asymmetry decreased or increased proportionally as the stimulation progressed. In female rats such dependence was not observed, and was replaced by a more complex dynamics. The above sexual dimorphism may be influenced by the differing reaction of individuals of different sexes to stress factors. At the same time, the specificity of the dynamics of interhemispheric asymmetry, which depend on the index used, and the kind of vocalization, seems to be determined by lateral differences in the central organization of the mechanisms which can modulate vocal reactions.

Summing up, it was possible to show the existence of the sexual dimorphism of functional interhemispheric asymmetry for control of pain vocalizations. Asymmetry was expressed more strongly in males than in females. In general, quantitative changes were noted, though it was also possible to observe some traces of qualitative asymmetry: The left and the right hemisphere could also control different measures of pain vocalizations. The asymmetry under consideration was left-sided, that is, the left hemisphere was dominant. An important characteristic of interhemispheric asymmetry for the control of pain vocalizations is the dynamic aspects of asymmetry, which prevailed in males. Under certain conditions the dominant left hemisphere appeared to show greater dynamic changes in males.

2.3. PAIN SENSITIVITY

In the preceding section we described the results of investigations of vocalization reactions as such. We will now consider rats' vocalization as an index of their pain sensitivity.

A substantial body of evidence has now been accumulated concerning the participation of a number of cortical and subcortical structures in the perception, processing, and modulation of pain information (Durinian, 1980; Kaliuzhny and Golanov, 1980; Fields and Heinricher, 1985). The data on the function of the descending antinociceptive system are also of great significance, in that they enlarge considerably our concepts of the mechanisms of regulation of pain sensitivity and the means of aleviation of pathological pain (Kaliuzhny, 1984; Willis, 1988). The results of investigations showing changes in pain sensitivity in humans after one-sided brain infarction and lesions (Nery *et al.,* 1985), and in animals with experimentally induced unilateral and bilateral cerebral lesions (Lapina *et al.,* 1973; Best *et al.,* 1975; Reshetniak and Kukushkin, 1989) are also of great significance. Finally, among other problems, we should focus on the question of the relation between pain sensitivity and lateral specialization of the brain hemispheres. Thus, in humans, lateral specialization of the specificity of pain sensitivity was observed, in both the normal and the pathological situation (Murray and Hagan, 1973; Merskey and Watson, 1979; Nevy *et al.,* 1985). At the same time, such systematic studies have hardly ever been carried out on animals. In connection with this, we thought it valuable to study the relation between pain sensitivity and lateral brain specialization in animals of both sexes.

The experiments were performed on 336 sexually mature male and female Wistar rats (Snarsky and Bianki, 1992). The threshold and latency of pain vocalizations were measured under conditions of intact brain functioning, and after inactivation of the right and left hemisphere by means of potassium chloride-induced spreading depression. It should be emphasized that, in such cases, data on different kinds of pain vocalizations (cries, squeals) were pooled. In determining the latency, vocalizations were evoked by electric current whose strength exceeded the threshold magnitude by approximately five times. During testing, the animal was fixed in a special semi-rigid hammock, and 12 electric stimulations of the base of tail were delivered by means of a bipolar electrode. The resulting pain vocalizations were tape-recorded and subsequently analysed.

Let us focus first on the general characteristic of the threshold magnitudes for pain vocalizations, which are adequate indices of pain sensitivity, and are determined in part by sufficiently high levels of the central nervous system (Carr and Uysal, 1985). It should be pointed out that, in the mixed sample, assessment of the body of experimental data did not reveal any significant influence of unilateral cortical inactivation, nor any significant differences in the reactions after left or right hemisphere inactivation. At the same time, some other results were obtained from a sample of males (Figure, 3, I). In this case the threshold current strength for intact animals significantly exceeded that which was used for the rats whose left hemisphere had been inactivated, but did not differ from the threshold magnitude measured during of right hemisphere inactivation. Under these conditions, the threshold for appearance of pain vocalizations was lower than that after right hemisphere inactivation. At the same time, in female rats no major influence of unilateral inactivation of the hemispheres upon threshold magnitude was found, nor any differences in the consequences of the unilateral inactivation of the right and the left cortex.

The most important of the above results appears to be the discovery of functional interhemispheric asymmetry of pain thresholds, characterized by left hemisphere dominance in male white rats (as distinct from females). It may be suggested that the left cortex in males is immediately involved in the antinociceptive regulation of sensory input for pain,

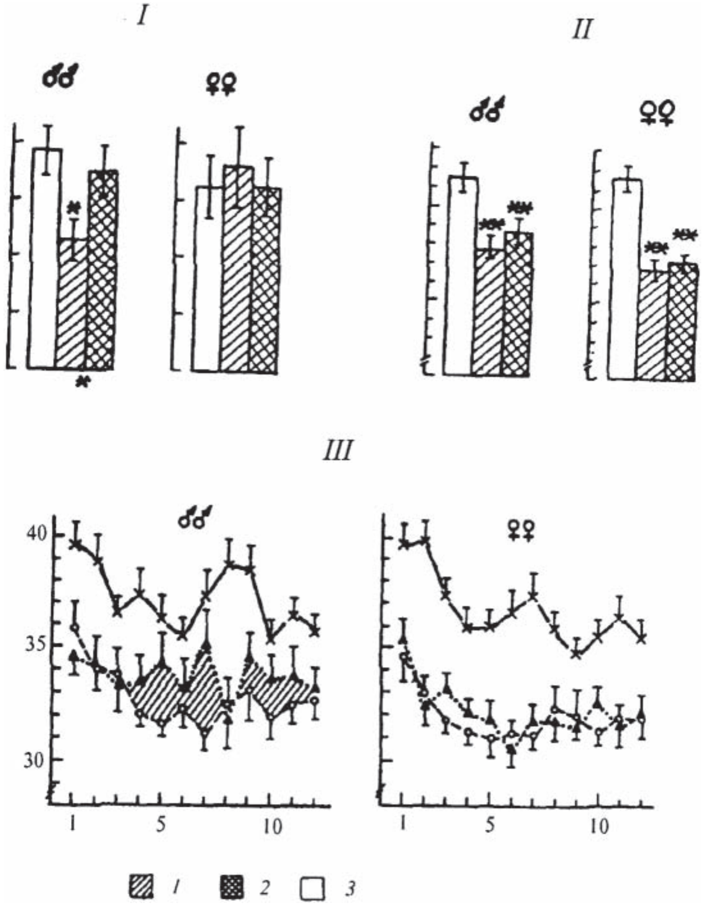


Figure 3: Functional interhemispheric asymmetry of pain sensitivity in rats of different sexes. **I**–threshold magnitude, relative units; **II**–latency, ms; **1, 2**–left (1) and right (2) hemisphere inactivation, **3**–the norm; asterisks above columns–difference from the norm, under columns–interhemispheric asymmetry; *– $p<0.01$; **III**–dynamics of the latency, ms; *abscissa:* stimulation number, *ordinate:* latency, ms; **lines with crosses;** the norm, **lines with circles**–left hemisphere inactivation, **lines with triangles**–right hemisphere inactivation; line slant marks the zone of interhemispheric asymmetry ($p<0.01$).

or else its influence is mediated by specific corticofugal connections with a number of subcortical centres acting upon spinal structures. The hyperalgesia developed against a background of reversible unilateral cortical inactivation, with the lowering of pain sensitivity thresholds has been found earlier in male rats after bilateral inactivation of the pre-frontal cortex in the area of the rhinal sulcus (using the indices of startle and jumping) (Cooper, 1975). It has also been found using bilateral stimulation of the medial prefrontal cortex as an analytic method (Hardy, 1985).

At the same time, a detailed comparison of our results (using extensive inactivation of the cortex) with the above consequences of local action on the cortex proved difficult. There may be specific cortical zones participating in the regulation of pain sensitivity. In this case, it is possible to obtain effects in opposite directions, observed particularly in cats for the orbito-frontal regions and the somatosensory cortex (Reshetniak and Kukushkin, 1989).

When comparing results obtained from different species (and even from different lines of animals) considerable differences are often revealed, which can be explained only partially by the methodological details of the experiments. Thus, for example, in cats, after unilateral cortical inactivation the thresholds of pain sensitivity in the contralateral limb fall, whereas, on the contrary, in Sprague Dawley rats they rise (Lapina *et al.,* 1973; Best *et al.,* 1975).

There is an increasing body of data on the biochemical and structural differences of a number of mediator systems in representatives of different species, lines, and even in animals of different sexes. In particular, this work refers to the endogenous morphines (and corresponding receptors) known to be the most important link in the system of nociception (Hammer, 1985; Marek *et al.,* 1990). The lateral and sex differences in question seem to be based on the mediator systems being different in left and right hemispheres in animals of different sexes.

Let us now turn to another characteristic of pain sensitivity, that is, the latency of pain vocalizations. First of all it should be noted that, in both male and female white rats, it was observed that the latency of pain vocalizations was reduced after left and right hemisphere inactivation, the latency being longer in males than in females. It should be noted that in our experimental model, unlike more traditional ones–the tail-withdrawal reaction, and the hot plate test–the main determinant of response latency was not so much the achieving of threshold magnitude, but rather the rate of conduction and switching-on of excitation in the neural circuit. This was connected with the considerable (almost fivefold) excess of the current strength over threshold magnitude, and also with the steep, momentary increase of the current strength up to the maximum value. This is supported indirectly by the fact that we found differences between the influence of unilateral cortical inactivation upon the thresholds and that on latency of the reactions under investigation. We have yet to clarify the neurophysiological mechanisms and brain structures by means of which the above reduction of the latency takes place. It may be associated with an imbalance between the transcallosal and corticofugal influences, arising as a result of unilateral cortical inactivation.

Distinct sex differences were found in white rats when we analysed the dynamics of the latency of pain vocalizations, after presentation of a series of painful stimulations. The average values for latency did not reveal any sex differences. When processing data obtained from a mixed sample of male and female rats, after several applications of the painful stimuli, functional interhemispheric asymmetry was found in the way the latencies for vocalization reaction changed: The latency decreased to a greater extent after left than after right hemisphere inactivation. With further stimulation, statistically significant asymmetry disappeared. Similar results were obtained from male rats (Fig. 3, III). It can be seen that functional interhemispheric asymmetry arose after several stimulations. This was established on the basis of the change of latency, and consisted of left hemisphere dominance. Such asymmetry was maintained throughout the action of all subsequent stimuli. In females no significant asymmetry was revealed in the latency of pain responses after inactivation of left and right hemispheres. Thus, it can be suggested that, in a mixed sample, initial symmetry of latency was produced by both males and females, asymmetry appeared with subsequent repetitions in males, and symmetry with subsequent repetitions in females. The above data indicate the dynamic aspects of functional interhemispheric asymmetry (Bianki, 1985, 1989) and pain sensitivity (Bykova *et al.,* 1987).

In summary of these data, it should be emphasized that there is a definite specificity in the influence of unilateral cortical inactivation upon pain sensitivity, which is influenced both by the animal's sex and by brain lateralization. This reflects the differential influence of the hemispheres upon the process under investigation. The interhemispheric differences revealed in this way are characterized by sexual dimorphism, with definite dynamic aspects, and may be based on structural and biochemical factors, as well as neurophysiological ones. The peculiarities of the modulations of threshold sensitivity, and the regulation of nerve transfer rate belong to the neurophysiological domain.

The following conclusion can be drawn, with regard to sexual dimorphism in functional interhemispheric asymmetry for the control of pain sensitivity in white rats. Functional interhemispheric asymmetry for control of pain sensitivity was found in white rats. It could be revealed only in males, using pain sensitivity thresholds and the dynamic characteristics of the latency measurements as indices. These data point to greater development of functional interhemispheric asymmetry in male rats, compared to females. Left hemisphere inactivation resulted in greater changes than right hemisphere inactivation in the parameters of the pain reactions we investigated, which testifies to left hemisphere dominance. The important peculiarity of left hemisphere control for pain sensitivity is the dynamic character of functional interhemispheric asymmetry.

The lowering of pain sensitivity thresholds in males, as a result of left hemisphere inactivation, points to the fact that it is the left hemisphere in males that dominates in the control of the antinociceptor function, which causes the analgesic effect. This may be of great biological importance for males, since it inhibits their pain sensitivity in the moments of danger.

2.4. MOTOR ACTIVITY

In this chapter several cases are demonstrated where the magnitude of functional interhemispheric asymmetry in males exceeds that in females. It should be noted that the above differences were quantitative, i.e. in males and females the same function was differentially controlled by the left (or the right) hemisphere. An example will be given below of qualitative sexual dimorphism of functional interhemispheric asymmetry: The same functions in males and females were controlled by different hemispheres. General motor activity appears to be a convenient model of this principle.

At present there is an abundance of data on lateral specialization of the human and animal brain, when carrying out motor control (Lomas and Kimura, 1976; Denenberg, 1981; Kimura, 1983; Bianki, 1985; Glick, 1985; Collins, 1988). Most of these data point to the dominance of the left hemisphere. The facts obtained from animals indicate the dominant role of the left hemisphere in limb preference, in motor and exploratory activity, in control of vocalization, in the interaction of transcallosal and thalamocortical streams of excitation etc. At the same time, if the motor behaviour of animals is connected with spatial orientation, the dominant role may be transferred to the right hemisphere. For example, this may be observed in rotatory movements, in the spatial-motor components of a conditioned reflex etc. Therefore it would seem that hemispheric lateralization of motor control is dynamic by its nature.

General motor activity of rats in the "open field" test is known to possess a biphasic motivational structure: It is connected both with the emotion of fear and with exploratory behaviour. Rather prolonged experiments are necessary to single out those phases, involving continuous recording of behaviour.

Such hour-long experiments were performed by us on 70 white Wistar rats of both sexes (Bianki, 1985; Filippova, 1985). In most of them, isolated inactivation of the left or the right cortex was carried out by means of unilateral spreading depression (Bureš and Burešova, 1962), while the remaining animals served as controls. The results obtained from males and females were so different that we immediately began to consider the corresponding data separately. First of all, it was found that motor activity in males and females possessed two peaks–at the beginning and in the second part of the experiment. Functional interhemispheric asymmetry was mainly observed during these maxima.

At the beginning of the experiment, significant left hemisphere dominance was noted, in both males and females (Figure 4, I). This points to the predominance of left-sided lateralization of motor activity. In the second part of the experiment asymmetry was also

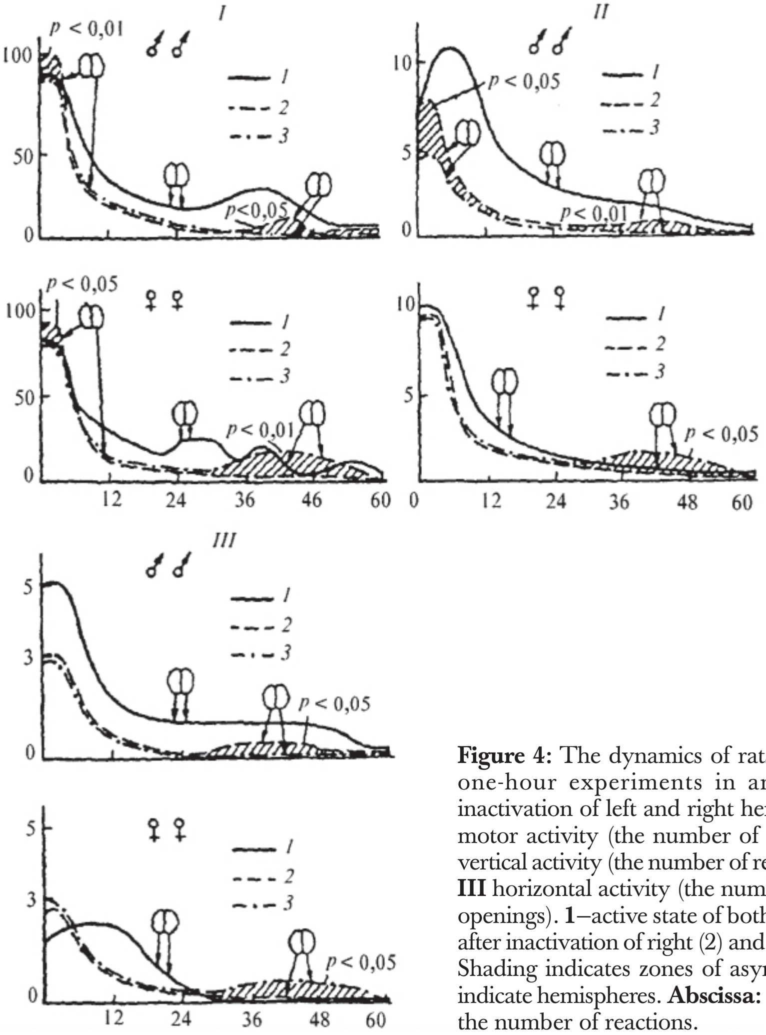


Figure 4: The dynamics of rats' behaviour during one-hour experiments in an open field after inactivation of left and right hemisphere. **I**–general motor activity (the number of squares crossed), **II** vertical activity (the number of rearings on hind legs), **III** horizontal activity (the number of peepings into openings). **1**–active state of both hemispheres; **2, 3**–after inactivation of right (2) and left (3) hemispheres. Shading indicates zones of asymmetry, hemicircles indicate hemispheres. **Abscissa:** time, min; **ordinate:** the number of reactions.

observed. As mentioned above, it was mainly manifested in exploratory activity. The essential point is that, in this experiment, sex differences were revealed: In the males the left hemisphere was dominant, whereas in the females it was the right.

Exploratory activity can also be studied in an open field test using other specific indices, for example, the number of times the animal reared on its hind legs (vertical activity) and the number of occasions it peeped into openings in the floor (horizontal activity). The corresponding results are presented in Figures 4 (II and III). It can be seen that, during these experiments, in males, functional interhemispheric asymmetry was observed either twice (at the beginning and in the second part of the experiment) or once only, whereas in females it happened only once, at the end of the experiment. However, the main point was that, in male rats, during the periods of asymmetry, the left hemisphere was always dominant, whereas in females it was the right. Hence the rats' exploratory activity is lateralized, and this lateralization is characterized by sexual dimorphism. In male rats the asymmetry may be stronger (since two phases of asymmetry were observed) and the main role in formation of asymmetry is played by the left hemisphere, whereas in females, the asymmetry is weaker and appears mainly due to dominance of the right hemisphere. We also emphasize that here the asymmetry appears in the dynamics of behaviour.

It should be added that, from the calculations performed, it was shown that, during concurrent action of the cerebral hemispheres, variance of the level of performance in male rats appeared to be more prominent than in females.

Thus, with respect to sex differences in motor and exploratory activity of white rats, it was possible to show that unlike most other cases described, in animals of different sexes, functional interhemispheric asymmetry differs not quantitatively but qualitatively: In male rats the left hemisphere is dominant, in females it is the right. Consequently we are dealing with the qualitative sexual dimorphism of interhemispheric asymmetry. Finally, male rats are characterized by a higher level of variance of behaviour.

2.5. ONTOGENETIC DYNAMICS

One of the most important properties of functional interhemispheric asymmetry (along with its relativity, its bilateral origin, its mosaic aspects, and the interaction between endogenous and exogenous asymmetry) is its dynamic aspects (Bianki, 1985, 1989). In preceding sections, we repeatedly pointed to the existence of certain sex differences in the dynamics of interhemispheric asymmetry. Let us focus on this question in greater detail, taking sexual dimorphism in ontogenetic development of several behavioural reactions as the first instance.

An important approach to understanding functional interhemispheric asymmetry and its sexual dimorphism in humans and animals is the study of the ontogenetic regulation of its formation. The data obtained on this question allow one to draw the conclusion that interhemispheric asymmetry may arise at early stages of postnatal development, or even during the prenatal period (Corballis and Morgan, 1978; Rogers and Anson, 1979; Denenberg, 1981; Ross *et al.,* 1982; Bianki, 1985; Makarova, 1986; Carlson and Glick, 1989; Rashid and Andrew, 1989). With increasing age, asymmetry undergoes different changes: It may intensify, or it may be inverted. In the course of individual development, the complex dynamics of asymmetry is determined on the one hand by exogenous factors, such as enriched or impoverished environments, or the action of stressful situations

(Denenberg, 1981; Bianki, 1985; Carlson and Glick, 1989; Petrov *et al.,* 1989). On the other hand, it is determined by endogenous shifts (Filippova *et al.,* 1989; Fitch *et al.,* 1990). To-date, there is no agreed concept of the regularities of the dynamic aspects of hemispheric specialization in man and animals during ontogenesis. According to one hypothesis some kinds of asymmetry are governed by the maturation gradient during the course of development of asymmetry (Corballis and Morgan, 1978), when the left hemisphere develops faster than the right. In the literature there are also additional arguments supporting this point of view (Rogers and Anson, 1979; Bianki and Filippova, 1982; Carlson and Glick, 1989). However, other experimental data are definitely in conflict with this hypothesis (Ross *et al.,* 1982; Bianki and Makarova, 1987; Rashid and Andrew, 1989; Farber *et al.,* 1990). In a number of cases it is possible to draw the conclusion that there is an earlier functional maturation of the right hemisphere. On the basis of the inductive-deductive concept of hemispheric specialization (Bianki, 1985, 1989) it can be assumed that in the course of ontogenesis, as well as in the process of learning, a change of the dominant hemisphere takes place, which is carried out according to the rule of the right-left or left-right gradients.

We investigated sex differences in the asymmetry of control of different behavioural acts in open field tests in the course of postnatal ontogenesis (Bianki and Makarova, 1995). For this purpose an ethological method of studying rats' behaviour in the open field was used. The experiments were performed on 124 Wistar rats (59 males and 65 females). Ontogenetic dynamics was assessed in four age groups: 18–24 days (group I), 30–37 days (group II), 52–56 days (group III) and 3–4 months (group IV). The age of the rat pups from group I corresponded to the end of suckling, and fell at the end of the period of early postnatal ontogenesis. At that age the pups were in the nest with their mother. Group II included the animals at the beginning of the post-nesting period and their transition to independent feeding. Group III included animals at the period of sexual maturation. Group IV included young sexually mature animals. In their individual behaviour the following elementary behavioural reactions were recorded:

1. Horizontal motor activity in the periphery of the field, in its centre, or summated over all the field.
2. Rearing on hind legs in the periphery, in the centre of the field or summated over all the field.
3. Peeping into openings.
4. Washing and grooming.
5. Sniffing, and body turns without changing body coordinates.
6. Freezing, or immobile stance by the animal.

Recording the succession and duration of behavioural acts was carried out using a special ethograph. To assess the specific contribution of the right and the left hemisphere to control of the corresponding behavioural reactions, the method of unilateral functional inactivation of each cerebral hemisphere was used by means of spreading depression. The possibility of effective application of spreading depression to rat pups of the younger age-groups is supported by the results of special investigations of J.Bureš and his colleagues (1980).

The results obtained testified primarily to the complex dynamics of the asymmetry of hemispheric control of rats' behaviour in the open field during the course of ontogenesis.

Two main types, or patterns of development were distinguished. According to the first type, control of behavioural acts was first carried out mainly by the right hemisphere, later, during the animals' maturation, by the left and then again by the right hemisphere. The second type of asymmetry dynamics was an inverse succession of the order of hemispheres participating in activity, that is, left-right-left.

Now let us consider in greater detail the sex differences in the patterns of asymmetry of hemispheric control over behavioural acts in the open field situation, in rats from the age groups investigated. In male rats, using indices of general motor activity (viz: general activity during the first minute and activity in the centre of the field) and rearing on hind legs, in the course of ontogenesis the patterns of asymmetry were left-right-left, whereas in females they were right-left-right or left-right or right in the same reactions (Figure 5, A–B). Using the criteria of motor activity in the periphery of the field, and the number of times the animal peeped into openings, washed, and sniffed, in males the pattern of change of the dominant hemisphere in the course of ontogenesis was right-left-right, while in the females it was left-right (Fig. 5, D–H). Finally, in freezing reactions (Fig. 5, I) the left-right shift of hemispheric dominance was observed both in males and in females.

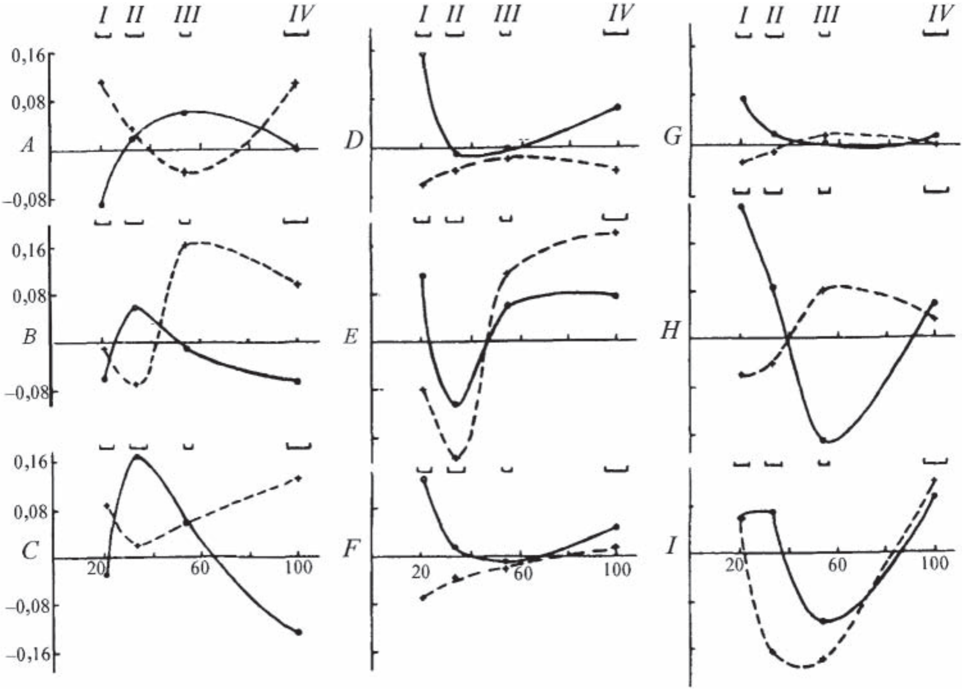


Figure 5: Comparative dynamics of asymmetry of hemispheric control of behavioural reactions in rats of different sexes and ages. **A, C, D, F**–the frequency of occurrence of reactions; **B, E, G, I** summated duration of reactions. **A**–general motor activity during 5 min in the centre of the field; **B**–rising on hind legs during 5 minutes of observation: **C**–motor activity during 5 minutes in the centre of the field; **D**–motor activity during 10 min in the periphery of the field; **E**–the number of peepings into openings during 10 minutes; **F**–motor activity during 5 minutes in the periphery of the field; **G**–sniffings during 10 min; **H**–washing during 10 min; **I**–freezing during 10 min. **Solid line**–males, **broken line**–females. **Abscissa:** age of animals, days; **I–IV**–age groups, **ordinate:** $\mathbf{K}_{as}$, *positive values* right hemisphere dominance, *negative values*–left hemisphere dominance.

The existence of two main patterns of the asymmetry of hemisphere control for behavioural reactions in the rats' ontogenesis, these being more-or-less mirror-reflections of each other, may be supposed to be associated with two main motivations for behaviour in the open field, namely those of avoidance and exploration. Indeed, as shown earlier, fear and exploratory activity can be considered as the principal factors determining the main part of behavioural variation in the open field, and the vector forming it (Markel' *et al.,* 1988). The relations of the above factors are also known to be mutually antagonistic, that is exploratory behaviour inhibits the emotion of fear accompanying avoidance reactions and, conversely, intensification of fear shifts the vector of behaviour towards inhibiting the exploratory component and the prevalence of the avoidance reaction (Titov and Kamensky, 1980). According to the hypothesis of emotional valence, control for comparatively strong emotions is taken over by the right hemisphere, control for comparatively weak ones by the left (Bianki, 1985). It should be noted that changes in asymmetry were approximately mirror images, for the reactions of different biological significance.

As shown by analysis of all the exploratory reactions investigated, the first pattern of hemispheric asymmetry, i.e. right-left-right, was revealed in males for the passive reaction of washing, and also for active behavioural acts (motor activity in the periphery, and peeping into openings). In females the same type of asymmetry dynamics was recorded for control of general motor activity during 10 minutes, and for rearing on hind legs. Control of the freezing reaction, a manifestation of passive behaviour, was also carried out according to a pattern of the first type in rats of both sexes. The asymmetry dynamics in the above reactions may be associated with the prevalence of the motivation of avoidance, and the emotion of fear accompanying it. A large expression of fear seems to have been conditioned by the "novelty" of the situation in which the animals were being tested, and also by its short duration. These factors may have determined the leading role of the right hemisphere for control of the above reactions in rats of both sexes.

The second ontogenetic pattern of change of asymmetry, i.e. left-right-left, was found in male rats in the reactions of general motor activity during the first minute, rearing on hind legs, and motor activity in the centre of the field. The appearance of the animal in the centre of the field is known to be accompanied by inhibition of fear and intensification of the exploratory components of behaviour. However, in females, behavioural acts associated with their appearance in the centre of the field were mainly controlled by the right hemisphere in all the age groups under investigation. Prevalence of the left hemisphere pattern of asymmetry in females took place only for the reaction of general motor activity in the periphery of the field.

Thus, on the whole, in female rats, the dynamics of asymmetry of hemispheric control over behaviour in the open field is more often carried out according to the first pattern, whereas in males it took place according to the second pattern. It should be emphasized that, in this sense, one could suggest that there is an advantage of the right hemisphere in females and of the left hemisphere in males for control of behavioural reactions. Under these conditions, the males' behaviour is determined more by the motivation of exploration, that of females by that of avoidance.

The above data suggest that sex differences in the patterns of behavioural asymmetry in rats are usually qualitative. Indeed, in the dynamics of asymmetry of hemispheric control over behavioural reactions in animals of different sexes, their opposite character was noted at certain ontogenetic phases. For instance, reactions of motor activity in the periphery of the field were carried out according to the first pattern in males, but according to the second pattern in females. At the same time, males typically possessed asymmetry dynamics of the second type for the reactions of general motor activity and activity in the centre of the field, and also for the total number of rearings on hind legs, whereas the females were characterized by the dynamics of the first type for such reactions. Indeed, while in the male rats from age-groups I and IV, control was carried out mainly by the left hemisphere, in the female rats from the same age-groups it was carried out by the right. These facts may be accounted for by differences between individuals of the two sexes in the involvement of the investigatory and exploratory components in carrying out the same behavioural acts.

An important peculiarity of the dynamics of asymmetry for hemispheric control of rats' behaviour in the open field is the inversion, or change of direction of asymmetry during certain age ranges.

In control of motor activity during the first minute, rearings on hind legs, and motor activity in the centre of the field, the first inversion of asymmetry was observed in animals of both sexes during their transition between age-groups I and II. Under natural conditions the rat pups of age 30–35 days first leave the precincts of their nest and begin to feed independently. This is one of the critical periods in the development of animals of this species. Under experimental conditions the first inversion of asymmetry coincided with biologically important changes in the pups' way of life: They were isolated from their mother and placed in new cages where they were kept with animals of the same age and sex but from different litters. Under these conditions the open field behaviour of the females from the group II was already controlled not by the right (as it had been the case in the group I) but by the left hemisphere. The reverse was observed in the males: Their asymmetry for most of the active behavioural reactions became right-hemisphere dominant. Hence the shift of asymmetry at that stage of ontogenesis was mostly left-right for the males and right-left for the females. There are also other indications in the literature of different shifts in interhemispheric asymmetry, accompanying the process of brain maturation and the development of behaviour, both in rodents (Diamond, 1982; Ross *et al.,* 1982) and birds (Rogers and Anson, 1979).

The second inversion of hemispheric control of behavioural reactions coincided with the onset of sexual maturity. In females, by the age of 50–56 days, i.e. during the transition between groups II and III, the direction of asymmetry could be reversed, and control over most reactions became right-hemispheric (as it had been in the case of group I), the asymmetry gradient then being left-right. At the same time, in males, as a rule, the second inversion was observed later, during the transition between groups III and IV; behavioural control became more left-hemispheric, the asymmetry gradient thus being right-left. The modulating influence of sex hormones upon the direction of interhemispheric asymmetry for the control of behaviour in the open field in rats had been shown earlier (Filippova *et al.,* 1989). Gonadectomy in adult animals caused inversion of the normal dominant control of behaviour: In males this control became right-hemispheric, in females left-hemispheric. Delay in the period of the second inversion of asymmetry in male rats, as compared to the females, may be associated with some degree of slowing of maturation of their central nervous system, of the onset of physiological maturity, and of completion of hemispheric specialization.

Finally, control of behavioural reactions in the periods of development investigated was more dynamic in males than in females. This was manifested by the fact that the ontogenetic dynamics of asymmetry in males was described by the triads of the two above types. At the same time, in females, in the course of individual development, hemispheric control for a number of behavioural acts mainly involved a single hemisphere, or was characterized by the left-right shift of asymmetry.

In summary, the purpose of the present work was not just to reveal the existence of dynamic changes of hemispheric control over different forms of behaviour in the course of ontogenetic development, but also to establish some regularities in such dynamics. These dynamic changes were shown to depend on several factors, such as the animal's age, its sex, the peculiarities of its behavioural reaction etc. In this context some of the contradictions in data from the literature can also be accounted for.

It was possible to establish two main types of the ontogenetic dynamics for interhemispheric asymmetry. The first was characterized by a right-left-right pattern of asymmetry, the second by the left-right-left shift. The first type of ontogenetic dynamics usually prevailed in females, the second in males. At different phases of development, hemispheric control over the same behavioural acts in animals of different sexes could be both out-of-phase and in-phase. The first type of the asymmetry dynamics was associated with hemisphere control for avoidance behaviour, the second for exploratory behaviour. The males' behaviour in the open field is determined more by the exploratory component, in females by the avoidance component. It should also be noted that the peculiarities of the ontogenetic dynamics of hemispheric control for different behavioural reactions points to the fact that in males the main role in the total control of behaviour is played by the left, in females by the right hemisphere. It should be emphasized that, in the above experiments, qualitative sexual dimorphism of functional interhemispheric asymmetry was revealed, so that at the same stages of ontogenetic development the same hemispheres in males and females control different forms of behaviour. We also note that, in the course of the ontogenesis, functional interhemispheric asymmetry in males was more dynamic than in females.

2.6. CONDITIONED REFLEXES

Let us consider the process of formation of conditioned reflexes as another example of sexual dimorphism in the dynamic characteristics of functional interhemispheric asymmetry. In I.P.Pavlov's school (1923) it was established that, at the beginning of the formation of any conditioned reflex, a phase of generalization is observed during which not only does the conditioned stimulus itself cause the conditioned reflex reaction but also other stimuli similar to it do the same. After consolidation of the conditioned reflex, the phase of specialization sets in, during which extraneous stimuli become less effective or even ineffective.

Our purpose was to study the sexual specificity in lateralization of the generalization and specialization phases of conditioned reflexes within the cortex of the rats' brain. Reflexes conditioned to sound were chosen. At different stages of formation of conditioned reflexes different conditioned signals were used, transformed in different ways, under conditions of isolated function of either the left or the right hemisphere (Bianki, 1985).

The experiments were carried out on white Wistar rats of both sexes using an automated "electrodefensive" technique involving active avoidance in a shuttle box. In the first variant of the experiments, in 238 rats (124 males and 114 females) the right or the left hemisphere was previously inactivated by means of spreading depression (SD), and then a conditioned reflex was elaborated, 100 or 300 combinations being presented. The results obtained are given in Figure 6A, I, III. In these experiments, asymmetry of the conditioned reflex was clearly revealed. It passed through two phases in its dynamics. During phase I, the conditioned reflex was formed more quickly and was more durable in the right than in the left hemisphere ($p<0.001$). It was revealed within about 200 combinations and was equally well expressed in both males and females. In females, the conditioned reflexes during right hemisphere functioning had a latent period 200 msec less (on average) than they had during the active state of the left hemisphere ($p<0.01$). In phase II, on the contrary, the conditioned reflex was more durable in the left hemisphere than in the right one ($p<0.001$). This phase started after approximately 200 combinations and was found only in males, females showing a symmetrical manifestation of the conditioned reflex.

In the second variant of the experiments, in 134 rats (58 males and 76 females) the conditioned reflex was elaborated and then the right or the left hemisphere was inactivated by means of SD. Before hemisphere inactivation, one subgroup of animals ($n=106$) was presented with 100 combinations, and the other subgroup ($n=28$) were presented with 480 combinations. As seen in Figure 6, A, II, IV, males revealed both the above phases of conditioned reflex formation. After 100 combinations, the reflex appeared to be more durable in the right hemisphere ($p<0.001$), and on average had a latent period shorter by 250 msec than that in the left hemisphere ($p<0.001$). After 480 combinations, a more durable reflex was observed in the left hemisphere ($p<0.05$) and it was characterized, on the average, by a latent period 700 msec less than that in the right hemisphere ($p<0.05$). In females, on the other hand, instead of phase II, a symmetrical manifestation of the conditioned reflex was observed.

In both variants of the experiments, the difference in the durability of the conditioned reflex between right and left hemispheres, on average, achieved 15% in phase I and 8% in phase II. This testifies to phase I being somewhat more strongly expressed. Let us note that the spatial component of the conditioned reflex did not noticeably affect its lateralization, since, in all the experimental series the difference in the number of movements from the right semi-chamber into the left one and back was not statistically significant.

Similar results were obtained during the study of electrodefensive conditioned reflexes of two-sided active avoidance to the sound [a], pronounced by a speaker, and taped. Before the onset of shock the sound was repeated twice, and its intensity was 92 db.

In the first experimental variant, the conditioned reflex to sound was previously elaborated in 60 rats, after which the right and then the left hemisphere were inactivated. The first inactivation of the hemispheres was performed after 80 combinations, and the second after 560 combinations. The results obtained are shown in Figure 6, B, II, IV. It can be seen that the asymmetry of formation of phase I of the conditioned reflex could be revealed, with right hemisphere dominance, only in males ($n=30$; $p<0.001$). Under the same conditions, females showed only a similar tendency but no statistically significant values were obtained ($n=30$; $p>0.05$). Phase II of the asymmetry of elaboration of the conditioned reflex to the sound was revealed both in males and females, the conditioned reflex in the left hemisphere being more durable than in the right hemisphere ($p<0.001$

and $p<0.05$, respectively). In addition, the left hemisphere reflex in males had (on average) a 200 msec shorter latent period that the right hemisphere reflex ($p<0.01$).

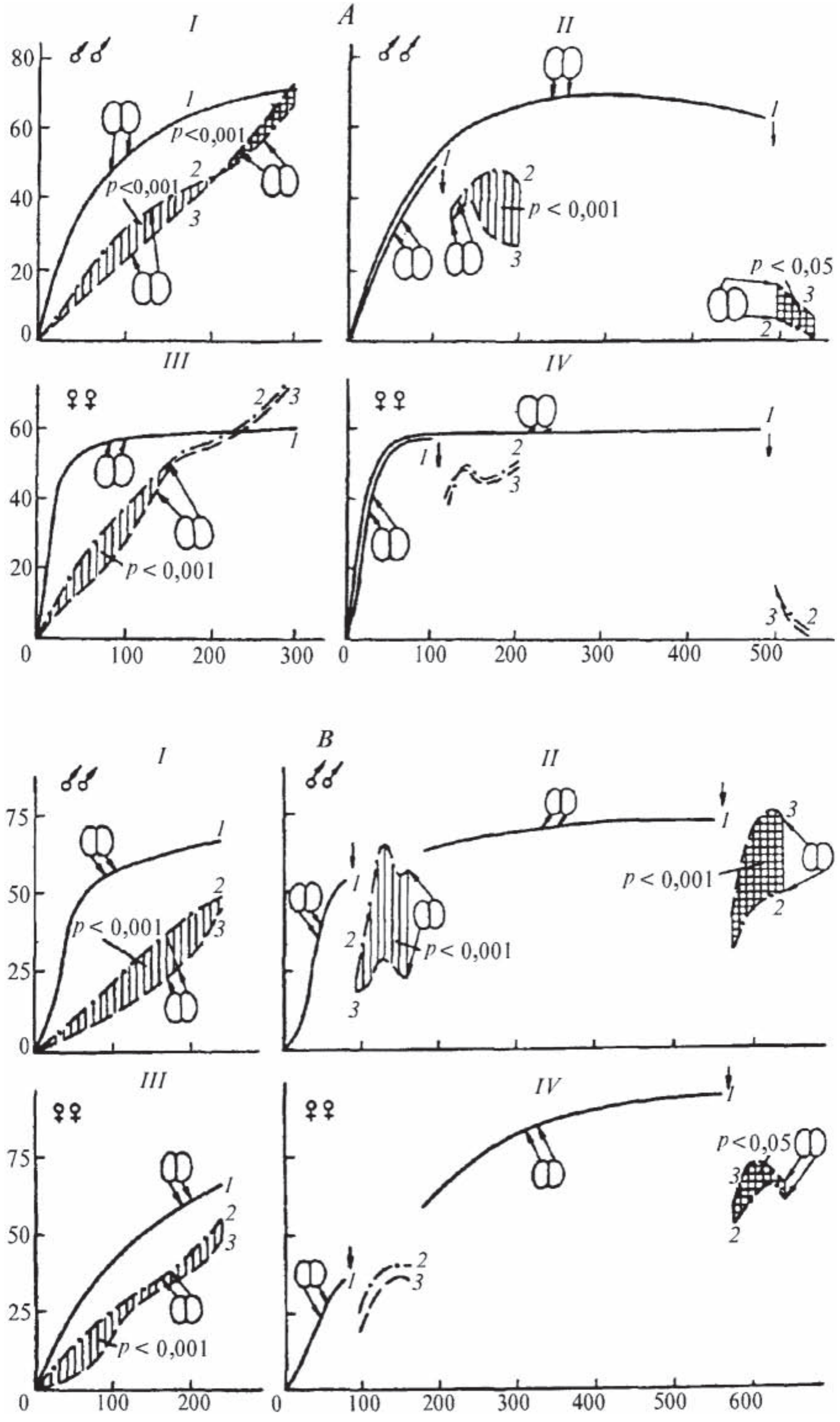
In subsequent experiments the sound stimuli used were subdivided into the "main" and the "test" stimuli. The main stimulus was a sound to which a conditioned reflex was formed, which was naturally reinforced every time an adequate reaction was produced to it, namely the animals' moving to the other part of the experimental chamber. The main stimulus was the English vowel sound [a] pronounced by a speaker, recorded on tape. The test stimulus was the basic sound but it was transformed, in its intensity, in the frequency of its main tone, or in its duration. The test stimuli were never reinforced and were always presented randomly. The main experiment consisted only of the main signals, whereas in the test experiment both the main and the testing stimuli were presented.

Thus in the initial stages of the formation of a temporary connection, the main objects of study were lateralization of generalization of the conditioned reflex to the basic sound, and lateralization of specialization of the conditioned reflex to this sound. Generalization of the conditioned reflex was measured by comparing its occurrence as a response to the transformed sound with that to the main stimulus. For this purpose the numbers of conditioned reactions to the test stimulus (or group of stimuli) and to the main stimulus were assessed. The hemisphere during whose function these differences were minimal (or were not observed at all) was held to be dominant. In other words, during operation of the hemisphere dominant for generalization, transformed signals were perceived as if they were the main ones. In contrast to this, during the functioning of the hemisphere dominant for specialization of the conditioned reflex, the animals responded to the test stimuli in a different way from the main, specific stimuli.

In the experiments described below the following procedure was used: First the reflex response to the main stimulus was formed while both hemispheres were active, then the left and the right hemispheres were successively inactivated, and the test experiment was performed. The main stimulus was the sound [a] pronounced by a male speaker, sound intensity being 92 dB, and duration 1.5 s. The test experiments were performed twice, after 100 and and 480 pairings of conditioned and unconditioned stimulus. Thirty rats were used. Inactivation of the cortex of one hemisphere was achieved by means of potassium chloride-induced spreading depression.

In male rats, presentation of test sounds which had been transformed in intensity, so that they were stronger than the main ones, revealed right hemisphere dominance for the degree of generalization during the first phase of formation of the conditioned reflex (i.e. after 100 pairings, with both hemispheres active): During right hemisphere function sounds of 98 and 104 dB intensity did not cause a statistically significant change in the rate of occurrence of conditioned reflexes, as compared to the reaction to the main stimulus; at the same time, during left hemisphere function, statistically significant differences were observed. On the contrary, when sound stimuli which were relatively weak compared to the main one (80, 86 dB) were presented, the left hemisphere was dominant for the degree of the conditioned reflex generalization. Under such conditions no asymmetry could be revealed in females.

Thus in male rats, during the first phase of formation of conditioned reflexes to the sound stimulus, with transformation of the signal intensity of the stimulus, the following facts were found: When strong stimuli were used, the right hemisphere was dominant for generalization, the left one for specialization of the conditioned reflex. If weak test stimuli


A
I
♂♂
80
60
40
20
0
1
2
3
p<0,001
p<0,001
II
♂♂
1
1
2
3
p < 0,001
p < 0,05
3
2
III
♀♀
60
40
20
1
2
3
p < 0,001
0
100
200
300
IV
♀♀
1
1
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3
3
2
0
100
200
300
400
500
B
I
♂♂
75
50
25
0
1
2
3
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II
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2
3
p< 0,001
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III
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75
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100
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IV
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1
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p<0,05
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300
400
500
600

Figure 6: The influence of right and left hemisphere inactivation in rats upon "electrodefensive" two-way avoidance conditioning during cross-reinforcement. **A**–conditioned reflexes to light, **B**–to sound. **I, III**–experiments with hemispheric inactivation before and during training, **II, IV**–with hemispheric inactivation after training (at time marked marked with an arrow). **1**–active state of both hemispheres, **2**–right hemisphere active, **3**–left hemisphere active. Semicircles indicate hemispheres; **single shading**–the first asymmetry phase, **double shading**–the second phase. **Abscissa:** the number of combinations; **ordinate:** percentage of correct responses.

were used, the left hemisphere dominated for generalization, the right one for specialization of the conditioned reflex.

During the second phase of elaboration of the conditioned reflex (i.e. after 480 combinations), when asymmetry appeared for generalization of the conditioned reflex to the sound [a] transformed in its intensity, the left hemisphere was dominant in female rats. It can be seen that when relatively strong sounds were used (98, 104 dB) the rate of occurrence of the conditioned reflex in the left hemisphere in response to the test stimuli was statistically indistinguishable from that to the main stimulus. With the right hemisphere active it was lower. No such changes could be found in males.

Consequently, in female rats, during the second phase of formation of the conditioned reflex to the sound stimulus, under conditions of increasing intensity, left hemisphere dominance was found in the degree of conditioned reflex generalization, whereas the right hemisphere was dominant for the degree of conditioned reflex specialization.

Another transformation of the sound [a] which was used in the present study was to change the frequency of the main tone. The main tone was pronounced by a male speaker, at an intensity of 92 dB, and lasting for 1.5 s. The test sound [a] was pronounced by another male speaker, or by a woman. The rest of the sound parameters were preserved. In the main experiments, carried out with both hemispheres remaining active, 80 pairings of the main stimulus were presented, and in the testing situation, 40 main and 20 test stimuli were presented. Thirty nine rats were used.

In female rats, during the first phase of formation of the conditioned reflex (after 80 pairings), when the female voice served as the test stimulus, right hemisphere dominance was observed for the degree of conditioned reflex generalization: When the right hemisphere functioned no statistically significant differences were observed in the occurrence of the conditioned reflex compared with responses to the main stimulus, whereas with the left hemisphere active, such differences did exist. Such a pattern was not observed in males.

During the second phase of establishment of the conditioned reflex (after 480 pairings) the female rats showed right hemisphere dominance for the degree of the generalization of the conditioned reflex to sound when the frequency of the main tone was varied. The right hemisphere dominated when the test stimulus was another male voice. In this case no statistically significant differences were observed between the occurrence of the conditioned reflex to the main and to the test stimuli during the function of the right hemisphere, whereas they were found when the left hemisphere was active. In males no such asymmetry was found.

Thus, in female rats, during the first and the second phase of formation of conditioned reflexes to a sound stimulus and after its transformation with respect to the main tone frequency, right hemisphere dominance was revealed for generalization of conditioned reflexes and left hemisphere dominance for specialization of them.

Finally, let us consider the case of transformation of the main signal with respect to its duration. The main stimulus was the sound [a] pronounced by a male speaker, at intensity of 92 dB, and duration of 1.5 s. For the test stimuli, only duration was changed. The rest of the signal parameters were preserved. The experimental design was also the same. The experiments were performed on 39 rats.

In female rats, during the first phase of formation of the conditioned reflex (80 pairings) functional interhemispheric asymmetry for generalization of the conditioned reflex could be revealed only in one case. When the sound [a], with duration of 1 s was used as the test stimulus, the right hemisphere appeared to be dominant: With the right hemisphere active, the rate of occurrence of reflexes in response to presentation of the main and a shorter test stimulus, did not differ significantly, though they did when the left hemisphere functioned. Such asymmetry was found only in females.

Consequently, in female rats, during the first phase of the formation of conditioned reflexes to a sound stimulus, after the transformation of the main tone, dominance of the right hemisphere was found for conditioned reflex generalization, and of the left hemisphere for its specialization.

What do the results obtained indicate? First of all, it should be mentioned that, in earlier works, we formulated the rule of the right-left gradient (shift) during learning (Bianki, 1985). According to this rule, in conditioned reflexes which are only weakly established (i.e. non-durable), the right hemisphere dominates, while, after they are firmly established, the left hemisphere is dominant. From the facts presented above, it follows that this rule may be expressed differently in males and in females. To be more exact, the rule does make its appearance in individuals of both sexes, but its "tempo" is different.

It should be pointed out once more that the first phase of formation of conditioned reflexes can be characterized as the phase of right hemisphere dominance for generalization of the conditioned reflex, and that of left hemisphere dominance for specialization. The second phase of the conditioned reflex formation can be considered as the phase of left hemisphere dominance for generalization of the conditioned reflex, whereas right hemisphere dominance was found for its specialization.

The facts obtained show that in males, under the above experimental conditions, 80 pairings of the conditioned and unconditioned stimuli seem to be sufficient for the occurrence of both phases of asymmetry, and the subsequent transition to symmetry, whereas in females, even after 480 pairings, the second, and even some traces of the first phase can be observed. These data suggest that male rats appear to be characterized by a faster dynamics (as compared to females) for the transition through the main stages of conditioned reflex formation, according to the rule of a right-left gradient.

Let us now consider some additional data from rats on the characteristics of functional interhemispheric asymmetry in the dynamics of formation of conditioned reflexes to the sound [a]:

In males during concurrent function of the hemispheres, on presentation of the main stimuli the following differences were observed (compared to females)[4]:

1. After formation of a durable conditioned reflex to a sound stimulus, the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.01$).
2. After formation of a durable conditioned reflex to a sound stimulus, the magnitude of asymmetry (assessed by the K_{as} criterion) is greater ($p<0.01$).

3. After formation of a non-durable (i.e. weakly established) conditioned reflex to a sound stimulus, the expression of asymmetry is greater ($p<0.05$).
4. After the formation of a durable conditioned reflex to a sound stimulus, the variance of the magnitude of asymmetry (assessed by the K_{as} criterion) is greater ($p<0.01$).
5. After the formation a durable conditioned reflex to a sound stimulus, the magnitude of the individual asymmetry is greater ($p<0.05$).
6. After transformation of a conditioned stimulus with respect to its intensity, and with a non-durable conditioned reflex to a sound stimulus, the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).
7. After transformation of a conditioned reflex with respect to its timbre, and with a durable conditioned reflex to a sound stimulus, the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.01$).
8. After transformation of a conditioned stimulus with respect to its duration, and with a durable conditioned reflex to a sound stimulus, the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).
9. After the transformation of a conditioned stimulus according to its duration, and with a durable conditioned reflex to a sound stimulus penetrance of asymmetry is greater ($p<0.05$).
10. After the transformation of a conditioned stimulus with respect to its duration, and with a non-durable conditioned reflex to a sound stimulus, expression of asymmetry (assessed by the difference criterion) is greater ($p<0.01$).
11. After transformation of the conditioned stimulus with respect to its duration, after a conditioned reflex to a sound stimulus had been established, variance of the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).
12. After transformation of a conditioned stimulus with respect to either its intensity, timbre or duration, and with a durable conditioned reflex to a sound stimulus, the magnitude of individual asymmetry is greater ($p<0.05$).

(In females the magnitudes of all these indices were smaller.)

On the basis of the data analysis, it can be concluded that in male rats, in the first and the second phase of elaboration of a conditioned reflex, when the main and test stimuli are presented (the latter transformed with respect to intensity, timbre or duration), during concurrent hemisphere function, species-specific and individual functional interhemispheric asymmetry is greater than in females; the same can be said about the penetrance and strength of expression of asymmetry, and about the magnitude of asymmetry expression, as compared to females.

Thus, on the basis of the data obtained, it can be concluded that functional interhemispheric asymmetry of the brain in males as compared to that in females is distinguished by a greater degree of expression, greater penetrance and greater variance.

2.7. STEREOTYPED AND PROBABILISTIC BEHAVIOUR

Depending on the nature of environmental changes, both human beings and animals can respond to these changes by either stereotyped or probabilistic behaviour. In this connection the models for studying sex differences were the “dynamic stereotype” (Pavlov, 1951a, b), or systemic behaviour and probabilistic learning.

The dynamic stereotype is one of the most remarkable ways in which animals carry out analysis and synthesis, based on conditioned reflexes. In this case the index of synthesis is known to be the ability of one of the stimuli to reproduce the whole series of elaborated reactions. At the same time the isolated stimuli of the stereotype do not completely lose their meaning as signals, but carry out both triggering and tonic functions. In our preceding studies it was shown that in carrying out the dynamic stereotype, analysis was mainly lateralized to the right hemisphere, and synthesis to the left (Bianki and Poletayeva, 1981; Bianki, 1985).

In the experiments under consideration, in 28 white Wistar rats of both sexes the dynamic stereotype was elaborated to the alternating presentation of a square and a circle. When a square was presented, the animals learned to open the right door in the experimental set-up, and when a circle was exposed they had to open the left door. In both cases food reinforcement was used. The intervals between the stimuli were constant, lasting 40 s.

After the establishment of a durable dynamic stereotype all stimuli were replaced by the first one, namely the square, which was presented both in "its own" place and in "the other's" place (in place of the circle). The experiments were carried out under the condition of temporary functional inactivation of one hemisphere, by means of spreading depression in the cortex (Bureš and Burešova, 1962). In the case of the first stimulus (the square) being presented in "the other's place" (instead of the circle) no sex differences were revealed in carrying out the dynamic stereotype. When the first stimulus (the square) was presented in "its own" place, sexual specificity was found: In male rats, variance of the level of analysis carried out by the right hemisphere was expressed more strongly than in females. These data point to a greater changeability, and variability of the analysis being performed by the right hemisphere in males than in females.

To study the process of probabilistic learning a model with partial reinforcement of the signal stimulus is to be preferred. Earlier it was shown (Bianki, 1985, 1988) that when the probability for reinforcement was low (25%) animals with both hemispheres functioning chose the strategy of levelling, which was determined by the action of the right hemisphere. Under the condition of a relatively high probability of reinforcement (50%) the animals resorted to the strategy of correspondence, in performance of which the left hemisphere plays the main role. At the beginning of elaboration of the above system of conditioned reflexes the strategy of "maximalization" was used, i.e. the animals responded positively to the stimuli presented in 100% of the cases.

D.N.Menitsky and V.V.Trubachev (1974), proceeding from game theory (and related experimental results) provide the following analysis of the behavioural strategies of animals in the probabilistic environment. The first strategy is that of averaging, which means a random, equiprobable choice. This is a stochastic equiprobable reaction, a chaotic choice, independent of reinforcement probability. Subjectively, it reflects a pessimistic prognosis of finding a solution to the task. The second strategy is that of correspondence, in which the choice is proportional to the event probability. This probabilistic correspondence is a proportional choice of alternatives. Such a strategy ensures a realistic approach. The third strategy is that of maximization, which means the choice of only the most frequently reinforced stimulus. This strategy reflects an optimistic prognosis of solving the problem. The above authors also introduce the idea of hierarchical levels in the perception of probabilistic sequences. The lowest level corresponds to the averaging strategy, the middle level to the correspondence strategy, and the highest one to the maximization strategy. In the light of these data it can be assumed that the rats' left hemisphere uses the strategy of a higher level (the correspondence strategy) than the right one (the averaging strategy).

To study the sexual specificity of probabilistic behaviour, the following experimental procedure was used: First, in 51 white Wistar rats of both sexes, motion-food conditioned reflexes were elaborated, in which the rat pushed aside the door with its head. The signal stimuli for different animals were representations of a square, a cross or an irregular polygon exposed on a screen. Altogether, about 100 pairings were presented during 3–4 experiments, with 100% reinforcement. The rats were then divided into two groups. In one of them, partial stereotyped reinforcement was practiced. The stimuli were divided into four groups each consisting of ten pairings: In the first ten pairings all the stimuli were reinforced, in the second ten alternate stimuli were reinforced, in the third ten every fourth, and in the fourth ten, every eighth stimulus was reinforced. In the other group of rats probabilistic reinforcement was used: In the first group of ten stimuli, 100% of the stimuli were reinforced, in the second group of ten stimuli, 50% (in random order), in the third, 25%, and in the fourth, 12.5%.

Using the above design, the experiments were performed over 36–53 days (40 experiments on average), after which it became evident that, in the variant with a fixed sequence of reinforcements, a complex response strategy (repeated for each repetition of the sequence) was not formed. It should be noted that a simpler response strategy is formed in rats with no particular difficulty. The absence of differences between the two variants of the experiment allowed us to combine the results and to consider them, as a whole, in terms of probabilistic learning.

After detailed consideration of the evidence obtained, our attention was drawn to the sex differences in probabilistic learning (Figure 7). Both males and females are seen to possess the two phases of interhemispheric asymmetry described above, the first, with right hemisphere dominance, carrying out the strategy of averaging, the second, with left hemisphere dominance, using the matching strategy. In both cases the left hemisphere ensured that the strategy of a higher hierarchical level occurred. Nevertheless, in female rats, functional interhemispheric asymmetry was expressed approximately 2.5 times more strongly than in males. This is a rather rare case of females showing an advantage over males for expression of interhemispheric asymmetry. It testifies to the fact that under certain conditions male and female rats can use the same hemispheric strategies of probabilistic behaviour,

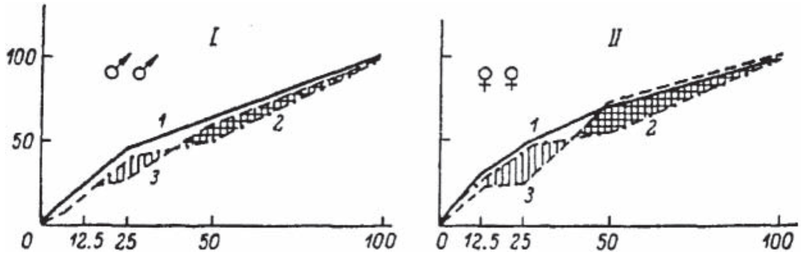

Figure 7: Asymmetry of probabilistic learning in rats. **I**–males, **II**–females. **Abscissa:** probability of reinforcement, %; **ordinate:** probability of correct reactions, %. **1**–both hemispheres are active, **2**–the left hemisphere, **3**–the right hemisphere. Single shading indicates the first phase of asymmetry, double shading indicates the second phase of asymmetry.

but, in realization of these strategies, the role of the left and the right hemisphere is considerably greater in female rats than in males.

A comparison of stereotyped and probabilistic behaviour was made in white rats of different sexes. In males, with the two hemispheres functioning concurrently while carrying out probabilistic behaviour (50% reinforcement), variance of the level of asymmetry (assessed by the K_{as} criterion) appeared to be greater than in females ($p<0.05$).

When *the left hemisphere was working in isolation* while carrying out probabilistic behaviour (50% reinforcement), variance of the effects of left hemisphere inactivation on the level of performance is greater than in females ($p<0.05$).

When the *right hemisphere was working in isolation* while carrying out stereotyped behaviour, variance of the level of performance by the right hemisphere (after left hemisphere inactivation) was greater ($p<0.05$) than in females.

(In females the values of the corresponding indices were smaller.)

It should be emphasized first of all, that sex peculiarities were found only when reinforcement was 50%, and were absent when it was 25%. Consequently they were revealed only during the second phase of interhemispheric asymmetry, characterized by left hemisphere dominance and the correspondence strategy, and not during the first phase of asymmetry, with right hemisphere dominance and the averaging strategy. Hence sex differentiation was inherent more in the right than in the left hemisphere. The left hemisphere of the male rats differed from that of the females by a more strongly expressed variance (changeability of the level of performance).

In addition, in male rats during stereotyped and probabilistic behaviour, with the cerebral hemispheres working concurrently or in isolation, a greater variance was observed compared to female rats in the level of performance, in the magnitude of interhemispheric asymmetry, and in the consequences of left hemisphere inactivation. In other words, these indices are more changeable in males than in females.

At the same time, in male rats, stereotyped behaviour assessed by the variance index, and changeability of the level of performance appeared to be associated more with the right hemisphere, and probabilistic behaviour more with the left one. Hence in male rats, control for different forms of behaviour may be more differentiated with respect to the hemispheres than in females.

Thus, the above data suggest that, in carrying out probabilistic behaviour, male and female rats use the same strategies of behaviour, but the functional interhemispheric asymmetry which appears is expressed more strongly in males than in females. Such an important adaptive character of stereotyped and probabilistic behaviour as variance or changeability appears to be expressed more strongly in male than in female rats, mainly on account of left hemisphere function. This may be evidence for a greater adaptive ability of the females. Finally, on the basis of the same index, namely variance and changeability of the performance level, it can be assumed that males, as distinct from female rats, use mainly the right hemisphere for stereotyped behaviour, and the left one for probabilistic behaviour.

2.8. DIFFERENTIATION OF VISUAL AND SOUND STIMULI

In order to clarify the problem of the dependence of sexual dimorphism of functional interhemispheric asymmetry upon its direction (i.e. on right or left hemisphere dominance) we investigated the differentiation of visual and sound stimuli of different complexity by animals.

2.8.1. Visual stimuli

In the literature, there are several indications that functional interhemispheric asymmetry depends on the difficulty involved in the discrimination task, asymmetry being observed to arise only when relatively difficult tasks are to be solved. Is this proposition always true, and are there any sex differences in this respect? Earlier it was shown that the right hemisphere was dominant in animals solving tasks by spatial analysis (Bianki, 1985). Is the right hemisphere advantage inherent in males and females to the same degree? It was demonstrated that, in the process of learning, a right-left gradient of asymmetry was observed, i.e. there was a gradual transition from right to left hemisphere dominance. Is this the case during an animal's solution of tasks of gradually increasing complexity, and if this is so, in what way is the gradient specific for males and females?

To study the above problems a typical right hemisphere task was chosen: differentiating between six pairs of light circles, gradually approaching each other in size (Figure 8, A). The diameter of the larger circle diminished from pair to pair, by equal increments, and the diameter of the small circle increased in the same way, by the same magnitude. As a result, the stimuli gradually came to approximate each other, discrimination between them becoming more and more difficult.

The experiments were performed on 40 white Wistar rats (20 males and 20 females). An automatized set-up for elaborating instrumental motion-food conditioned reflexes was used. For the initial signals, two light circles of different sizes were used–a large one (33 mm in diameter) and a small one (7 mm in diameter). In the first pair the ratio of areas was 25:1, in the second, 7.05:1, in the third, 3.5:1, in the fourth, 2.44:1, in the fifth, 1.67:1, and in the sixth, 1.15:1. The large and small circles of each pair were exposed simultaneously, in randomized position, to the right and to the left of the screen doors. The elaboration of the discrimination responses was carried out step by step, with gradual replacement of very different circles by ones which, relatively, were only slightly different. The final phase of the experiment consisted of six successively presented series of stimuli, of increasing difficulty. Each pair was exposed ten times running, and consequently the experiment consisted of 60 presentations. In all cases, the positive signal was the large circle, on presentation of which the rat had to push aside the corresponding door with its head, after which it received food reinforcement. Temporary inactivation of the cortex of one hemisphere was achieved by means of potassium chloride-induced spreading depression.

After processing the corresponding experimental evidence, both general and specific characteristics of analytic/synthetic brain activity of males and females were revealed (Figure 8, B). First of all, it was shown that when both hemispheres of the brain were working concurrently, male and female rats achieved approximately equal levels of discrimination of the size of the visual stimuli (and in every case, no significant differences were found). The exception was the presentation of the fifth pair of stimuli, which were the most difficult to differentiate. In this case, it was possible to reveal the females' advantage over the males during the process of discrimination of the stimuli. The sixth pair of stimuli could not be differentiated either by males or females. It should be emphasized that the male and female rats achieved approximately the same results, using somewhat different hemispheric strategies.

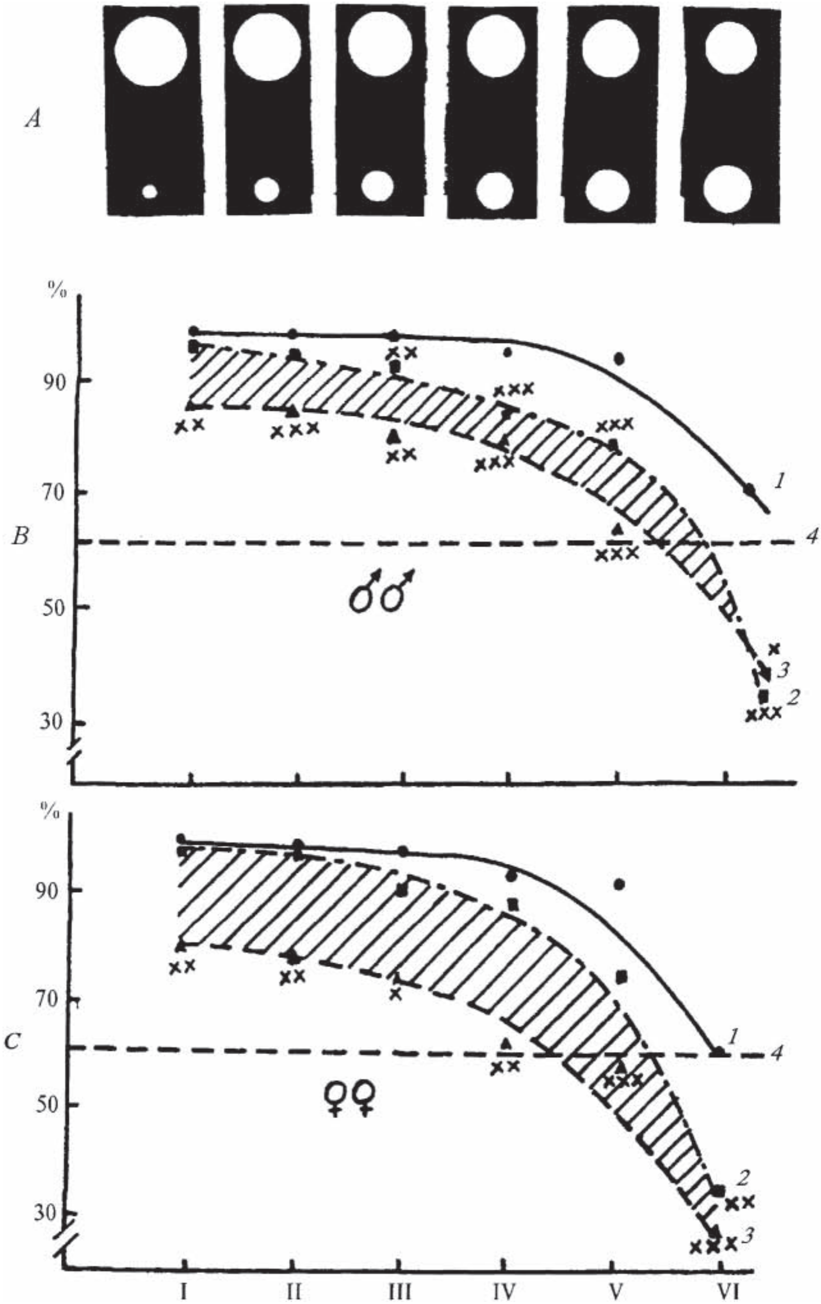

Figure 8: Sex differences in rats solving a visual task of increasing difficulty. **A**–visual stimuli to be discriminated, **B**–males, **C**–females, **1**–both hemispheres active, **2**–right hemisphere active (left hemisphere inactivated), **3**–left hemisphere active (right hemisphere inactivated), **4**–the level at which discrimination becomes significant. **Abscissa:** successive steps of tasks of increasing difficulty; **ordinate:** percentage of correct responses. Significant differences in the level of discrimination between animals with both hemispheres active and with one hemisphere active; *– $p<0.05$, **– $p<0.01$, ***– $p<0.001$.

In male and female rats, during tasks of increasing difficulty involving discrimination of the size of visual stimuli, functional interhemispheric asymmetry was observed. However it was expressed more strongly in females than in males, and this difference increased as the task became more difficult. It was shown that when male and female rats discriminated visual stimuli of increasing difficulty, the right hemisphere played the leading role, in other words, it was dominant. Moreover, the right hemisphere took a greater part in the discrimination of the above stimuli in females than in males. This testifies to the advantage of the right hemisphere in females compared to males, under the conditions of this experiment.

When male and female rats performed discriminations of the size of visual stimuli of increasing difficulty, only the right (dominant) hemisphere was involved in the solution of simple tasks; but as their difficulty grew, the left hemisphere was also mobilized. This seems to be a peculiar modification of the right-left gradient of hemisphere dominance, with the only difference being that, during the solution of a typical right hemisphere task, the right hemisphere was always dominant, the left one becoming involved only gradually. The essential point is that, in females, left hemisphere involvement started when more difficult tasks were being solved than in males. This also points to the advantage of the right hemisphere in females as compared to the males. Consequently, in solving the same task, namely differentiation of visual stimuli of increasing difficulty, male and females rats use the same right-left hemisphere strategy, although in males it is carried out faster than in females.

From the above data it follows that male rats carry out differentiation of the size of visual stimuli at approximately the same level as females, in the case of tasks of low and medium difficulty, but are inferior to the latter in the level of discrimination of relatively difficult signals. Males are characterized by a weaker functional interhemispheric asymmetry, a smaller involvement of the right hemisphere, and an earlier participation of the left hemisphere as compared to females. In their turn, female rats carry out analysis of relatively difficult stimuli at a higher level, they possess a more strongly expressed interhemispheric asymmetry, and their left hemisphere starts working only during the solution of more complicated tasks compared to males.

Subsequent processing of the experimental evidence allowed us to draw conclusions concerning not only the level of discrimination of the size of visual stimuli by rats, but also such an important index as its variance (Table 1). In male rats, with both hemispheres working concurrently, variance of the level of discrimination is greater (Table 1: 1a, 2a), and so is the variance of functional interhemispheric asymmetry (Table 1: 3a). The first of those characteristics, i.e. variance of the level of discrimination, is determined by the right hemisphere (Table 1: 5a, 6a, 7a). In females, the level of discrimination of the size of visual stimuli (Table 1: 1b), while solving difficult tasks, is higher, and the magnitude of functional interhemispheric asymmetry is greater (Table 1: 2b, 3b, 4b). The first of these characteristics (level of discrimination) is determined by right hemisphere activity (Table 1: 5b).

Summing up the above, when rats analyse the magnitude of visual stimuli differing in difficulty, the following characteristics come to light: Females reveal a higher level of discrimination when solving difficult tasks. This is achieved by right hemisphere function, a more strongly developed functional interhemispheric asymmetry, a more strongly expressed right hemisphere dominance, and only later by an involvement of the left hemisphere when solving tasks increasing in difficulty (a prolonged modification of the right-left gradient). Male rats can be characterized by a greater variance of the level of discrimination, and of functional interhemispheric asymmetry, the values of the first parameter (variance of level of discrimination) depending on left hemisphere function, which can be considered to be the dominant one.

Table 1. Sex differences in analysing visual stimuli of different complexity

Males	*Females*
Concurrent hemisphere function	
1a. In analysing the size of visual stimuli of the IInd difficulty step, variance of the level of discrimination is higher ($p<0.05$).	1b. In analysing the size of visual stimuli of the Vth difficulty step, variance of the level of discrimination is higher ($p<0.05$).
2a. In analysing the size of visual stimuli of the Vth difficulty step, variance of the level of discrimination is higher ($p<0.05$).	2b. In analysing the size of visual stimuli of the IVth difficulty step, the magnitude of asymmetry (assessed by the K_{as} criterion) is greater ($p<0.05$).
3a. In analysing the size of the Vth difficulty step, variance of the magnitude of asymmetry (according to the difference criterion) is greater ($p<0.01$).	3b. In analysing the size of visual stimuli of the IVth difficulty step, the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).
Isolated activity of the left hemisphere	
4a. In analysing the size of visual stimuli of the IInd difficulty step, variance of the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.01$).	4b. In analysing the size of visual stimuli of the I-IVth difficulty step, the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).
Isolated activity of the right hemisphere	
5a. In analysing the size of visual stimuli of the Ist difficulty step, variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is greater ($p<0.01$).	5b. In analysing the size of visual stimuli of the I-IVth difficulty step, the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).
6a. In analysing the size of visual stimuli of the IInd difficulty step, by the right hemisphere (after left hemisphere inactivation) variance of the level of discrimination is greater ($p<0.01$).	
7a. In analysing the size of visual stimuli of the VIth difficulty step, variance of the consequences of right hemisphere inactivation upon the level of discrimination is greater ($p<0.05$).	

In a more general form it can be assumed that, in solving right hemisphere visual tasks, a more perfect ability in differentiation, and a right hemisphere advantage were revealed in females as compared to males.

2.8.2. Sound stimuli

Earlier it has been shown that white rats are capable of differentiating between the English vowels [a] and [i], and the English consonants [b] and [d] in the sound combination [ba] and [da], achieving a sufficiently high level of correct reactions–90% on average (Bianki, 1985,1988; Bianki *et al.,* 1989a). However, it should be pointed out that before such a result can be obtained, prolonged training is needed. It took about 25 experiments (from 18 to 33) to stabilize the discrimination of the sounds [a] and [i], whereas the ability to differentiate between the consonants [b] and [d] took 29 experiments on the average (from 21 to 45 in different individuals). In addition, it was established that left hemisphere inactivation during the differentiation of both the vowels and the consonants resulted in deterioration of performance, whereas right hemisphere inactivation somewhat increased its level. Thus, in animals with an intact brain, left hemisphere function appeared to improve analysis, and the activity of the right hemisphere seemed to make it inferior. These data testified to the dominance of the left hemisphere when rats analysed the above vowels and consonants.

In experiments whose purpose was to study the influence of functional inactivation of the left and the right hemisphere upon the rats' differentiation between different vowels and consonants, 24 males and 24 females were used. Cortical inactivation was achieved by means of spreading depression. In Figure 9 it can be seen that, when the animals analysed the vowels [a] and [i], no sex differences were revealed in the level of discrimination by the intact brain. Left hemisphere inactivation in the animals of both sexes resulted in a significant deterioration of discrimination, whereas right hemisphere inactivation appeared to be ineffective, in both males and females.

A somewhat different picture was observed when the rats analysed the consonants [b] and [d], the males seeming to differentiate between these sounds a little better (5%) than females. In addition, when consonants were analysed, both left and right hemisphere inactivation appeared to be effective. In the first case, differentiation deteriorated, while in the second it improved. This picture was observed in both males and females. Hence it follows that, when analysing vowels, rats use a one-hemisphere mechanism to create functional interhemispheric asymmetry, and when differentiating consonants a two-hemisphere mechanism is employed.

It can be suggested that the above sex differences are associated with certain levels of difficulty of the tasks presented. Analysis of vowels must have been a simpler task, which is evidenced by a relatively fast establishment of differentiation. In this case no sex differences in the level of discrimination level were observed, and left-sided interhemispheric asymmetry was determined only by left hemisphere function. In differentiating between consonants the task was hampered by the fact that the animals had to analyse not isolated stimuli, as in the case described above, but the binomial complexes [ba] and [da] differing in one (consonant) component. The sex differences manifested themselves in some advantage of males over females. Left-sided interhemispheric asymmetry was established as the result of the opposite shifts of the functional state of both hemispheres. The above data reveal sex differences in animals only when tasks of a certain level of difficulty are presented.

In addition, males surpass females not only in the level of discrimination, but also in the expression of functional interhemispheric asymmetry in differentiating vowels (Table 2: 1a, 2a, 3a). Consequently, in males, under certain conditions, strongly expressed asymmetry occurs more often and is characterized by a greater changeability than in females. At the same time, females also possess a certain advantage over males: In differentiating between both vowels and consonants the variance of their level of discrimination is greater than that in males (Table 2: 1b, 2b).

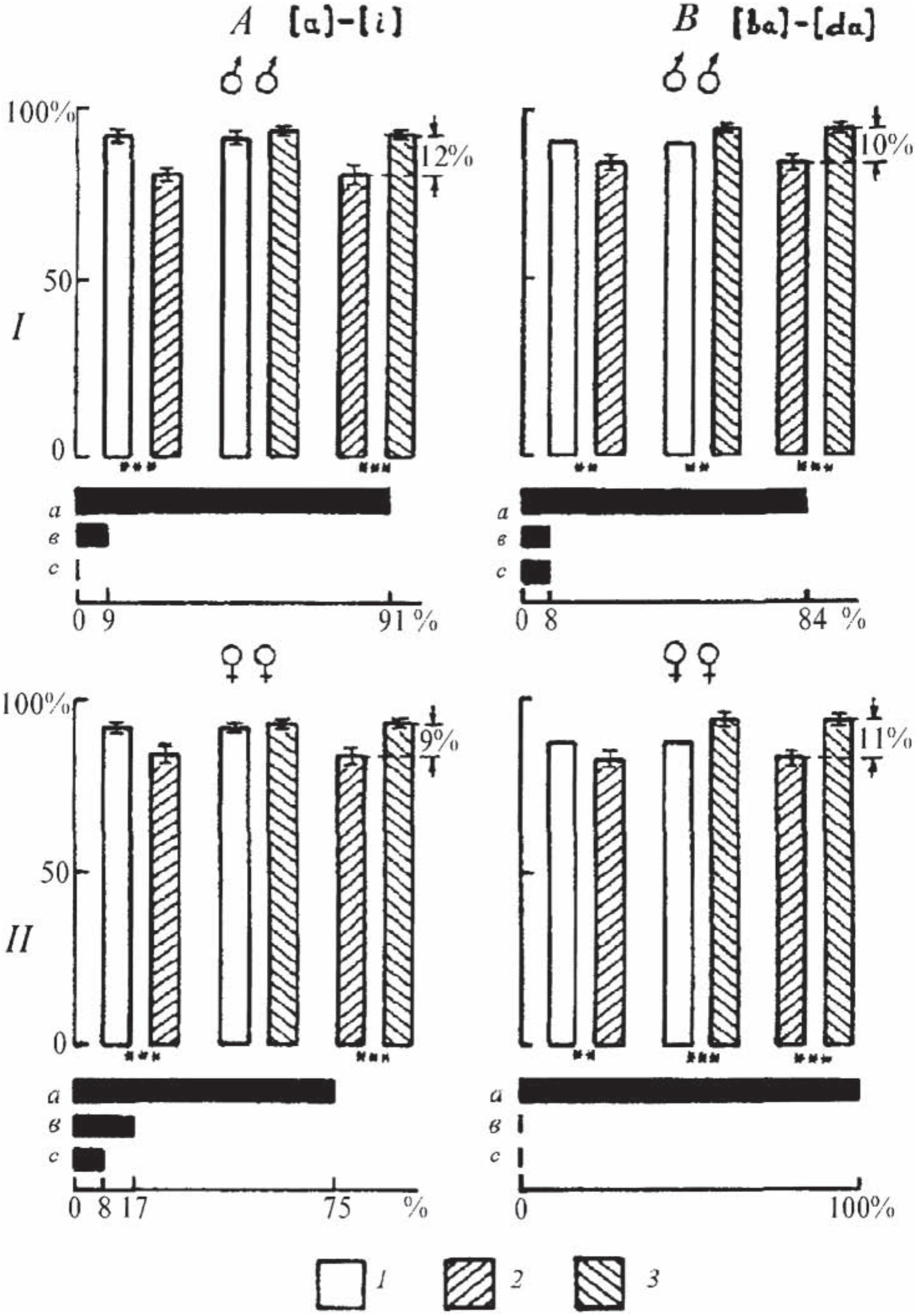

Figure 9: Sex differences in the analysis of vowels and consonants by rats. **A**–analysis of vowel sounds [a] and [i], **B**–analysis of consonant sounds [b] and [d] in the [ba]– [da] syllables, **I**–males, **II**–females. **1**–both hemispheres intact, **2**–left hemisphere inactivated, **3**–right hemisphere inactivated, **a**–percentage of individuals with left hemisphere dominance **b**–with right hemisphere dominance, **c**–percentage of ambidexters. **– $p<0.01$, ***– $p<0.001$.

Table 2. Sex differences in the analysis of vowels and consonants

Males	*Females*
Concurrent hemisphere function	
1a. In differentiating the consonants in [ba]-[da] syllables the level of discrimination is higher ($p<0.01$).	1b. In differentiating the consonants in [ba]-[da] syllables variance of the level of discrimination is greater ($p<0.01$).
2a. In differentiating the [a]-[i] vowels variance of asymmetry (assessed by the difference criterion) is greater ($p<0.01$).	2b. In differentiating the [a]-[i] vowels and consonants in [ba]-[da] syllables, presented concurrently, variance of the level of discrimination is greater ($p<0.05$).
3a. In differentiating the [a]-[i] vowels expression of asymmetry is greater ($p<0.05$).	
Isolated activity of the right hemisphere	
4a. In differentiating the [a]-[i] vowels variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is greater ($p<0.05$).	
5a. In differentiating the [a]-[i] vowels and the [b]-[d] consonants in the [ba]-[da] syllables variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is greater ($p<0.05$).	

It should be noted that some peculiarities of sex specificity during the analysis of vowels and consonants by male rats were determined by the function of their right hemisphere (Table 2: 4a, 5a). However, in females, it proved impossible to find any dependence of sex specificity when differentiating between vowels and between consonants upon the function of a single hemisphere.

In further experiments, a task was devised which complicated the analysis of the stimuli to be differentiated by the rats. For this purpose, animals had to differentiate not only between vowels and between consonants, but also to analyse these signals under conditions of transformation of one of the components with respect its intensity, timbre or duration.

Sex differences in the analysis of transformed vowels and consonants were as follows. We consider first the peculiarities revealed *in males.*

Concurrent function of both hemispheres:[5]

1. During differentiation between the consonants in syllables [ba]– [da], transformed with respect to their timbre, the magnitude of asymmetry (assessed by the difference criterion) was greater ($p<0.01$).
2. During differentiation between consonants in the syllables [ba]– [da], transformed with respect to their intensity and timbre, the magnitude of asymmetry was greater ($p<0.05$).
3. During differentiation between the consonants in the syllables [ba]– [da], transformed with respect to their timbre and duration, the magnitude of asymmetry (assessed by the difference criterion) was greater ($p<0.05$).
4. During differentiation between the vowels [a]– [i], transformed with respect to their intensity, the magnitude of individual asymmetry (assessed by the difference criterion) was greater ($p<0.05$).

5. During differentiation between the consonants in the syllables [ba]– [da], transformed with respect to their intensity and timbre, the magnitude of individual asymmetry (assessed by the difference criterion) was greater ($p<0.05$).
6. During differentiation between the vowels [a]– [i] and the consonants in the syllables [ba]– [da], transformed with respect to their intensity, the magnitude of individual asymmetry (assessed by the difference criterion) was greater ($p<0.05$).
7. During differentiation between the vowels [a]– [i], transformed with respect to their intensity, variance of asymmetry (assessed by the difference criterion) was greater ($p<0.01$).
8. During differentiation between the vowels [a]– [i] and the consonants in the binomial syllables [ba]– [da], transformed with respect to their intensity, variance of asymmetry (according to the difference criterion) was greater ($p<0.05$).

Isolated left hemisphere activity:[6]

9. During differentiation between the vowels [a]– [i], transformed with respect to their intensity, the level of discrimination by the left hemisphere (the right one being inactivated) was higher ($p<0.05$).
10. During differentiation between the vowels [a]– [i], transformed with respect to their duration, the level of discrimination by the left hemisphere (the right being inactivated) was higher ($p<0.05$).
11. During differentiation between the vowels [a]– [i], transformed with respect to their intensity, timbre and duration, the level of discrimination by the left hemisphere (the right being inactivated) was higher ($p<0.01$).
12. During differentiation between the vowels [a]– [i], transformed with respect to their intensity, variance of the level of discrimination was higher ($p<0.01$).
13. During differentiation between the vowels [a]– [i], transformed with respect to their intensity, timbre and duration, variance of the level of discrimination was higher ($p<0.01$).
14. During differentiation between the vowels [a]– [i] and the consonants in the syllables [ba]– [da], transformed with respect to their intensity, variance of the level of discrimination was greater ($p<0.01$).
15. During differentiation between the vowels [a]– [i] and the consonants in the syllables [ba]– [da], transformed according to their intensity, timbre and duration, variance of the level of discrimination was greater ($p<0.05$).

Isolated right hemisphere activity[7]

16. During differentiation between the consonants in the syllables [ba]– [da], transformed with respect to their timbre, the level of discrimination by the right hemisphere (the left hemisphere being inactivated) was higher ($p<0.01$).
17. During differentiation between the consonants in the syllables [ba]– [da], transformed with respect to their intensity and timbre, the level of discrimination by the right hemisphere (the left hemisphere being inactivated) was higher ($p<0.05$).
18. During differentiation between the consonants in the syllables [ba]– [da], transformed with respect to their intensity, timbre and duration, the level of discrimination by the right hemisphere (the left being inactivated) was higher ($p<0.05$).

19. During differentiation between the vowels [a]– [i] and the consonants in the syllables [ba]– [da], transformed with respect to their intensity, timbre and duration, the level of discrimination by the right hemisphere (the left being inactivated) was higher ($p<0.05$).
20. During differentiation between the vowels [a]– [i], transformed with respect to their intensity, variance of the level of discrimination was greater ($p<0.01$).

(In the females, the values of the corresponding indices were smaller.)

From the data obtained it follows that, during the concurrent activity of the cerebral hemispheres, male rats were characterized by a greater magnitude of species-specific and individual functional interhemispheric asymmetry, and variance of this was greater than in females (points 1–8). Male rats also appeared to surpass females in the isolated activity of both the left and the right hemisphere. In both cases (i.e. during the function of each hemisphere singly) the males carried out analysis of vowels and consonants at a higher level, and with greater variance than females (points 10–20). It is of interest that, in males, there was a tendency for the left hemisphere to be specialized in the analysis of vowels (7 cases out of 8), and for the right to dominate in differentiating between consonants (4 cases out of 5). However it cannot be ruled out that this effect was determined not by the sounds being vowels, but by the relative difficulty of the stimuli to be differentiated.

What does the above evidence show? First of all, it points to the existence, within certain limits, of a direct relation between the difficulty of analysis and the manifestation of sex specificity. Sex differences are mainly found when a sufficiently difficult task is presented; in relatively simple tasks such differences are not found, as a rule. Probably this is determined by different mechanisms underlying the appearance of functional interhemispheric asymmetry: In simple tasks it is uni-hemispheric, in difficult ones, bi-hemispheric.

During the analysis of vowels and consonants, certain advantages of males over females were found in the level of discrimination of the above stimuli, in the greater magnitude of species-specific and individual functional interhemispheric asymmetry, in greater expression of asymmetry, and in the greater variance of the degree of asymmetry. However, under certain conditions, female rats reveal a definite advantage over males, in the degree of variance of the level of discrimination. Sex differences when rats analyse vowels and consonants are also observed during the isolated function of either hemisphere. In such cases the males' advantage over the females is very distinct. In males, analyses of both vowels and consonants can be carried out in the left and in the right hemisphere at a higher level, and with greater variance than in females.

Generally, it is suggested that, when male rats solve "left-hemisphere" tasks, both hemispheres are more differentiated than in females.

2.9. INVARIANT RECOGNITION OF SOUND AND VISUAL STIMULI

The above data clearly indicate the existence of some sex peculiarities of functional interhemispheric asymmetry. Quite naturally, a question arises about which of the hemispheres determines the specificity of interhemispheric asymmetry in the brains of males and females. Some data on this topic are given below.

2.9.1. Sound stimuli

In the process of sound perception, the subject of perceptual invariance or constancy is becoming of increasing significance. Such invariance ensures the ability of the organism to neglect differences in signal parameters, within certain limits, and to refer them to one category, in other words, to ascribe the same meaning to them. In studies on humans, natural speech signals are usually used as stimuli, for example, isolated vowels and syllables with the "vowel-consonant" structure. As shown in earlier investigations, during the perception of speech sounds in new-born human infants, and in animals, division of such sounds into phonemic categories is based mainly on the inborn properties of the auditory system, unrelated to speech (Burdick and Miller, 1975; Kuhl, 1979). However, learning also makes a considerable contribution to the formation of the phonemic system (Lisker and Abramson, 1967). In this respect two mechanisms are important for the formation of categories: generalization, which provides for transferring the response elaborated to one signal, to other stimuli different from it; and differentiation, which results in the "singling out" of signals referring to one category from all others.

Our previous experiments were performed in line with the traditional design for studying the properties of perceptual constancy. According to this, differentiation of two sounds was elaborated in animals, and then the transfer of learning was assessed to signals differing in some non-phonetic parameters, i.e. intensity, duration, or the basic tone frequency (Bianki, 1985, 1988; Bianki *et al.,* 1989a). In experiments performed on white rats not divided according to their sex, the animals' perception of phonemes was shown to be characterized by perceptual constancy (invariance), i.e. they had the ability to refer the signals with different acoustic parameters to the same category. In addition, the rats were observed to possess interhemispheric differences in expression of this property: At the stage of well-established performance, their dominant hemisphere was, as a rule, the left.

In the present work we were interested mainly in the sex differences in perceptual constancy, or invariance of perception of the sound stimuli by rats. The experiments were performed on white Wistar rats, using the motion-food technique for forming instrumental conditioned reflexes. The sound source was placed above the experimental chamber. Under the action of one stimulus the rat was required to push aside a certain door with its head, and when the other stimulus was presented the other door was to be pushed aside. The main differentiated stimuli were the English vowels [a] and [i], and the consonants [b] and [d] in the consonant-vowel type of syllables [ba]– [da], pronounced by a speaker, and recorded on tape. The test stimuli were both basic sounds, but were transformed according to their intensity, the frequency of the basic tone, or their duration. The test stimuli were never reinforced. The experimental procedure was the preliminary elaboration of the discrimination of the vowels or consonants used, and the subsequent performance in the test experiments, under the conditions of inactivation of the right or left cortex by means of spreading depression. It should be pointed out that one or other hemisphere was considered to be dominant for invariance if, during its function, reactions to transformed test stimuli did not differ significantly from those to the main stimuli.

First of all, let us consider data obtained from presentation of the vowels [a] and [i], differing in intensity (Figure 10.I). The main stimuli were the sounds pronounced by a male speaker, with intensity 92 dB, and duration 1.5 s. For test stimuli, the same sounds were used, but with intensity of 80 and 104 dB. In the diagrams, it can be seen that in two cases, in male rats, left hemisphere dominance was observed in the animals' ability to neglect changes in the signal intensity, when the test stimuli were either relatively weak or strong sounds [i] (80 and 104 dB). When the left hemisphere was active, reactions to the main and test stimuli were not significantly different, whereas, during right hemisphere activity, the differences were statistically significant.

In another experimental variant, vowels with a different tone frequency were used (Figure 10.II). The basic sounds were pronounced by a male speaker, with intensity 92 dB and duration 1.5 s, while the test stimuli were pronounced by another male speaker, or by a female speaker. Left hemisphere dominance was found for male and female rats, in their ability to neglect the differences between the speakers, in pronunciation of the sounds [a] and [i], when the main male speaker was replaced by a female, or by another male speaker. In this case, significant differences between the levels of reaction to the main and the test stimulus were observed when the right hemisphere was active, and were not observed during the activity of the left.

Still more distinctive results were obtained when vowels differing in duration were used (Figure 10.III). The main stimuli were the sounds [a] and [i] pronounced by a male speaker, with intensity of 92 dB and duration 1.5 s. For the test stimuli, only duration was changed, to either 1 or 2 s. In these experiments, in male rats, left hemisphere dominance was found for invariant recognition of the sound [a], in cases where test sounds of 1 and 2 s duration were used: When the left hemisphere was functioning, differences in the level of occurrence of the conditioned reaction to the main and to the test stimuli were not significant, whereas during right hemisphere function they were. In female rats, left hemisphere dominance was also revealed for invariant recognition (regardless of duration) of the sounds [a] and [i]: When the duration of presentation was reduced to 1 s, no significant differences in the level of discrimination were observed when the left hemisphere was active, but they were present when the right was working. Finally, under similar experimental conditions, right hemisphere dominance could be observed when the main signals [a] and [i] were transformed with respect to their duration, and were presented for 1 or 2 s. The differences were not significant when the right hemisphere was active, whereas left hemisphere activity produced significant differences.

In the next experimental series, also performed on 24 rats, lateralization of the faculty of perceptual constancy in perceiving consonants by animals of both sexes was studied (Figure 11.I). In the first variant of these experiments, as in the case of vowels, transformation of the consonants [b] and [d] were used, pronounced by a male speaker, with intensity of 92 dB and duration 1.5 s. The test stimuli were the same sounds, but with intensities of 80 and 104 dB. In experiments performed on male rats, left hemisphere dominance was found for the invariant perception of the sound [b] when its intensity was changed to 80 and 104 dB, and for that of the sound [d] when its intensity was increased to 104 dB. In the dominant (left) hemisphere, statistically significant differences between the levels of reactions to the main and the test stimuli were not observed, whereas they occurred in the nondominant (right) hemisphere. In one case, right hemisphere dominance was found in male rats for invariant recognition of the sound [d] when its intensity was changed to 80 dB. In female rats, it was also possible to find left hemisphere dominance for invariant perception of the sounds [b] and [d], when their intensity was changed to 80 and 104 dB. Right hemisphere dominance was observed for invariant recognition of the sound [b] when its intensity was changed to 104 dB.

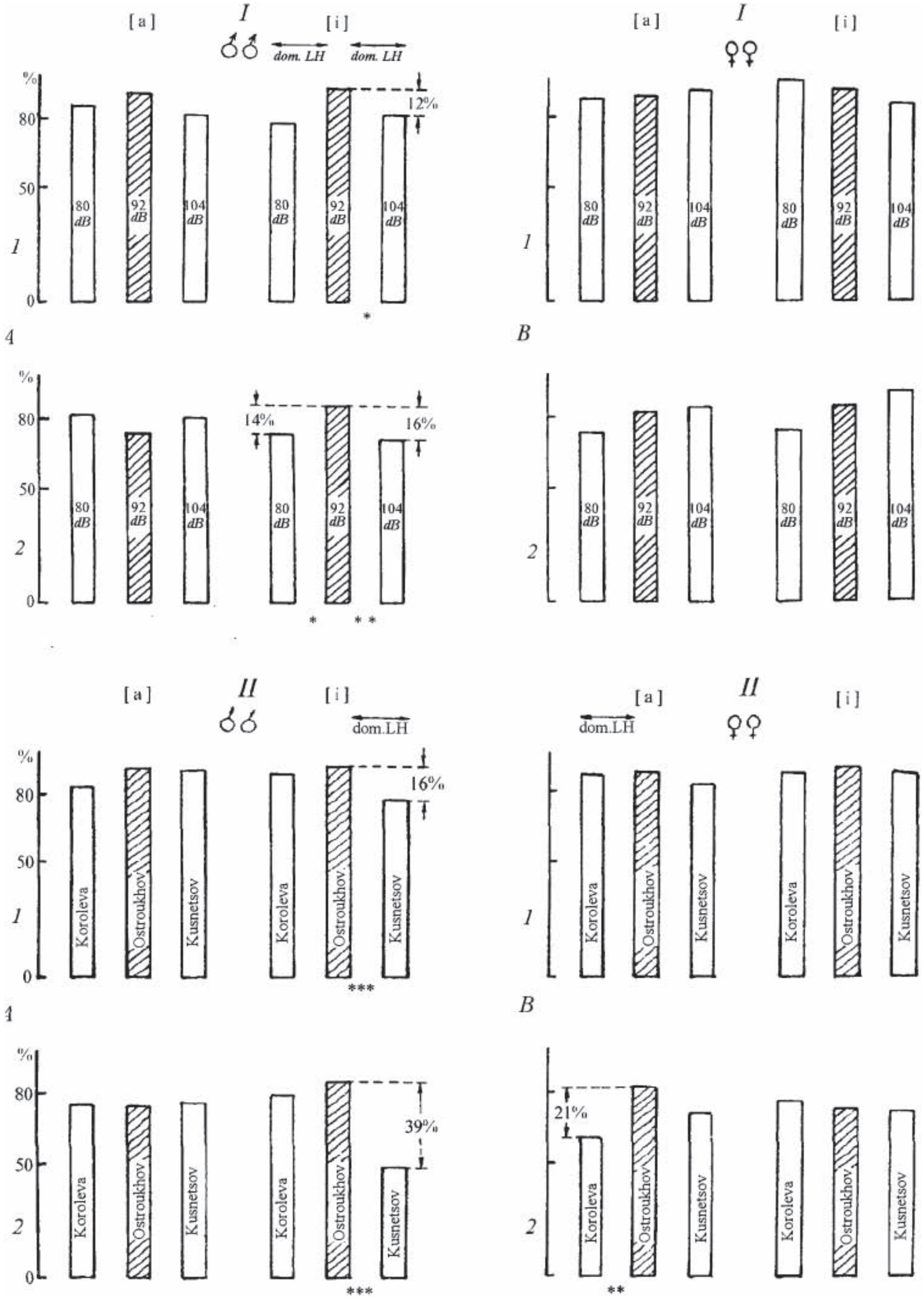

Figure 10: Invariant recognition of vowel sounds after left and right hemisphere inactivation. **A**–males, **B**–females, **I**–transformation with respect to intensity, **II**–with respect to frequency of the main tone, **III** with respect to duration; after right **(1)** or left **(2)** hemisphere inactivation. The signal characteristics are indicated. **Shaded columns**–reaction to the main stimuli; **non-shaded ones**–reactions to the test stimuli. **Ordinate:** the level of discrimination (%). *– $p<0.05$; **– $p<0.01$; ***– $p<0.001$.

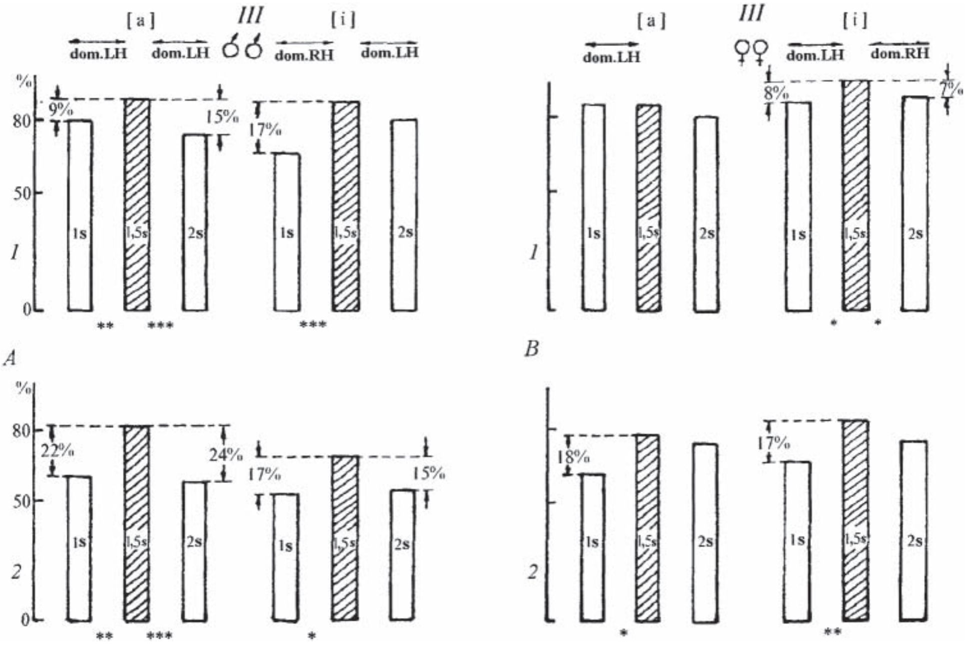

Figure 10: Continued

In the second series of experiments, consonants with different tone frequencies were used (Figure 11.II). The basic sounds were pronounced by one male speaker, the test ones, by another male speaker or by a female speaker. Left hemisphere dominance for maintaining perceptual constancy in discriminating between the consonants [b] and [d] was found in males, both after replacing one male speaker by the other, and after replacing him by a woman speaker. In both cases, during dominant (left) hemisphere activity, differences between the levels of reactions to the main and the test stimuli were not significant, while they became significant during nondominant (right) hemisphere activity. In female rats, left hemisphere dominance for invariant perception was found during analysis of the consonant [b] under the condition of replacing one male speaker by the other, and also during differentiation between the consonants [b] and [d] under the condition of replacing by either speaker. At the same time, in female rats, right hemisphere dominance was also observed during the analysis of the consonant [b] after the male speaker had been replaced by the woman speaker.

The above data testify to the fact that in both male and female rats, phoneme perception is characterized by the property of perceptual constancy, or invariance. At the same time, in realization of such invariant phoneme perception, the left hemisphere dominates in most cases. The following trend may be of interest: In male rats, in almost all cases, left hemisphere dominance is observed for perceptual invariance, whereas in female rats dominance of left and right hemisphere is equiprobable. This points to a greater degree of brain asymmetry in males, and a relative symmetry in females. Hence it follows that the left hemisphere advantage for maintaining perceptual constancy, noted earlier in the population as a whole, is determined mainly by males (Bianki, 1985, 1988).

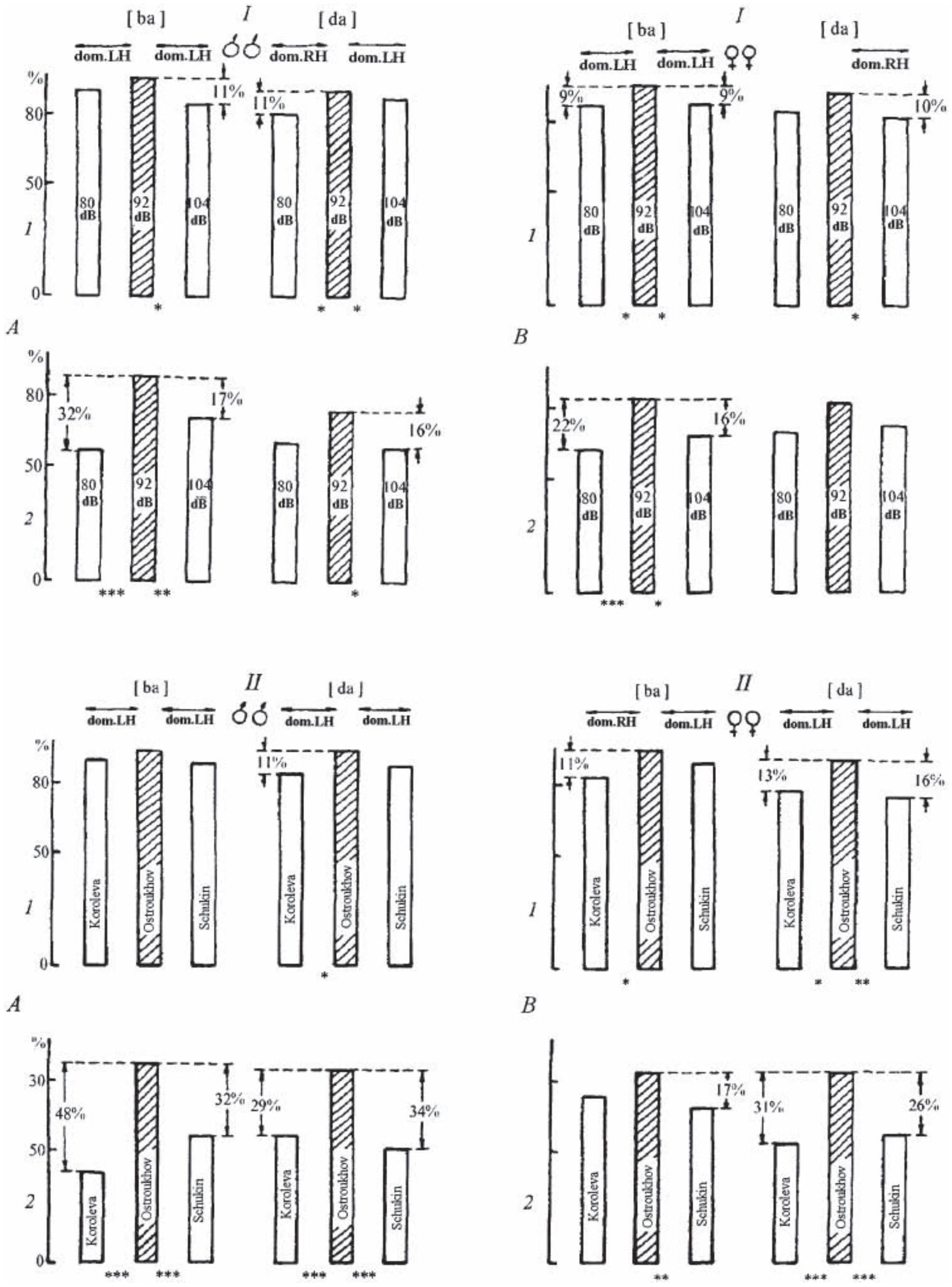

Figure 11: Invariant recognition by rats of both sexes of consonant sounds after left and right hemisphere inactivation. **A**–males, **B**–females, **I**–transformation with respect to intensity, **II**–with respect to the frequency of the main tone; after right **(1)** or left **(2)** hemisphere inactivation. The signal characteristics are indicated. **Shaded columns**–reaction to the main stimuli; **Non-shaded ones**–reactions to the test stimuli. **Ordinate:** the level of discrimination (%). *– $p<0.05$; **– $p<0.01$; ***– $p<0.001$.

On the basis of the above data on invariant recognition of vowels and consonants by rats of both sexes, one can gain an inkling of the comparative character of the processes of specialization and generalization of the conditioned reflexes in the two cerebral hemispheres of male and female rats. For this purpose it would be instrumental to introduce a "coefficient of specialization-generalization". This is the difference between the levels of expression of the conditioned reflex under the action of the main and the test stimuli. The greater this coefficient, the more strongly is specialization of the conditioned reflex expressed; the lesser it is, the more highly developed is generalization of the conditioned reflex. Corresponding calculations were made on the basis of all experimental data obtained from the rats' invariant recognition of vowels and consonants.

The results of the calculations suggest that, during concurrent function of the two hemispheres, the coefficient of specialization-generalization in male rats is greater than in females (on the average, 14 and 10 respectively, $p<0.05$). This testifies to greater role of the hemispheres in specialization in males, as compared to females, and to a greater role in generalization in females as compared to males. At the same time, during left hemisphere activity, the specialization-generalization coefficient appeared also to be greater in males than in females (on the average, 10 and 6 respectively, $p<0.05$). This suggests a greater role of the male left hemisphere in specialization as compared to that of females, and a greater role of the female left hemisphere function in generalization as compared to males.

The above data point to the fact that the greater hemispheric differentiation of the male brain is maintained mainly by the role of the left hemisphere in the function of specialization. At the same time, the relatively undifferentiated hemispheric activity of the female rats' brain was determined to a certain degree by the greater role of their left hemisphere in the function of generalization.

2.9.2. Visual stimuli

Invariance for recognition of visual stimuli is the ability to recognize objects independent of their transformation with respect to their position, size, orientation, brightness, colour etc. There is an opinion that, in humans, two kinds of description of images are associated with the function of different hemispheres (Levashov, 1976; Leushina *et al.,* 1981, 1982). According to the data of A.A.Nevskaya and L.I.Leushina (1990), in adult humans, the type of image description is a constant property of each hemisphere, since it does not change with time, and does not depend on the type of image transformation. In most people, the mechanisms of initial invariance (i.e. inborn invariance) are associated with the left hemisphere, those of the secondary invariance (i.e. that acquired in the course of training), with the right hemisphere. It should be noted that in a considerable group of right-handers (about 20%), the initial invariant description is carried out in the right, the secondary one, in the left hemisphere. Animals are known to possess left hemisphere dominance for invariant recognition of visual stimuli with some kinds of visual image transformation (Bianki, 1985, 1988).

To study invariant recognition of visual stimuli in Wistar rats, a motion-food technique was used for forming instrumental conditioned reflexes, with simultaneous presentation of two stimuli. The experiments were performed on 27 males and females. The experiments were subdivided into the main and the test ones. The main experiment consisted of 30 presentations of a pair of the main stimuli, exposed simultaneously on two doors in random position. To obtain reinforcement the rat was required to push aside with its head the door upon which the positive signal was projected. Such experiments were performed for several months until a criterion level of performance was achieved.

The test experiments consisted of 30 presentations of the main pair of stimuli, alternating with 20 presentations of the test stimuli. Temporary functional inactivation of the cortex was achieved by means of potassium chloride-induced spreading depression.

In the experiment, standard shapes were used (Glezer *et al.,* 1970). The main stimuli were: a cross and a circle, a square and a triangle, and two polygons with symmetrical and asymmetrical sides (Figure 12). The stimuli mentioned first in each of the above pairs were meant to be positive signals. The main and the test stimuli were (as a rule) black contours, each with the same length of perimeter, and presented against a light background. Six kinds of transformations of the test figures were used: with respect to their size, by filling up of the contour, with respect to their contrast, their background, by rotation to the angle of 45°, or by mirror-transformation with a rotation round the vertical and horizontal axes, and also by presentation of elements of the figures. Initially, differentiation between

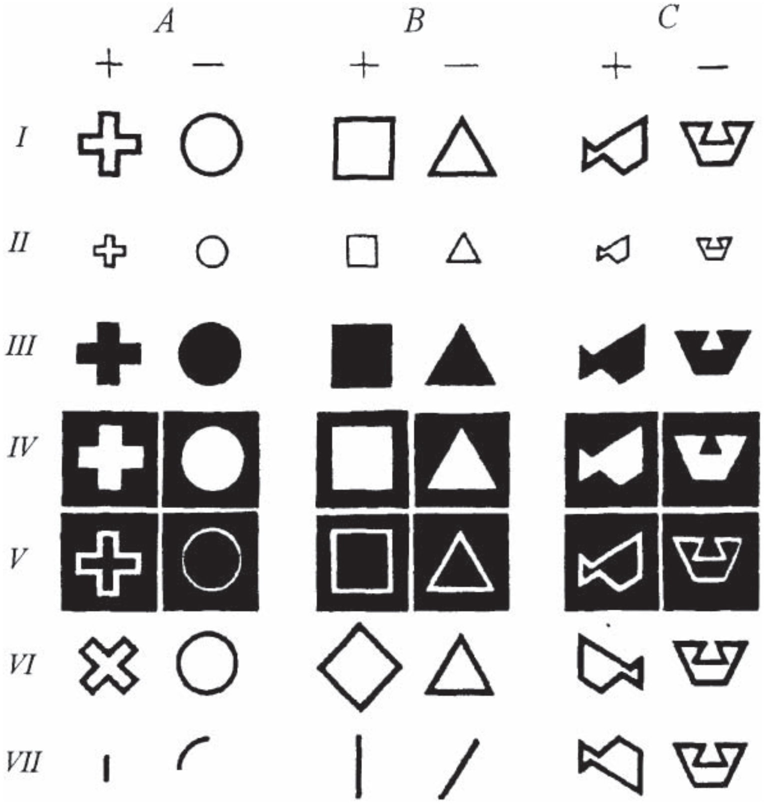

Figure 12: Tests used for studying invariant recognition of visual stimuli (According to Glezer *et al.,* 1970). **A**-**C**–variants of stimuli presented. **I**–the main figures, **II**–transformation with respect to size, **III**–by filling up contours, **IV**–with respect to contrast, **V**–with respect to background, **VI**–by rotation (turning of one of the figures at an angle of 45°, or mirror-image transformation with rotation around the vertical and the horizontal axes), **VII**–presentation of elements of figures.

the main figures was established, and then the action of the test stimuli was tested. The correct choice of the transformed positive figure was taken to be the index of invariant generalized recognition. A mistaken choice (a positive reaction to another transformed stimulus) was considered to be an index of reaction to concrete variants.

It was shown (Bianki, 1985, 1988) that when the first three kinds of transformations were used–with respect to their size, by filling in of the contour, and with respect to contrast–invariant recognition, and assessment of concrete variants deteriorated equally, both after left and right hemisphere inactivation, although individual asymmetry was observed. In contrast to the above, when the other transformations were used–with respect to the background, by rotation, or by breakdown into elements–it was possible to find lateral brain specialization. Left hemisphere inactivation resulted in a deeper disruption of invariant recognition than did inactivation of the right hemisphere. Right hemisphere inactivation influenced the assessment of concrete variants more than that of the left hemisphere. In both cases, asymmetry was, on the average, 16%.

After processing the experimental evidence, differentiated according to sex, no sex differences could be revealed in invariant recognition of visual stimuli by rats. Both in males and females, left hemisphere dominance was observed for invariant recognition and right hemisphere dominance for analysis of concrete stimuli.

In contrast to this, sex differences *were* found when such an important characteristic of analytic/synthetic activity was considered as variance. We hold variance (changeability of reaction) as an important biological factor, which under certain conditions may assume considerable adaptive importance.

During concurrent activity of the cerebral hemispheres, males surpass females in variance of functional interhemispheric asymmetry, under the condition of transformation of visual stimuli with respect to their size (Table 3: 1a). Sex differences in variance of reactions were also found when isolated activity of each hemisphere was considered. Thus, a left hemisphere advantage was found in males for variance of the level of discrimination, under the conditions of transformation of visual stimuli by filling in contours, and in

Table 3. Sex differences in invariant discrimination between visual stimuli

Males	*Females*
Concurrent hemisphere function	
1a. In transforming visual stimuli with respect to their size (Figure 12, II) variance of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).	
Isolated activity of the left or the right hemisphere	
2a. In transforming visual stimuli by filling-up (Figure 12, III) variance of the level of discrimination by the left hemisphere (after right hemisphere inactivation) is greater ($p<0.01$).	2b. In transforming visual stimuli by rotation (Figure 12, VI) variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is greater ($p<0.05$).
3a In transforming visual stimuli with respect to contrast (Figure 12, IV) variance of the consequence of left hemisphere inactivation upon level of discrimination is greater ($p<0.05$).	3b. In transforming visual stimuli by rotation (Figure 12, VI) variance of the consequence of right hemisphere inactivation on the level of discrimination is greater ($p<0.05$).

contrast (Table 3: 2a, 3a). At the same time, a right hemisphere advantage was revealed in females for the same index during transformation of visual stimuli by rotation (Table 3: 2b, 3b). Hence it follows that in males, the left hemisphere dominates for the degree of variance, whereas in females the right hemisphere is dominant. However, this dominance is revealed under different conditions, i.e. when different transformations of visual stimuli are used. In males the left hemisphere appeared to be capable of more perfect activity, whereas in females it was the right one.

Thus, under certain conditions, in male rats a higher level of analytic-synthetic activity (according to the index of variance) was found, compared to females. In addition, males mainly use their left hemisphere to achieve better results, whereas females resort to the right hemisphere.

2.10. INTERMODAL AND INTRAMODAL INTEGRATION

Earlier, proceeding from conceptions concerning the diffuse function of the human right hemisphere, and a more focal activity of the left, it was suggested that the right hemisphere was specialized for multimodal, the left, for unimodal integration (Semmes, 1968; Goldberg and Costa, 1981). To test this proposition, a special model was developed which consisted of unimodal and multimodal stimulus-complexes. The animal was required to differentiate between the *complexes* and *components* of such kinds of stimuli, when either the right or the left hemisphere was functioning in isolation. If the hypothesis proved to be correct, right hemisphere inactivation was expected to be more influential upon multimodal synthesis, whereas left hemisphere inactivation was more likely to affect unimodal synthesis.

The experiments were performed on 30 white Wistar rats. Temporary functional inactivation of the cortex was achieved by means of potassium chloride-induced spreading depression. The motion-food instrumental technique for establishment of conditioned reflexes was used.

The multimodal simultaneous stimulus-complex consisted of the following components: light (100 lx), tone (1000 Hz, 63 dB), and vibration (10 Hz, amplitude 4 mm). The unimodal simultaneous visual complex included the illumination of three lamps (50, 100 and 200 lx). The unimodal simultaneous sound complex consisted of three sounds (55, 63, and 69 dB). In response to the stimulus-complex the rat was required to push aside a certain door with its head, while, in response to isolated components, it was required to push aside another door. Thus, after the conditioned reflexes had been elaborated, the rats performed the unimodal or multimodal integration of the corresponding components. They responded to each of them by the same instrumental reaction of pushing the same door. They also distinguished the complex from its components, i.e. they differentiated between two integrated systems–the initial complex stimulus, and the newly formed complex of components.

From analysis of the evidence obtained, we found that during differentiation between both unimodal and multimodal stimulus-complexes and their components, the right hemisphere is dominant. This corresponds to the concept of more diffuse function of the right hemisphere as compared to the left hemisphere. In fact, it proved impossible to support the suggestion of right hemisphere specialization for multimodal, and the left hemisphere specialization for unimodal integration and coordination (Bianki, 1985, 1988).

The above conclusion was drawn from the results of analysing evidence obtained from males and females together. It could be suggested that differentiating the data to be analysed with respect to sex would be more effective. This experimental model also seemed appropriate for studying sex differences in concurrent and isolated hemisphere activity when stimuli of different complexity and modality are presented.

Let us analyse the results obtained (Table 4) with reference to appropriate points in the table. First of all, a peculiarity of the concurrent hemisphere ability in males and females should be considered: Males surpass females in at least two respects: They show greater penetrance of asymmetry (1a) and greater variance of asymmetry (2a). Nevertheless, females surpass males for magnitude of asymmetry (1b) and variance of the level of discrimination (2b, 3b). The above characteristics can be taken naturally as manifestations of a certain advantage of the respective sex. Indeed, we consider functional interhemispheric asymmetry as an important biological character, and therefore characteristics such as its penetrance (percentage of individuals possessing asymmetry), its dispersion (variance, changeability) and the magnitude of asymmetry also indicate biological advantages, just as does the level of discrimination of corresponding stimuli by animals. It is clear from the above that, under the same conditions, males would possess certain advantages, under

Table 4. Sex differences in the analysis of unimodal and multimodal complexes and their components

Males	*Females*
Concurrent hemisphere function	
1a. In responding to the strong light component of the unimodal visual stimulus-complex variance of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).	1b. In responding to the multimodal and unimodal stimulus-complexes concurrently, the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).
2a. In responding to the unimodal sound stimulus-complex, variance of the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).	2b. In responding to the unimodal visual stimulus-complex, variance of the level of discrimination is greater ($p<0.01$).
	3b. In responding to the strong light component of the unimodal visual stimulus-complex, variance of the level of discrimination is greater ($p<0.01$).
Isolated activity of the left or the right hemisphere	
3a. In responding to the unimodal sound stimulus-complex, the influence of left hemisphere inactivation upon the level of discrimination is greater ($p<0.05$).	4b. In responding to multimodal and unimodal stimulus-complexes concurrently, the level of discrimination by the right hemisphere (after left hemisphere inactivation) is higher ($p<0.05$).
4a. In responding to the unimodal sound stimulus-complex variance of the influence of left hemisphere inactivation upon the level of discrimination is greater ($p<0.001$).	
5a. In responding to all the components of the unimodal sound stimulus-complex concurrently, variance of the influence of left hemisphere inactivation upon the level of discrimination is greater ($p<0.05$).	

others it would be the females. What can be those conditions? Analysis of our experimental evidence allowed us to suppose that they may be associated with the complexity of the stimuli used, and their modality.

The biological advantages of males manifest themselves during the analysis of unimodal complexes (2a), while those of females, are seen during differentiation between unimodal and multimodal stimuli (1b, 2b, 3b). Consequently, female rats surpass males in analysis of multimodal complex stimuli, this advantage being conditioned by right hemisphere function (4b).

Some of the sex differences are also revealed during differentiation between unimodal stimulus-complexes of different modality, judging by the parameters of interhemispheric asymmetry. Males analyse both visual (1a) and sound (2a) stimuli and their components better than females. In females the only advantage was found was during differentiation between visual complexes and their components (2b, 3b). Consequently, males surpass females in the analysis of unimodal stimulus components. The above advantage of males is maintained by left hemisphere activity (3a, 4a, 5a).

The above data suggest that, in males, the left hemisphere functions more focally than in females, whereas the female right hemisphere is more diffuse than the male one. Thus a suggestion made by J.Semmes and her colleagues (1968) of a more diffuse character for the right hemisphere and a more focal one for the left hemisphere (which could not be proved when the approach to the experimental evidence was not differentiated according to sex), found support when data obtained from males and females were analysed separately. This is one more reason for the necessity of considering physiological functions separately for males and females.

Thus on the whole, the above data testify to the fact that males surpass females in differentiating unimodal sound stimulus-complexes, this being maintained by their left hemisphere. In their turn, females analyse multimodal complexes better than males, this being determined by the function of their right hemisphere.

2.11. ANALYSIS OF SPACE AND TIME STIMULI

Recently, it has been suggested repeatedly that sex differences in the human psyche are determined by the fact that men and women use different strategies of information processing. Experiments are described below whose purpose was to attempt to find a similar regularity in animals.

One of the most firmly-established propositions in studies of brain asymmetry is the right hemisphere dominance for visuospatial analysis in humans and animals. In particular, it has been shown, in a number of experiments on rats, that the right hemisphere plays the leading role in differentiating between various visuospatial stimuli (Bianki, 1979b, 1980a,b, 1983, 1985; Bianki and Poletayeva, 1978; Bianki *et al.,* 1981). By now, a considerable amount of experimental evidence has been collected, which has allowed us to suggest the presence of sexual dimorphism in the role of the left and the right hemisphere in spatial orientation (Bianki, 1985, 1988). We shall return to this problem later.

The experiments were performed on 130 white Wistar rats, using the motion-food technique, with visual discrimination between stimuli, usually presented simultaneously. Seven visuospatial tasks were presented. The following seven types of stimuli were used: In the case of differentiating a point on a vertical plane, a light round spot with an area of

20 mm^2 was exposed on the screen to the right and to the left of the vertical line. When the position of the dot was analysed with respect to its depth, the area of the light spot was 300 mm^2, the distance between its different positions was 60 mm. To distinguish the slope of a line, a light vertical line, 15 mm long, served as a positive stimulus, another identical line positioned at a different angle to it being a negative stimulus. Analysis of a geometrical shape was carried out by presenting different solid light figures, of identical areas (2.25 cm^2). In discriminating the orientation of the same solid geometrical figures with an area of 2.25 mm^2, the figures were usually rotated by an angle of 90°. If the task was to differentiate between the sizes of the same geometrical figures they were light, solid, and had areas of 2.25 and 1.125 cm^2. Finally, when chequered patterns were analysed, the latter consisted of 18 white squares randomly positioned against a black background; representations of patterns occupied the whole screen (15 cm^2); one of them served as a positive stimulus, the others were distinguished from it.

The following experimental design was used. Previously, discrimination of some of the above stimuli was elaborated in rats, and then successive temporary functional inactivation of one and then the other hemisphere was carried out by means of potassium chloride-induced spreading depression (Bureš and Burešova, 1962).

The four main conclusions drawn from the analysis of the evidence obtained are given below (Table 5).

1. During concurrent activity of the cerebral hemispheres, male rats possessed a higher level of the discrimination of visuospatial stimuli, while solving a wide range of tasks–all the seven tests of spatial discrimination (1a)–whereas females are characterized by a greater variance of the level of discrimination of all the visuospatial stimuli (2b).
2. A higher level of discrimination is maintained chiefly by the right hemisphere in male rats, and by the left one in females (5a, 3b).
3. A greater variance of the level of discrimination is determined by the left hemisphere in males, and by the right in female rats (4a and 5b, 6b, 7b).
4. The rats' brain on the whole, and its hemispheres can be relatively specialized for different forms of visuospatial analysis.

Thus, for instance, both when the brain was intact, and when the left and the right hemispheres were working in isolation, male rats analyse the position of relatively small point stimuli better (3a, 4a, 6a). At the same time, female rats with an intact brain, or with isolated function of the left or right hemispheres possess an advantage for discrimination of relatively complex and large stimuli, such as chequered patterns, or geometrical figures (1b, 3b, 4b).

How can the above facts be interpreted? Probably, two forms of adaptation of the organism to the environment can be distinguished here. One of these forms is characterized by adaptation to a comparatively narrow span of the environment, the other, by adaptation to a comparatively wide range of factors. The first of these is attained by achieving a relatively high level of discrimination, the second, by a comparatively greater changeability or variance of the level of discrimination. The first form of adaptation (high level of discrimination) is inherent mainly in males, the second one (high level of variance), is characteristic chiefly of females. Some structural and functional peculiarities of the brains of males and females may underlie this sexual dimorphism. The facts obtained point to

Table 5. Sex differences in spatial analysis

Males	*Females*
Concurrent hemisphere function	
1a. In differentiating all the visuospatial stimuli used the level of discrimination is higher ($p<0.05$).	1b. In differentiating chequered patterns the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.01$).
2a. In differentiating all the visuospatial stimuli used the asymmetry magnitude (according to the difference criterion) is greater ($p<0.01$).	2b. In differentiating all the visuospatial stimuli used variance of the level of discrimination is greater ($p<0.05$).
3a. In differentiating the position of the dot on the vertical plane variance of the level of discrimination is greater ($p<0.05$).	
Isolated activity of the left hemisphere	
4a. In differentiating the position of the dot on the vertical plane variance of the level of discrimination is greater ($p<0.05$).	3b. In differentiating the chequered patterns, the level of discrimination by the left hemisphere (after right hemisphere inactivation) is higher ($p<0.01$).
	4b. In differentiating all the visuospatial stimuli used, variance of the influence of left hemisphere inactivation upon the level of analysis is greater ($p<0.05$).
Isolated activity of the right hemisphere	
5a. In differentiating the chequered patterns the influence of right hemisphere inactivation upon the level of discrimination is greater ($p<0.01$).	5b. In differentiating the geometrical shapes of visual stimuli, variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is greater ($p<0.01$).
6a. In differentiating the position of the dot on the vertical plane, variance of the influence of right hemisphere inactivation upon the level of analysis is greater ($p<0.05$).	6b. In differentiating the chequered pattern, variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is greater ($p<0.01$).
	7b. In differentiating all the visuospatial stimuli used, variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is greater ($p<0.01$).

the conclusion that the intact brain of male rats may be more differentiated, focal, that of females more diffuse.

The relative exent to which the forms of adaptation under the conditions in question may be distributed between the two hemispheres of the male and the female brain approximate to a mirror-image: In males, the left hemisphere controls the level of variance to a greater degree, the right one is responsible more for the level of discrimination. On the contrary, in females the left hemisphere mainly maintains the level of discrimination, the right one, the level of variance. In accordance with this, in this experimental model, the male rats' left hemisphere is more diffuse, the right one, more focal. In contrast, the female rats' left hemisphere is more focal, the right one, more diffuse.

As mentioned above, adaptation by achieving a higher level of discrimination of a narrow range of stimuli is typical of male rats with an intact brain, whereas female rats with both hemispheres functioning concurrently can be characterized by adaptation with the help of response variance, and changeability of discrimination for a wider range of stimuli. In male rats, the right hemisphere is characterized by a higher level of analysis and a relatively low level of variance. Females show an inverse picture: The right hemisphere maintains a higher level of variance and a relatively low level of discrimination. This may be accounted for by differences in the degree of expression of focality and diffusion of the male and female right hemisphere. The male right hemisphere may be more focal than the female one, that of females may be more diffuse than the male one. This is supported by the fact that the male right hemisphere analyses focal stimuli better than diffuse ones. The female right hemisphere shows an inverse picture.

The presentation of the above results allows us to draw the following conclusions. The existence of two means of adaptation to the spatial factors in the environment is suggested. The first one can be associated with adaptation to a relatively narrow range of the environment, is carried out by means of a more perfect discrimination, and is inherent mainly in males. The second can be characterized by adaptation to a relatively wide range of stimuli, is determined by a greater variance of the level of discrimination, and is observed mainly in females. These data can be accounted for as indicating the existence of two different strategies of spatial adaptation, according to an animal's sex. The above forms are represented in both hemispheres of males and females, in mirror fashion.

The sex peculiarities of adaptation to spatial factors are determined mainly by the dominant right hemisphere. There are grounds to suppose that the male brain as a whole, and its right hemisphere, are more differentiated, focal, than those in females. In females, under these conditions, the left hemisphere is more focal than that in males.

Let us now turn to the results of the study on the sex specificity for analysis of time. Some facts have been described, testifying to dominance of the left hemisphere in humans, during the analysis of the temporal factors in the environment. Similar data were also obtained from animals (Bianki, 1980a, 1983, 1985). Now we will make an attempt to analyse sex differences in animals, revealed when they were differentiating time.

In white Wistar rats (20 individuals of both sexes) a motion-food instrumental conditioned reflex to a light stimulus was elaborated. The intervals between successive conditioned stimuli lasted for two minutes. The index of the conditioned reflex to time was the dynamics of intersignal reactions. After prolonged training, when the animals had achieved a durable conditioned reflex to time, the curve describing the dependence of the intersignal reactions on time became ascending (Figure 13), i.e. the number of intersignal reactions gradually increased up to the moment of action of the conditioned stimulus. The curve was ascending during the concurrent activity of both hemispheres, and also during the isolated activity of the left hemisphere, whereas during the function of the right hemisphere it was descending. In the second half of the intersignal period left-sided hemispheric asymmetry appeared, characterized by the specialization of the left hemisphere for discrimination of time. The latter was absolute, and manifested itself in all the animals tested. As for the descending curve of the intersignal reactions during the isolated function of the right hemisphere, it seems to reflect the trace of excitation by food. To judge from the crosswise intersection of the two curves of intersignal reactions (for the left and for the right hemisphere), in the first half of the intersignal interval, a further phase of interhemispheric asymmetry was observed–the asymmetry of trace excitation, this being characterized by right hemisphere dominance.

Sex differences of hemispheric specialization during time differentiation attract special attention. Comparison of graphs A and B (Figure 13) suggests that left-sided asymmetry during temporal analysis was characteristic of both males and females, yet it was expressed more (approximately twofold more) in females. Similarly, right-sided asymmetry of trace excitation was observed in animals of both sexes but its magnitude was also larger in female rats. Consequently, in these experiments, consideration of sexual dimorphism revealed a unidirectional asymmetry in both sexes, which, however, was expressed more in females, rather than in males (as is usually the case).

In the next experimental series, discrimination between different durations of action of the same stimulus was elaborated in 24 white rats. An electric bulb was switched on for either 5 or 10 s, and acted as a signal for an instrumental response, directed either to the deflecting door on either the right or the left (respectively). Food reinforcement was used.

When a mixed sample of animals (without sex differentiation) was examined, inactivation of the left hemisphere was found to result in deterioration of temporal analysis, whereas inactivation of the right hemisphere appeared to be ineffective. Left-sided asymmetry was statistically highly significant, amounting, on average, to 13%, and it was found in all the subjects. Consequently, the hemispheric specialization revealed was absolute.

The results of studying sexual dimorphism during discrimination of the duration of action of a light stimulus by rats (Table 6) suggests that male rats with both hemispheres active surpass females in the level of discrimination (on the average, by 8%), in the resulting degree of asymmetry (approximately, twofold) and in the degree of expression, and level of variance of discrimination (1a, 2a, 3a). With respect to the action of one hemisphere, under given experimental conditions, females appeared to possess a higher level of variance, which could be associated both with left (1b) and right (2b) hemisphere function.

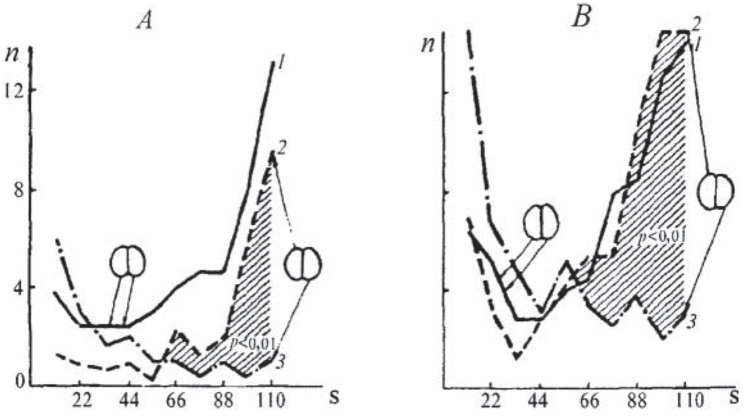

Figure 13: The influence of left and right hemisphere inactivation in male and female rats during the formation of the light conditioned reflex to time, with 2 min intervals between the stimuli. **A**–males, **B**–females, **1**–both hemispheres active, **2**–the right hemisphere inactivated, **3**–the left hemisphere inactivated. **Abscissa:** time, s; **ordinate:** number of reactions between two signals, n.

Table 6. Sex differences in time analysis

<table>
<tr><th>Males</th><th>Females</th></tr>
<tr><td colspan="2">Concurrent hemisphere function</td></tr>
<tr><td>1a. In differentiating the time period of light stimuli action, 5 and 10 s, the level of discrimination is higher (p<0.01).</td><td></td></tr>
<tr><td>2a. In differentiating the time period of light stimuli action, 5 and 10 s, the magnitude of asymmetry (assessed by the difference criterion) is greater (p<0.05).</td><td></td></tr>
<tr><td>3a. In differentiating the time period of light stimuli action, 5 and 10 s, variance of the level of discrimination is greater (p<0.05).</td><td></td></tr>
<tr><td colspan="2">The isolated activity of the left hemisphere</td></tr>
<tr><td></td><td>4b. In differentiating the time period of light stimuli action, 5 and 10 s, variance of the level of discrimination by the left hemisphere (after right hemisphere inactivation) is higher (p<0.05).</td></tr>
<tr><td colspan="2">The isolated activity of the right hemisphere</td></tr>
<tr><td></td><td>5b. In differentiating the time period of light stimuli action, 5 and 10 s, variance of the influence of right hemisphere inactivation upon the level of discrimination is greater (p<0.05).</td></tr>
</table>

Comparison of data obtained from the study of spatial and temporal analysis, under the condition of an intact brain, showed that, in both cases, male rats surpassed females in the level of discrimination, in the degree of functional interhemispheric asymmetry, and in the variance of the level of discrimination. It is important that the above advantage was revealed for both right hemisphere functions (spatial analysis) and left hemisphere functions (time differentiation).

It should also be noted that, under other experimental conditions, during formation of a conditioned reflex to a fixed period of action of a visual stimulus, females were found to possess an advantage over males in the degree of functional interhemispheric asymmetry.

It should be emphasized that two different strategies in spatial behaviour were revealed, according to the animal's sex: The males analysed a relatively narrow range of signals using a higher level of discrimination, while the females analysed a relatively wide span of stimuli, using a greater variance of the level of discrimination.

2.12. DISCRIMINATION OF SIMULTANEOUS AND SUCCESSIVE COMPLEXES

According to a hypothesis included in a number of summaries, the human right hemisphere is specialized for simultaneous information processing, the left hemisphere for successive processing (White, 1969, 1972; Kimura and Durnford, 1974; Pirozzolo, 1977; Polich, 1978; Simernitskaya, 1978). J.Levy-Agresti and R.Sperry (1968) suggested that the left hemisphere is characterized by analytic information processing, the right by synthetic processing or Gestalt perception. G.Cohen (1973) called these differences successive and parallel information processing. Earlier, in experiments on rats, we used the following experimental models: Simultaneous and successive stimulus complexes, the period of signal recognition, and territorial exploration (Bianki, 1985, 1988). It was possible to show that, in animals, the right hemisphere was also specialized for parallel (simultaneous) information processing, while the left was specialized for successive (serial) analysis. Of course, such specialization is not absolute: First, one can speak only of the prevalent role of each hemisphere in specific information processing; second, the character of one or another principle of information processing could, in some way, be connected with its degree, i.e. the actual nervous apparatus may have different capacities.

In accordance with the general purpose of this work, a task was devised to study sex differences in the discrimination of simultaneous and successive stimulus complexes by

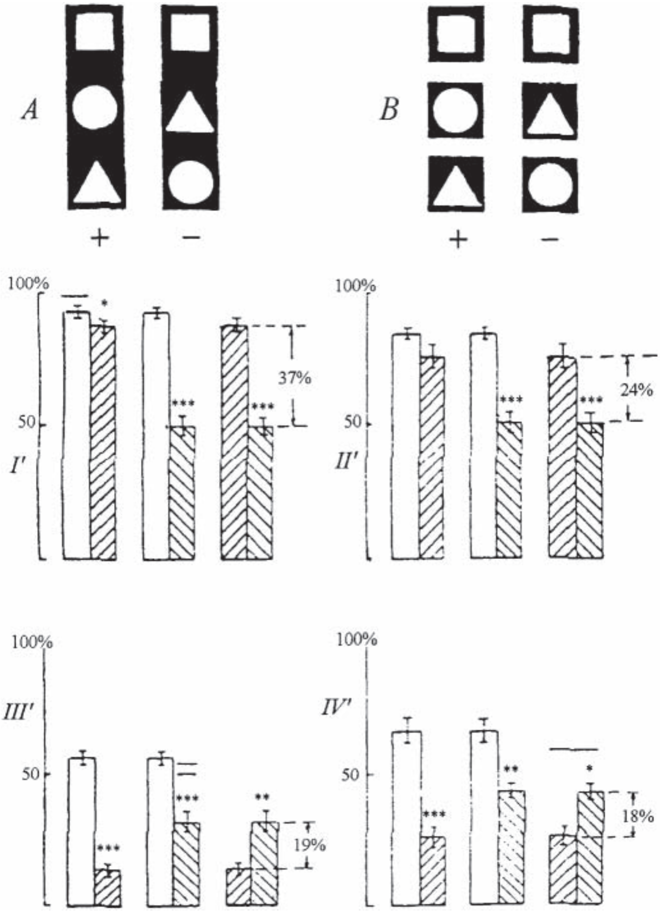

Figure 14: *See opposite for caption*

rats. The rats had been previously taught to differentiate between two stimuli: In one case, three-component simultaneous complexes of geometrical figures, in the other, three-component successive complexes of the same figures. The members of each pair could also be presented for discrimination either simultaneously or successively. After establishment of differentiation, each hemisphere was temporarily inactivated by means of potassium chloride-induced spreading depression.

The experiments were performed on 53 white Wistar rats of both sexes. Motion-food instrumental conditioned reflexes were elaborated. Simultaneous and successive three-component stimulus complexes were used as conditioned signals, consisting of solid light geometrical figures. All the figures differed in the order (or position) of presentation of the second and the third component (Figure 14). The simultaneous complex consisted in one case, of a square, a circle, and a triangle positioned vertically, and in the other, of a square, a triangle, and a circle. Successive complexes consisted of the same stimuli, but they were presented successively. In the case of simultaneous presentation of complexes both stimuli

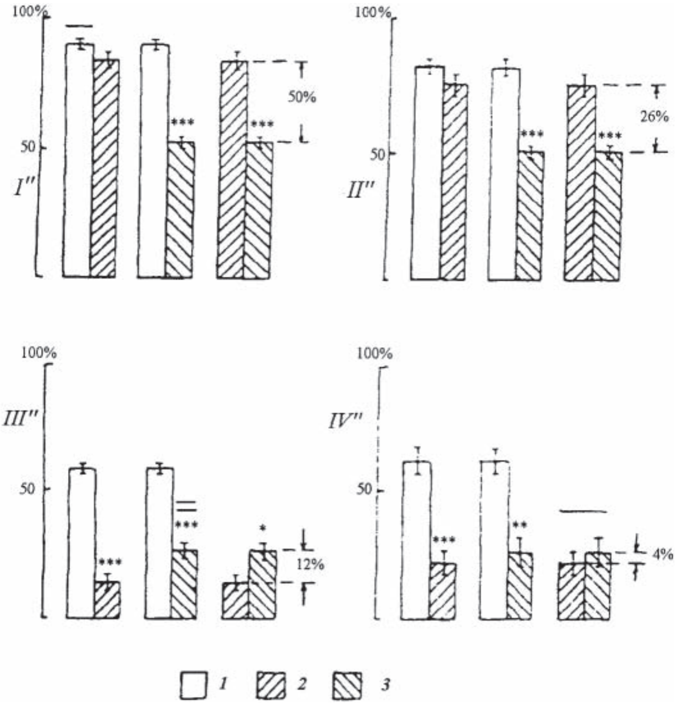

Figure 14: The influence of left and right hemisphere inactivation upon discrimination of simultaneous and successive complexes of visual stimuli during their simultaneous and successive presentation by rats of both sexes. **A**–simultaneous, **B**–successive stimuli complexes. **I', I?, II', II?**–discrimination of simultaneous (I', I?) and successive (II', II?) complexes during their simultaneous presentation in males (I', II') and females (I?, II?); **III', III?, IV', IV?**–discrimination of simultaneous (III', III?) and successive (IV', IV?) complexes during their successive presentation in males (III', IV') and females (III?, IV?). **1,2,3**–percentage of adequate responses before hemisphere inactivation (1), after left (2) and right (3) hemisphere inactivation. The stars indicate differences between the level of discrimination in the animals of one series: *– $p<0.05$, **– $p<0.01$, ***– $p<0.001$. The lines indicate differences in the level of discrimination between males and females: **single line–** $p<0.05$, **double line–** $p<0.01$.

were simultaneously exposed on both screen doors, the side of presentation being random. The rat was required to push aside the door showing the positive stimulus with its head. When the complexes were presented successively, this was done in the same way as in classical differentiation, i.e. on a single door, the presentation of the negative complex being unaccompanied by reinforcement.

In the results obtained (Figure 14) one circumstance leaps to the eye. Both in male and in female rats, a common regularity was found: The dominance of one or other hemisphere was determined first of all, not by the structure of the stimulus complex itself (simultaneous or successive), but by the manner of its presentation. Both simultaneous and successive stimulus complexes presented *simultaneously* appeared to be analysed by means of the right hemisphere, while those presented *successively* were processed by the left hemisphere.

At the same time, a definite sex specificity could be observed: In male rats the level of discrimination of simultaneous stimulus-complexes presented simultaneously, is a little higher (by 3%, on the average) than in females (Figure 14, I’, I?). This suggests some advantages of analytic-synthetic activity in males. Further, it was found that in males, when differentiating successive signal complexes presented successively, functional interhemispheric asymmetry was, on the average, stronger by 14% than in females (Figure 14, III’, III?). The above data indicate the fact, that under certain conditions, male rats may be characterized by a higher level of discrimination, and by a more strongly expressed functional interhemispheric asymmetry, as compared to females; whereas females, in their turn, differ from males by a more frequent dominance of the right hemisphere.

Now let us turn to the results of a more detailed analysis of the experimental evidence. Sex differences in the analysis of simultaneous and successive complexes were as follows.

Concurrent hemisphere function in males

1. During discrimination of simultaneously presented simultaneous visual stimulus complexes, the level of discrimination was higher ($p<0.05$).
2. During discrimination of successively presented simultaneous visual stimulus complexes, variance of the level of discrimination was greater ($p<0.05$).
3. During discrimination of successively presented successive visual stimulus complexes, the magnitude of asymmetry (assessed by the difference criterion) was greater ($p<0.05$).
4. During discrimination of successively presented simultaneous and successive visual stimulus complexes, the magnitude of asymmetry (assessed by the difference criterion) was greater ($p<0.05$).
5. During discrimination of simultaneously presented successive visual stimulus complexes, variance of the magnitude of asymmetry (assessed by the K_{as} criterion) was greater ($p<0.01$).
6. During discrimination of simultaneously presented successive visual stimulus complexes, variance of the magnitude of asymmetry (assessed by the difference criterion) was greater ($p<0.05$).
7. During the analysis of simultaneously presented simultaneous and successive visual stimulus complexes, variance of the magnitude of asymmetry (according to the K_{as} criterion) was greater ($p<0.05$).

Isolated left hemisphere activity in males

8. During discrimination of successively presented simultaneous and successive visual stimulus complexes, the level of discrimination performed by the left hemisphere (after inactivation of the right) was higher ($p<0.05$).
9. During discrimination of simultaneously presented successive visual stimulus complexes, variance of the level of discrimination performed by the left hemisphere (after inactivation of the right) was greater ($p<0.05$).
10. During discrimination of simultaneously presented successive visual stimulus complexes, the level of discrimination performed by the left hemisphere (after inactivation of the right) was greater ($p<0.01$).
11. During discrimination of simultaneously presented simultaneous and successive visual stimulus complexes, variance of the level of discrimination performed by the left hemisphere (after inactivation of the right) was greater ($p<0.05$).

Isolated activity of the right hemisphere in males

12. During discrimination of simultaneously and successively presented simultaneous visual stimulus complexes, variance of the influence of right hemisphere inactivation upon the level of discrimination was greater ($p<0.01$).
13. During discrimination of simultaneously presented simultaneous and successive visual stimulus complexes, variance of the influence of right hemisphere inactivation upon the level of discrimination was greater ($p<0.05$).

Isolated right hemisphere activity in females

14. During discrimination of successively presented simultaneous visual stimulus complexes, the influence of right hemisphere inactivation upon the level of discrimination was greater ($p<0.01$).
15. During discrimination of simultaneously presented simultaneous visual stimulus complexes, the influence of right hemisphere inactivation upon the level of discrimination was greater ($p<0.05$).
16. During discrimination of successively presented successive visual stimulus complexes, the influence of right hemisphere inactivation upon the level of discrimination was greater ($p<0.05$).
17. During discrimination of successively presented simultaneous visual stimulus complexes, variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) was greater ($p<0.05$).
18. During the analysis of simultaneously presented successive visual stimulus complexes, variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) was greater ($p<0.05$).

First of all, let us dwell on sex differences in rats during concurrent hemisphere activity. Here advantages of males over females are very distinct: In male rats the level of discrimination of visual complex stimuli is higher (1), functional interhemispheric asymmetry is more strongly expressed (3, 4), and variance of the values of these indices is greater (2, 5–7) as compared to females.

A similar advantage of males over females could be observed when only the left hemisphere was active. In this case males showed a higher level of discrimination of visual complex stimuli (8) and greater variance of this measure (9, 11).

During the isolated function of the right hemisphere, in some cases the advantage was to males, in others, to females. Thus, females surpassed males in the degree of influence of inactivation of the right hemisphere upon the level of discrimination of visual complex stimuli (14, 15, 16), and in the variance of the level of discrimination during right hemisphere activity (17, 18). In their turn, males surpassed females in the variance of the consequences of right hemisphere inactivation upon the level of discrimination of visual complex stimuli (12, 13).

In addition, it should be pointed out that, in female rats, the highest level of discrimination, and its greatest variance, were achieved when their right hemisphere differentiated between simultaneous complexes of visual stimuli if they were presented successively (14, 15, 16, 17, 18). Male rats, on the contrary, showed no hemispheric differences during right hemisphere function when complexes were presented successively. This may mean that the right hemisphere maintains the advantage of females over males in analysing successively presented stimuli. It should be borne in mind that differentiation between successively presented stimuli is carried out mainly in the left hemisphere. In other words the cerebral hemispheres of the female rats' brain act more ambivalently while analysing sequences of visual stimuli than do those of males, i.e. they are functionally more symmetrical.

All the above is concerned mainly with species-specific functional interhemispheric asymmetry, i.e. characteristic of the species or the population as a whole (Bianki, 1979b). In addition to this, there is also individual functional interhemispheric asymmetry, peculiar to an individual. Of course, species-specific asymmetry includes individual asymmetry, but goes beyond it. Usually asymmetry is not unidirectional in all the population of individuals constituting a species. Only the statistical majority of its representatives possesses unidirectional asymmetry, whereas isolated individuals can possess asymmetry directed in the inverse direction. It would be of interest to analyse individual interhemispheric asymmetry in males and females separately while they differentiate between complex visual stimuli. In this case it would be necessary to determine the dominant and the nondominant hemisphere, and not right and left hemisphere function, as was done when the species-specific form of functional interhemispheric asymmetry was being considered.

What was actually found in this case? In male rats, under certain conditions of discrimination of visual complex stimuli, the magnitude of individual functional interhemispheric asymmetry, and its variance, is greater than in females. At the same time, in males, a higher level of discrimination was found when their dominant hemisphere was active, and a greater variance during nondominant hemisphere function, as compared to females. The conclusions which can be drawn seem to be rather important. They suggest that, both in male and in female rats, the strategy of differentiating between complex stimuli is that the dominant hemisphere has an advantage in the level of discrimination of the signals presented, whereas the nondominant hemisphere surpasses the dominant one in the variance of the level of such discrimination. However, the above strategy is more frequently used by males than by females.

What general conclusion can be drawn from the above evidence as a whole? It can be formulated as follows. During discrimination of different complex stimuli, both males and females showed right hemisphere dominance, when the stimuli were presented simultaneously, and left hemisphere dominance during successive presentation. Under certain conditions, with both hemispheres active, male rats may surpass females in the level of the discrimination of visual stimulus complexes, in the magnitude of species-specific and individual asymmetry, and in the variance of those indices. The above advantages of males are to a great extent determined by the function of their left hemisphere. At the same time, under other conditions of discrimination of complex visual stimuli, a right hemisphere advantage was found in females, compared to males, which manifested itself in a higher level of discrimination and its variance. There are indications that the right hemisphere of female rats ensures them advantage over males in the discrimination of successively presented stimuli. In general all this points to greater asymmetry of the male rat brain compared to the female one.

Finally, here again we face the problem of hemispheric sex specificity in the strategy of the complex stimulus analysis by animals: In animals of either sex, the dominant hemisphere was mainly used for achieving a higher level of discrimination, the nondominant one maintaining a wider variance of the level of this discrimination. The above strategy was more often used by males than by females.

2.13. DISCRIMINATION OF ABSOLUTE AND RELATIVE CHARACTERISTICS

Analysis of the evidence contained in the literature on humans (and also our own data) allowed us to come to the following conclusion: In animals, as well as in humans, perception of concrete stimulus characteristics may be closely connected (at least under certain conditions) mainly with right hemisphere function, while that of the abstract characteristics, is connected with left hemisphere activity (Bianki, 1985, 1988). This conclusion, as far as it concerns animals, was based on the results of experiments obtained by using the following three models: conditioned reflexes to stimulus ratios, conditioned reflex transfer, and invariant stimulus recognition. In particular, when we studied lateralization of conditioned reflexes in rats to the *ratio* of the length of straight line segments, under conditions of the varying task difficulty, right hemisphere dominance was shown for analysis of the absolute characteristics of the above stimuli; but left hemisphere dominance was observed when relative stimulus characteristics were analysed. In the latter case, functional interhemispheric asymmetry was more strongly expressed than in the former case.

Some data indicate the existence of definite sexual dimorphism in the discrimination of absolute and relative visual stimulus characteristics are given below. The conditioned signals were representations of dark straight line segments, presented against a white background on two screen doors. Motion-food instrumental conditioned reflexes were elaborated, with simultaneous presentation of stimuli, animals being require to open one of the doors of the experimental chamber with their head. Segments of a straight line with a length-ratio of 2:1 were used as the main stimuli, the greater segment being taken as the positive stimulus, and the smaller segment as the negative one. Pairs of segments with a length ratio of 1:2, 1:1.75; 1:1.5, and 1:1.25 were used as test stimuli, the smaller segment always being equal to the greater one of the main pair of stimuli. Under such conditions, choice of the smaller test stimulus was always taken as an indication of analysis in terms of absolute stimulus characteristics, while choice of the greater one was taken as an indication of analysis in terms of relative stimulus characteristics. In the experiments, 60 white Wistar rats of both sexes were used. Inactivation of one hemisphere was achieved by means of potassium chloride-induced spreading depression.

Table 7. Sex differences in analysing absolute and relative characteristics

Males	*Females*
1a. In analysing the absolute characteristics of visual stimuli (the segment length), variance of the magnitude of asymmetry (assessed by the difference criterion) is greater (p<0.01).	1b. In analysing the absolute characteristics of visual stimuli (the segment length), expression of asymmetry is greater (p<0.01).
2a. In analysing the relative characteristics of visual stimuli (the segment length), variance of the magnitude of asymmetry (assessed by the difference criterion) is greater (p<0.01).	2b. In analysing the relative characteristics of visual stimuli (the segment length), expression of asymmetry is greater (p<0.01).

Let us note that, during the discrimination of relative stimulus characteristics, sex specificity could be revealed only in the most difficult case, i.e. when the length-ratio was 1:1.25. From the above data (Table 7) it follows that, during concurrent hemispheric activity, male rats surpassed females when discriminating in terms of both absolute and relative visual stimulus characteristics, and (from Table 7: 1a, 2a) in the variance of the magnitude of interhemispheric asymmetry. At the same time, in female rats, under similar conditions, an advantage over males was observed for the degree of expression of functional interhemispheric asymmetry (1b, 2b).

Thus we could not reveal sex differences in rats in the efficiency of discrimination in terms of absolute and relative characteristics of visual stimuli. At the same time, the results obtained indicate a greater dispersion, i.e. changeability (variance) of functional interhemispheric asymmetry being more inherent in the male rat brain.

The conceptions of penetrance and expression, widely used in genetics for characterizing the phenotypic characteristics of changeability, should also be taken into account (Timofeev-Resovsky and Ivanov, 1966) and used by us in physiology (Bianki *et al.,* 1991b). Penetrance means "...the ability of a gene to manifest itself phenotypically, which is measured by the percentage of individuals in which the given character is revealed." Expression is defined as "...the degree of expression of the character. Quantitatively it may be expressed as the percentage of individuals with the fullest expression of the character, among all the individuals manifesting this character" (Timofeev-Resovsy and Ivanov, 1966, p. 126). It should also be noted that the concept of variance has much in common with that of penetrance. Hence it may be suggested that, under the given experimental conditions, males are characterized by a greater penetrance of functional interhemispheric asymmetry, i.e. by responses, carried out at the average level, by a comparatively greater number of individuals, whereas females possess a greater expression of functional interhemispheric asymmetry, manifested in responses of a relatively small number of individuals, but carried out at a high level.

2.14. EMOTIONS

There are a number of facts in the literature concerning the preferential role of the human right hemisphere in emotionality, although they are not without contradiction (Campbell, 1982). The morpho-functional basis of this phenomenon may be the prevalence, in the right hemisphere, of cortico-diencephalic connections with the activating system of the brainstem reticular formation (Dobrokhotova and Bragina, 1977). As for animals, in earlier experiments on rats, we tested different hypotheses of the lateralization of hemispheric control of emotional reactions (Bianki, 1985, 1988; Bianki *et al.,* 1989a). The results of the experiments performed did not support the hypothesis of the dependence of lateralization of emotions on their valence: It was found out that either the right or the left hemisphere might dominate for control of positive or negative emotions. At the same time, hemispheric lateralization of control for both positive and negative emotions was found to be determined by their intensity: For strong emotional reactions, the right hemisphere was dominant, while for weaker reactions, it was the left. These data support the hypothesis of the lateralization of the intensity of emotions (Bianki, 1985, 1988).

The so-called emotional resonance phenomenon was chosen as a model for studying the problem of the sex specificity for lateralization of hemispheric control of emotional state. Emotional resonance shows itself in the form of avoidance of the cry of pain of another individual, emitted in response to painful electrical stimulation (Simonov, 1981). This phenomenon demonstrates, at the population level, the reinforcing function of emotions. In corresponding experiments, the natural preference of rats for a limited dark space was used. In response to another individual's cry of pain the animal was required to leave the preferred chamber, thereby stopping the painful electrical stimulation. Thus, in fact, a conflict of two motivations was observed: a striving to avoid the cries of the stimulated individual and, (probably phylogenetically more ancient and ecologically conditioned), a preference for a limited, dark space.

The experiments were performed on 70 white Wistar rats of both sexes. Inactivation of one hemisphere was carried out by means of spreading potassium chloride-induced depression. The following three experimental series were performed: In the first series, the reaction of emotional resonance was developed in rats, when the preferred and the unpreferred experimental chambers were lit identically, and the "victims" and "recipients" were of the same sex. In the second experimental series, a stronger emotional excitation was produced. For this purpose, the motivational preference for the smaller chamber was reinforced by diminishing its illumination tenfold, as compared to the illumination of the larger chamber. In the third experimental series, the reaction of emotional resonance was studied under the following conditions: with a tenfold difference in the illumination of the chambers, and using individuals of different sexes as "victims" and "recipients". The purpose of these changes was to reinforce the emotional conflict by stronger motivation.

An important characteristic of the interhemispheric asymmetry of emotional resonance appeared to be its sexual dimorphism. First of all, let us consider results obtained in all the above experimental series as a whole. It should be noted that the reaction of emotional resonance was developed faster in female than in male rats. In addition, female rats made more transitions between the chambers of the experimental set-up than did males. All this points to greater emotionality of females compared to males.

Comparison of results of the consequences of right *versus* left hemisphere inactivation in male and female rats (Figure 15) shows that, amongst animals with an established reaction of emotional resonance, the magnitude of functional interhemispheric asymmetry is greater in males than in females. This is manifested by the difference in time during which the animals of different sexes stayed in the dark (preferred) chamber. It is also

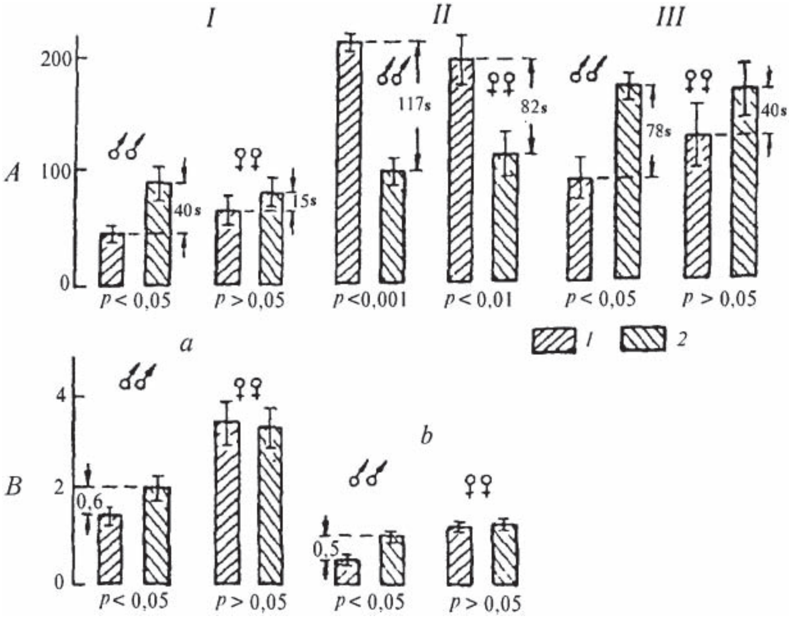

Figure 15: Sex differences in interhemispheric asymmetry during emotional reactions. **A**–reaction of “emotional resonance”: **I, II**–“recipients” and “victims” of one sex (I–right, II–left hemisphere dominance); **III**–“recipients” and ”victims” of different sexes. **Ordinate:** the period of staying in the preferred chamber (seconds) after left **(1)** and right **(2)** hemisphere inactivation. **B**–defecation **(a)** and urination **(b)** reactions in the open field. **Ordinate:** the number of reactions after left (1) and right (2) hemisphere inactivation.

shown by the speed of the restoration of this reflex, after hemispheric inactivation: In females this did not differ between hemispheres, while in males a significantly greater number of experiments was necessary to achieve a stable level of reaction after inactivation of the dominant than of the nondominant hemisphere. This difference in functional interhemispheric asymmetry for control of emotional resonance between male and female rats is associated with the different level of their emotional reactivity, mentioned above. This is also supported by the greater dominance of the right hemisphere in males, and of the left in females.

Now let us turn to the results which characterize concurrent and isolated hemisphere activity obtained from the second experimental series (Table 8). The male rats with an intact brain were characterized by a greater magnitude of interhemispheric asymmetry as compared to the females (1a), whereas the female rats surpassed the males in the variance of both the performance level and the level of asymmetry (1b, 2b, 3b). The first of these was observed both during concurrent and isolated left and right hemisphere activity

A good index of the rats’ emotional state in the open field test may be the reactions of defecation and urination, studied in experiments on 50 Wistar rats of both sexes. They reflect the level of the excitation of the peripheral nervous system, and depend upon the level of fear. During the first 3 min of the animals’ stay in the open field, the males were shown to possess a distinct left-sided asymmetry of the cortical control for the above reactions, whereas the females were shown to be symmetric. The males’ asymmetry was statistically significant. The corresponding diagrams (Figure 15, B) demonstrate a more

Table 8. Sex differences in carrying out the reaction of "emotional resonance"

Males	*Females*
Concurrent hemisphere function	
1a. In carrying out the reaction of "emotional resonance" the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).	1b. In carrying out the reaction of "emotional resonance" variance of the magnitude of asymmetry (assessed by the difference criterion) is greater ($p<0.05$).
The isolated activity of the left hemisphere	
	2b. In carrying out the reaction of "emotional resonance" variance of the level of discrimination by the left hemisphere (after right hemisphere inactivation) is greater ($p<0.05$).
The isolated activity of the right hemisphere	
	3b. In carrying out the reaction of "emotional resonance" variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is greater ($p<0.01$).

strongly expressed functional interhemispheric asymmetry in male, as compared to female rats.

What do the above experimental results show? They testify to the fact that female rats are more emotional than males. At the same time, male rats are characterized by stronger functional interhemispheric asymmetry for control of emotional reactions, as compared to females. The latter differ from males by a greater variance of both the performance level and the magnitude of functional interhemispheric asymmetry.

2.15. NOISE-RESISTANCE

We shall consider noise-resistance in its widest general biological sense. In this case it can be assumed that, in the real environment, recognition of any stimulus by humans and animals usually takes place against a background of various kinds of noise. There should be special neurophysiological mechanisms maintaining the processing of relevant information, and inhibiting the processing of irrelevant information. According to P.K.Anokhin (1964), a useful signal, as applied to the living system, can be regarded as a complex of physiologically-significant stimuli, integrated within the system used for synthesis of incoming signals. Noise, on the other hand, is defined as an aggregate of stimuli (from both the internal and external environment) which impedes the perception of the useful signals (and so reduces the probability of initiation of a response) or disrupting its adequacy. R.Lorenz (1973) believed that distinguishing the useful signal from noise is the most important indication of abstract perception.

In the literature, there are data testifying to the fact that, in humans, in the process of "singling-out" the useful signal against the background of noise, dominance of both the right and left hemisphere may be observed (Kock, 1967; Meyerson, 1975, 1980; Balonov and Deglin, 1967; Udalova, 1983). In experiments on animals, the advantage of the right hemisphere for recognition of visual stimuli with interference by light noise was shown (Bianki and Udalova, 1975, 1976, 1983; Udalova, 1976a,b, 1977, 1979, 1980, 1990; Bianki, 1985, 1988).

To study sexual dimorphism of the noise-resistance function, 64 white Wistar rats were used. Instrumental conditioned reflexes were developed in animals, with food and drink as reinforcement. Differentiation between the signals was worked out under the condition of their simultaneous reinforcement. Unilateral cortical inactivation was carried out by means of potassium chloride-induced spreading depression.

To study the role of the right and the left hemisphere in control of noise-resistance in the visual system, three models were used. In two of them the stimuli were computer-designed textures–varying in mean density–while in the third, they were chequered patterns. The first model was used to analyse textures against visual noise in the signal to be differentiated. As conditioned stimuli, textures composed of black elements randomly placed against a white background were used. "Visual noise" meant presenting images with a greater probability "p", coupled with the positive signal. The second model was used for the analysis of a textured geometrical shape (a square), against a background of Gaussian additive noise, as visual noise presented with the positive signal. The reinforced signal had a signal/noise ratio of 1.4, the one to be differentiated from it of 0.2. During visual noise, the signal/noise ratio of the positive stimulus was gradually reduced from 1.4 to 0.3 (by steps of 0.1), while the stimulus to be differentiated did not change. Finally, the third model was the analysis of chequered patterns, with visual noise imposed upon both positive and negative signal. The main stimuli consisted of 18 white squares, placed randomly against a black background. For the positive signal, noise was introduced as an additional 4–16 white squares. Images composed of the same number of randomly-placed white squares as in the corresponding positive signal served as stimuli to be differentiated.

Sexual dimorphism of noise-resistance during visual recognition was considered in the following respects: sex differences in the intact brain, interhemispheric asymmetry, the callosotomized brain, and also sex differences at the level of discrimination, and in its variance.

First of all let us consider noise-resistance in the intact brain. Significant sex differences in animals were found (Figure 16). Thus, for the whole range of signal/noise ratios, in females the level of the recognition of a geometrical figure against a textured background (Model II) was higher, on average by 7%, than in males (Figure 16, I, a). However, when we studied recognition of visual stimuli against a background of noise, and noise-resistance in this experiment (Model III), and the processing of the whole range of noise, a higher level of discrimination was observed in males, not in females (Figure 16, I, b, c), the corresponding indices in animals of different sexes differing, on average, by 5–7%.

In several cases sexual dimorphism could be revealed only in some parts of the range of the noise ratio used. For instance, during texture analysis (Model I), when the interference by noise was strong, (in the range p=0.6-0.8) the level of texture recognition in males was higher than in females (Figure 16, I, e). For all the other p values it was lower in males than in females (Figure 16, I, d). When a geometrical figure was being distinguished from noise (Model II), the level of visual stimulus recognition (with the signal/noise ratio of 0.7-0.2), and its noise-resistance, were higher in females, and not in males (Figure 16, I, f). The difference between the levels of recognition was, on the average, rather large, attaining as much as 14%.

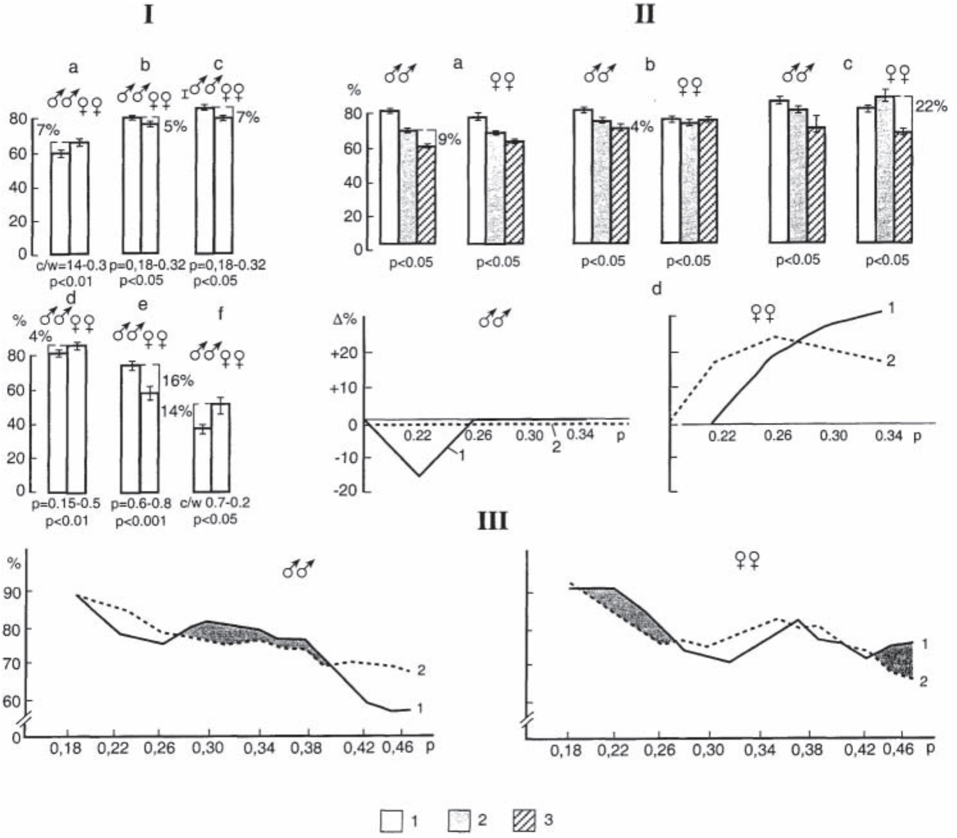

Figure 16: Sex differences in interhemispheric asymmetry for noise resistance in visual discrimination. **I**–noise protection of the intact brain in males and females (**a**–image discrimination, model II; **b**–image discrimination, model III, **c**–noise resistance in discrimination, model III; **d, e**–image discrimination, model I; **f**–noise resistance in discrimination, model II; **white columns**–intact hemispheres). **II**–asymmetry of noise resistance in males and females; **1**–intact hemispheres, **2**–left, **3**–right hemisphere inactivation; **a, b**–image discrimination, model I and II, **c**–noise resistance in discrimination, model I, **d**–change in noise resistance during recognition by animals with right **(1)** and left **(2)** hemisphere inactivated as compared to its level in the intact brain, model III. **Abscissa:** probability of the presence of the stimulus (white squares against the black background), conditioned stimuli, **ordinate:** the difference between the number of correct responses in animals with one hemisphere inactivated and in intact animals, %. **Positive values**–improvement in noise resistance; **Negative values**–deterioration. **III**–dependence of percentage of correct reactions (model III) in intact (1) and callosotomized **(2)** rats. **Abscissa:** probability of the presence of stimuli (white squares against the black background), conditioned stimuli; **ordinate:** percentage of correct responses.

Thus, greater noise-resistance in the visual system of an intact brain could be observed both in males and females, under different conditions of analytic-synthetic activity. When Models I and III were used, the males were usually characterized by greater noise-resistance, whereas when Model II was presented the advantage usually belonged to the females.

Of considerable interest is the asymmetry of noise-resistance, which is revealed when a comparative situation is created, the consequences of inactivation of left and right hemisphere. In some cases, even when the sample size used was comparatively small, sex differences in interhemispheric asymmetry were revealed. During the process of distinguishing visual stimuli from noise (Models I and III), the magnitude of asymmetry in males usually exceeded that in females for the whole range of noise intensity (Figure 16, II, a, b). Sometimes, when Model III was used, only right hemisphere influences were revealed in males with an intact brain, which intensified resistance to visual recognition in the face of noise, whereas in females an influence of both hemispheres was observed, which weakened noise-resistance (Figure 16, II, d). In one case, when noise-resistance in visual recognition was determined, the asymmetry was stronger not in males, but in females (Figure 16, II, c). The above data suggest that functional interhemispheric asymmetry occurs more often in males than in females.

One more case which allowed us to reveal sexual dimorphism refers to the comparison of the consequences of corpus callosum section in male and female rats (Udalova and Mikheev, 1982). In these experiments, Model III was used, namely the recognition of a chequered pattern against a background of noise. Comparison of the whole range of visual stimuli used showed that, after corpus callosum section in males, recognition of visual stimuli improved more than in females (Figure 16, III). The phasic dependence of the effect of callosotomy upon the magnitude of noise was especially distinct, the phases being almost mirror reflections, opposite in males and females. In male rats, recognition improved as noise increased, then it deteriorated and improved again. On the contrary, in females deterioration of analysis was first observed, then it improved, and then deteriorated again.

It should be pointed out that mirror-image forms of asymmetry were observed in some of the above cases in males and females with an intact brain when they were solving certain tasks.

Finally, let us consider sex differences in noise-resistance assessed by such indices as the level of discrimination and its variance (Table 9). Both during the concurrent function of both hemispheres, and when the right or the left hemisphere functions in isolation, under the conditions of noise-interference of visual stimuli, at some noise intensity levels, a greater variance of the level of discrimination was found in female rats than in males (1b–4b). In their turn, male rats surpassed females in the level of discrimination carried out by the right hemisphere when the degree of interference of visual stimuli by noise was low (1a). These data were obtained by means of Model II.

Thus, the above facts suggest there does exist a definite sexual dimorphism in noise-resistance to visual discrimination in rats. When the brain is intact, noise-resistance of the visual system is sometimes observed in males, sometimes in females under different experimental conditions. The resulting functional interhemispheric asymmetry in the control of noise-resistance against recognition of visual stimuli is somewhat more frequent in males than in females. The results of experiments on callosotomized rats point to the possibility of mirror-image reactions in males and females during discrimination of visual stimuli within noise.

Finally, under certain conditions, males were found to surpass females in the level of discrimination of visual stimuli against a background of noise, whereas females, as compared to males, are characterized by greater variance, and changeability of the level of discrimination. These facts, as other data presented in this chapter, point to the existence of two different strategies of behavioural adaptation, according to sex.

Table 9. Sex differences in noise resistance

Males	*Females*
Concurrent hemisphere function	
	1b. In analysing a textured geometrical figure without noise-interference of the positive signal, variance of the level of discrimination is greater ($p<0.05$).
Isolated activity of the left hemisphere	
	2b. In analysing a geometrical textured figure with noise-interference of the positive signal of the Vth step, variance of the level of discrimination by the left hemisphere (after right hemisphere inactivation) is greater ($p<0.05$).
Isolated activity of the right hemisphere	
1a. In analysing a textured geometrical figure with noise-interference of the positive signal of the IInd step, the level of discrimination by the right hemisphere (after left hemisphere inactivation) is higher ($p<0.05$).	
	3b. In analysing a textured geometrical figure with noise-interference of the positive signal of the IInd step, variance of the level of discrimination by the right hemisphere (after left hemisphere inactivation) is higher ($p<0.01$). 4b. In analysing a textured geometrical figure with noise-interference of the positive stimulus of the Vth step, variance of the influence of the right hemisphere upon the level of analysis is greater ($p<0.05$).

2.16. CONCLUSION

Let us briefly summarize some facts presented in this chapter (Tables 10–13).

In a number of cases, in animals, sex differences were observed in carrying out analytic-synthetic activity. As a rule an advantage of males was revealed, and only in the solution of one task did females show a higher level of performance. Males differentiated at a higher level relatively complicated stimuli. These include sound stimuli, which can be treated as two-item complexes, differing in the sequential order of the components (Table 10: 2a), a light stimulus, which can be treated as a complex signal with a constant visual component and a variable time component (Table 10: 3a), and visuospatial stimulus-complexes characterized by the same area of the components but differing in their position (Table 10: 4a). At the same time, in one case, an advantage was observed in females in their level of analytic-synthetic activity, in solving a very complicated visual task which reached the limit of the animals' analytic-synthetic potential (Table 10: 1b).

Another important characteristic of analytic-synthetic activity is the variance of the level of performance, its changeability and variability, which can also illustrate the animal's

Table 10. Concurrent hemisphere activity. Analytic and synthetic activity

Males	*Females*
Level of discrimination	
1a. In analysing sound stimuli, the level of discrimination is higher (differentiating the [b]-[d] consonants in [ba]-[da] syllables—Table 2: 1a). Left hemisphere dominance.	
	1b. In analysing visuospatial stimuli, the level of discrimination is higher (differentiating the area of circles with the area proportion of 1:1.67—Table 1: 1b). Right hemisphere dominance.
2a. In analysing simultaneously presented complexes of visual stimuli, the level of analysis is higher (differentiating concurrently presented simultaneous complexes of visual stimuli—p. 77, 1). Right hemisphere dominance.	
3a. In analysing the duration of action of a visual stimulus, the level of discrimination is higher (differentiating the duration of the light stimulus action, 5 and 10 s,—Table 6: 1a). Left hemisphere dominance.	
4a. In analysing visuospatial stimuli, the level of discrimination is higher (differentiating all the visuospatial stimuli studied—Table 5: 1a). Right hemisphere dominance.	
Variance of the level of discrimination	
5a. In analysing successively presented complexes of visual stimuli, variance of the level of discrimination, is greater (differentiating successively presented simultaneous *** complexes—p. 76, par. 2). Left hemisphere dominance.	
	2b. In analysing sound stimuli, variance of the level of discrimination is greater (differentiating the [a]-[i] vowels and [b]-[d] consonants in [ba]-[da] syllables—Table 2: 1b, 2b). Left hemisphere dominance.
6a. In analysing visuospatial stimuli, variance of the level of discrimination is greater (differentiating the area of the circles—Table 1: 1a, 2a; differentiating the dot location—Table 5, 3a). Right hemisphere dominance.	
	3b. In analysing the components of the visual stimulus-complex, variance of the analysis level is greater (differentiating a unimodal visual stimulus-complex and its components—Table 4: 3b). Right hemisphere dominance.

Table 10. continued

Males	*Females*
7a. In analysing the duration of action of a visual stimulus variance of the level of discrimination is greater (differentiating the duration of action of the light stimulus, 5 and 10 s,—Table 6: 3a). Left hemisphere dominance.	
	4b. In analysing visuospatial stimuli, variance of the level of discrimination is greater (differentiating all the visuospatial stimuli studied—Table 5: 2b). Right hemisphere dominance.
8a. During motor activity in the open field, variance of the level of performance is greater. Left hemisphere dominance.	

adaptive possibilities. A tendency for greater variance of the level of discrimination was observed a little more frequently in males, and less frequently in females. In males this was observed during differentiation between successively presented visual stimulus-complexes (Table 10: 5a), discrimination of isolated visuospatial stimuli (6a), differentiation between periods of action of visual stimuli (7a), and in carrying out motor activity (8a). In females variance of the level of performance surpassed that in males when the females were required to differentiate the components of a unimodal visual stimulus complex (Table 10: 3b), during visuospatial analysis of a wide range of stimuli (4b), and during differentiation between sound stimuli (2b).

Let us focus on the problem of strategies of each sex in behaviour. To some extent they can be judged on the basis of the level and variance of performance. There seem to be at least two different forms of species-specific adaptation to environmental conditions. The first is characterized by a comparatively high level of discrimination, within a relatively narrow range of stimuli. Let us designate this as the strategy of "specialized response". The second form of adaptation is, on the contrary, distinguished by a relatively low level of discrimination, but within a wider range of stimuli. Let us call this the strategy of "generalized response". Males appeared to resort more frequently to the strategy of specialization, while females used, as a rule, that of generalization. Analysis of sound stimuli and visuospatial stimuli may serve as examples (Table 10: 1a, 2b; 4a, 4b). However a reverse form of regularity could also be observed: Males, when differentiating visual stimuli of different complexity, resorted to the strategy of generalization, females preferring that of specialization. It should also be noted that sometimes both males and females used the same strategy of specialization, though it was expressed more strongly in males (Table 11: 3a, 4a). On the whole, the sex specificity of each strategy still proves difficult to find. Sometimes males and females may use the same strategy in solving different tasks.

The magnitude of species-specific interhemispheric asymmetry proved, as a rule, to be greater in males than in females. This was observed during the analysis of isolated stimuli (Table 11: 1a, 2a, 3a), during differentiation of isolated and complex visual stimuli (Table 11: 4a, 5a, 6a), and when controlling emotional reactions (8a) and pain vocalizations (7a). At the same time, sometimes the magnitude of functional interhemispheric asymmetry could be greater in females, for example, during the analysis of some spatial stimuli (Table 11: 1b), and of unimodal and multimodal stimulus complexes (2b). A greater role in this may be played by the biological significance of the corresponding reactions (Bianki *et al.,* 1992). The essential point is that the magnitude of the observed asymmetry was predominantly due to left hemisphere function in males, and to right hemisphere function in females

Similar regularities held true for another parameter of species-specific functional interhemispheric asymmetry–its variance. Again, when differentiating between isolated sound stimuli (Table 11: 9a, 10a), discrimination of isolated and complex visual signals (11a, 12a), probabilistic learning (13a) and discrimination of absolute and relative characteristics (14a), variance of functional interhemispheric asymmetry was greater in males, compared to females. Only in one case, when carrying out emotional reactions (3b), did it prevail in females.

It should be noted that sexual dimorphism in interhemispheric asymmetry could be observed in two forms: quantitative and qualitative. In the case of the quantitative sexual dimorphism of asymmetry, one and the same function was controlled by the same hemispheres in males and females, but to different degrees. For instance, this was the case during control of pain vocalizations and pain sensitivity, when the left hemisphere dominated. If sexual dimorphism was qualitative, different hemispheres controlled the same function in males and females. For instance, during general motor activity, the left hemisphere was dominant in males, the right in females.

The study of such important properties of interhemispheric asymmetry as its penetrance and expression, characterizing it quantitatively, points to the prevalence of at least the former in males. Thus, in males greater penetrance and expression of asymmetry were revealed during the discrimination of isolated sound stimuli (Table 11: 15a, 17a) and complex visual stimuli (16a, 18a). In males, a greater expression of asymmetry was found during differentiation between absolute and relative characteristics of visual stimuli (4b).

As mentioned above, in addition to species-specific interhemispheric asymmetry, there is also individual asymmetry. In several cases studied, this was also expressed more strongly in males, compared to females. For instance, this picture was observed in the cases when a durable conditioned reflex to a sound stimulus was established (Table 11: 19a), when analyses were performed of a transformed sound stimulus (20a), and also when discrimination of successively presented successive stimuli was carried out.

In addition, sexual dimorphism of functional interhemispheric asymmetry is found for such an important property as its dynamism. In some cases, at least, the dynamism of asymmetry is more strongly expressed in males than in females, for example, during the formation of a conditioned reflex, and during control of pain vocalizations.

As a result of analysis of the experimental evidence, it was possible to obtain some data pointing to the existence of sexual dimorphism of the lateralization of the dominant hemisphere. Thus, in males, dominance of the left hemisphere was observed more frequently, whereas in females it was that of the right. Nevertheless, it should be emphasized that, in representatives of both sexes, dominance of each hemisphere could be observed. For instance, under some experimental conditions, an advantage of males over females in the level of performance was accompanied by left hemisphere dominance (discrimination of some sound stimuli, visual complexes, the period of the action of a visual stimulus, control of motor activity–Table 10: 1a, 3a, 4a, 6a, 8a). Under other conditions the right

Table 11. Concurrent hemisphere activity. Interhemispheric asymmetry

Males	*Females*
The magnitude of species-specific interhemispheric asymmetry	
1a. In discriminating transformed sound stimuli, the magnitude of asymmetry is greater (differentiating syllables [ba]-[da] transformed with respect to loudness, timbre and duration—p. 45, par. 6–8. Left hemisphere dominance.	1b. In discriminating visuospatial stimuli, the magnitude of asymmetry is greater (differentiating the area of circles in chequered patterns—Table 1: 2b, 3b, 4b). Right hemisphere dominance.
2a. In forming a stable conditioned reflex to a sound stimulus, the magnitude of asymmetry is greater (a conditioned reflex to the sound [a]—p. 44, par. 1,2). Left hemisphere dominance.	2b. In discriminating the components of unimodal and multimodal stimulus-complexes, the magnitude of asymmetry is greater (unimodal complexes of visual and sound stimuli, a multimodal complex of visual, sound, vibrational stimuli—Table 4: 1b). Right hemisphere dominance.
3a. In forming unstable and stable conditioned reflexes to a sound stimulus, and its transformation, the magnitude of asymmetry is greater (a conditioned reflex to the sound [a], transformed with respect to its loudness, timbre and duration—p. 45, par. 3, 6, 10). Left hemisphere dominance.	
4a. In discriminating visual stimulus-complexes presented successively, the magnitude of asymmetry is greater (differentiating simultaneous and successive stimuli complexes presented successively—p. 76, par. 3,4). Left hemisphere dominance.	
5a. In discriminating visuospatial complexes, the magnitude of asymmetry is greater (differentiating all the visuospatial stimuli studied—Table 5, 1a). Right hemisphere dominance.	
6a. In discriminating the duration of action of visual stimuli, the magnitude of asymmetry is greater (differentiating the duration of action of the light stimulus, 5 and 10 s,—Table 6: 2a). Left hemisphere dominance.	
7a. In controlling pain vocalizations, the magnitude of asymmetry is greater. Left hemisphere dominance.	
8a. In emotional reactions to a sound stimulus, the magnitude of asymmetry is greater (reaction of emotional resonance to a cry of pain of another individual). Left hemisphere dominance.	
Variance of species-specific interhemispheric asymmetry	
9a. In discriminating untransformed and transformed sound stimuli, the variance of the magnitude of asymmetry is greater (differentiating the sounds [a]–[i]—p. 56, par. 7; differentiating the sounds [a]-[i] and the syllables [ba]-[da] transformed according to loudness—p. 56, par. 7,8). Left hemisphere dominance.	

Table 11 continued

Males	*Females*
10a. During the formation of a conditioned reflex to a sound stimulus and its transformation, the variance of the magnitude of asymmetry is greater (the conditioned reflex to the sound [a]; transformation of the sound [a] according to its duration—p. 45, par. 11. Left hemisphere dominance.	3b. During emotional reactions to the sound stimulus, variance of the magnitude of asymmetry is greater (reaction of emotional resonance to a cry of pain of another individual. The IInd group of animals, Table 8, 1b).
11a. In discriminating visual stimulus-complexes presented simultaneously, variance of the magnitude of asymmetry is greater (differentiating simultaneous and successive visual stimulus-complexes presented simultaneously—p.***, par. 5,6,7,8). Right hemisphere dominance.	
The magnitude of species-specific asymmetry	
12a. In discriminating transformed visual stimuli, variance of the magnitude of asymmetry is greater (transformation with respect to magnitude—Table 3: 1a). Individual asymmetry.	
13a. After probabilistic learning to a visual stimulus, variance of the magnitude of asymmetry is greater (50% probabilistic reinforcement—p. 48). Left hemisphere dominance.	
14a. In analysing the absolute and relative characteristics of visual stimuli, variance of the magnitude of asymmetry is greater—Table 7: 1a, 2a). Right and left hemisphere dominance respectively.	
Penetrance and expression	
15a. In establishing a stable conditioned reflex to a sound stimulus and its transformation, penetrance of asymmetry is greater (formation of the conditioned reflex to the sound [a] and its transformation with respect to duration—p. 45, par. 9). Left hemisphere dominance.	4b. In discriminating the absolute and relative characteristics of visual stimuli, expression of asymmetry is greater (differentiation of segment lengths—Table 7: 1b, 2b). Right and left hemisphere dominance respectively.
16a. In discriminating the components of the unimodal complex of visual stimuli, penetrance of asymmetry is greater (reaction to a strong light component of the visual stimuli complex). Right hemisphere dominance.	
17a. In forming an unstable conditioned reflex to a sound stimulus and its transformation, expression of asymmetry is greater (formation of the conditioned reflex to the sound [a] and its transformation with respect to duration—p. 45, par. 3,10). Right hemisphere dominance.	

Table 11. continued

Males	*Females*
The magnitude of species-specific asymmetry	
18a. In discriminating the components of a unimodal stimulus-complex, expression of asymmetry is greater (reaction to the strong light component of the visual stimuli complex). Right hemisphere dominance.	
19a. In forming a stable conditioned reflex to a sound stimulus and its transformation, the magnitude of asymmetry is greater (formation of the conditioned reflex to the sound [a] and its transformation according to loudness, timbre and duration—p. 45, par. 5,12). Left hemisphere dominance.	
20a. In analysing transformed sound stimuli, the magnitude of asymmetry is greater (differentiation of the sounds [a]-[i] and [ba]-[da] transformed according to loudness, timbre and duration—Ch. 2, p. 86, par. 4, 5, 6, 7). Left hemisphere dominance.	

hemisphere was dominant (for instance, analysis of some visuospatial stimuli, and visual complexes–2a, 5a, 6a). In females, under different experimental conditions, dominance of the right hemisphere was also observed (e.g., in analysis of some visuospatial stimuli and components of visual complexes–Table 10: 1b, 3b, 4b), whereas under some conditions their left hemisphere was dominant (analysis of some sound stimuli–2b).

The data obtained during the isolated study of right and left hemisphere function in males and females (Tables 12, 13) allow us to compare the functions both of the same and different hemispheres in animals of different sexes.

The same hemispheres in males and females possess both common and specific characteristics. Thus, the left hemisphere in males and females may dominate during the analysis of some visual spatial stimuli (Table 12: 1b, 2a). The male left hemisphere usually plays the main role when analysing transformed sound stimuli (Table 12: 1a, 3a), while that of females dominates during discrimination of the duration of action of a visual stimulus (2b) and in carrying out the reaction of emotional resonance (4b). The right hemisphere of males and females dominates in carrying out some forms of visuospatial analysis (Table 13: 2b, 4b, 5a) and in differentiating between unimodal complexes of visual stimuli (1b, 3a). An advantage of the right hemisphere of males was observed when they had to discriminate transformed sound stimuli (2a, 4a), in distinguishing a sound signal from noise (2a), and in carrying out the dynamic stereotype (6a). In females, the right hemisphere dominates during the analysis of sound stimuli (Table 13: 3b), visual stimulus-complexes (5b), analysis of transformed visual stimuli (6b), and reactions of emotional resonance (7b). Hence, it follows that the same hemispheres in individuals of different sexes may have both common and different characteristics. Further study of the peculiarities of their function is an urgent task of the future.

Table 12. Left hemisphere function

Males	*Females*
The level of analysis	
1a. In discriminating transformed sound stimuli, the level of discrimination is higher (differentiation of the sounds [a]-[i] transformed with respect to loudness, timbre and duration—p. 56, par. 9,10, 11).	1b. In discriminating visuo-spatial stimuli, the level of discrimination is higher (differentiation of geometrical statistics and chequered patterns—Table 5: 3b).
2a. In discriminating visual stimulus-complexes presented successively, the level of discrimination is higher (differentiating of simultaneous and successive complexes—p. 77, par. 9).	
Variance of the analysis level	
3a. In discriminating transformed sound stimuli, variance of the level of discrimination is greater (differentiation of the sounds [a]-[i] and [ba]-[da] transformed with respect to loudness, timbre and duration—p. 56, par. 12–14,15).	2b. In discrimination the duration of action of visual stimuli, variance of the level of discrimination is greater (differentiating the period of the light stimulus action, 5 and 10 s.—Table 6: 4b).
4a. In discriminating visual stimulus-complexes presented simultaneously, variance of the level of discrimination is greater (simultaneous and successive complexes—p. 77, par. 10, 12).	3b. In distinguishing a visual signal from noise, variance of the level of discrimination is greater (differentiating the period of light stimuli action, 5 and 10 s—Table 6, 1b).
5a. In discriminating visuospatial stimuli, variance of the level of discrimination is greater (differentiating the dot position—Table 5: 4a).	4b. In emotional reactions to sound stimuli, variance of the level of discrimination is greater (reaction of emotional resonance to a cry of pain from another individual—Table 8: 2b).
6a. In discriminating transformed visual stimuli, variance of the level of discrimination is greater (transformation of geometrical figures according to filling-up—Table 3, 2a). Individual asymmetry.	

Comparing the functions of different hemispheres in males and females shows that they also possess common and specific characteristic properties. Thus, the male left hemisphere and the female right hemisphere dominate in discrimination of transformed visual stimuli (Table 12: 6a; Table 13: 6b), and of some complex visual stimuli (Table 12: 2a, 4a; Table 13: 1b, 5b). The male right hemisphere and the female left hemisphere dominate during the analysis of some visuospatial stimuli (Table 12: 1b; Table 13: 5a) and in distinguishing visual stimuli from noise (Table 12: 3b; Table 13: 2a). Consequently, in some cases a mirror-image relation of hemispheric dominance between males and females is revealed.

Consideration of the experimental evidence sometimes points to the fact that, under certain conditions, the male brain is functionally more specialized, differentiated, and more focal than the female brain. This is mainly determined by the left hemisphere. The female brain seems to be functionally less specialized, less differentiated, more diffuse. These peculiarities may depend both on the right and the left hemisphere. The corresponding facts were obtained from study of the invariant recognition of sound stimuli,

Table 13. Right hemisphere function

Males	*Females*
The level of discrimination	
1a. In discriminating transformed sound stimuli, the level of discrimination is higher (differentiating the sounds [a]-[i] and [ba]-[da] transformed with respect to loudness, timbre and duration—p. 56–7, par. 16–19).	1b. In discriminating the components of unimodal (visual, sound) and multimodal stimulus-complexes, the level of discrimination is higher—(Table 4, 1b).
2a. In distinguishing a visual signal from noise, the level of discrimination is higher (differentiation of a textured figure with noise-inerference of the positive signal (IInd step)—Table 9: 1a).	2b. In discriminating visuospatial stimuli, the level of discrimination is higher (differentiating the area of circles—Table 1, 5b).
Variance of the level of discrimination	
3a. In discriminating the components of a unimodal complex of sound stimuli, variance of the level of discrimination is greater (Table 4: 6a, 7a, 8a).	3b. In discriminating sound stimuli, variance of the level of discrimination is greater (differentiating the sounds [a]-[i] and [ba]-[da]—Table 2: 2b).
4a. In discriminating transformed sound stimuli, variance of the level of discrimination is greater (differentiating the sounds [a]-[i] transformed with respect to loudness—p. 57. par. 20).	4b. In discriminating visuospatial stimuli, variance of the level of discrimination is greater (differentiating all the visuospatial stimuli studied—Table 5: 5b, 6b; Table 9: 3b).
5a. In discriminating visuospatial stimuli, variance of the level of discrimination is greater (differentiating the area of circles—Table 1: 5a, 6a).	5b. In discriminating visual stimulus-complexes presented simultaneously and successively, variance of the level of discrimination is greater (differentiating simultaneously presented successive stimulus-complexes and successively presented simultaneous complexes—p. 77, par. 17,18).
6a. In stereotyped behaviour in response to visual stimuli, variance of the level of discrimination is greater (dynamic stereotype to visual stimuli—p. 72).	6b. In discriminating transformed visual stimuli, variance of the level of discrimination is greater (transformation of geometrical figures with respect to rotation—Table 3: 2b).
	7b. In emotional reactions to sound stimuli, variance of the level of performance is greater (reaction of emotional resonance to a cry of pain from another individual—Table 8: 3b).

which showed a greater specialization of the male brain, mainly conditioned by their left hemisphere, and a relatively generalized activity of the female brain, which also depends to a certain degree on its left hemisphere activity. Similar results were obtained during the analysis of complex stimuli. Under certain conditions, males appeared to differentiate unimodal complexes better, this depending mainly on left hemisphere function, whereas females did better on the multimodal complexes. This peculiarity of the female brain was determined by their right hemisphere.

Summing up the above factual evidence, the data on the sexual dimorphism of behavioural reactions could be formulated as the following conclusions. Males, as a rule, are characterized by a somewhat higher level of discrimination, some tendency for a greater degree of the variance in the level of performance, a greater magnitude of functional interhemispheric asymmetry and its variance, a greater dynamism of functional interhemispheric asymmetry as compared to females. Under certain conditions, the males' behaviour is determined by the strategy of a specialized response, in which the left, more specialized hemisphere plays the leading role. Under some conditions, the females' behaviour is determined by the strategy of generalized response, where the leading role belongs to a less specialized hemisphere (the right or the left).

3. Electrophysiological Characteristics

3.1. INTRAZONAL CALLOSAL CONNECTIONS

The transcallosal response (TCR), described by H.J.Curtis (1940) is, as a rule, a positive-negative component, arising in the cortex of one hemisphere during electrical stimulation of the symmetrical cortical site on the other side. In most cases it is mediated by conduction of excitation via the corpus callosum. The exception is the sensorimotor cortex, amongst whose symmetrical connections are also included extracallosal commissures (Bianki and Bozhko, 1987). In addition to these "homotopical" TCRs, there have also been described "heterotopical" TCRs, which are recorded during stimulation of asymmetrical cortical sites. Heterotopical TCRs are supposed to be produced by the interaction of several streams of excitation, spreading in both the stimulated and the receiving hemisphere (Bianki *et al.,* 1978). Streams of heterotopical transcallosal excitation spread not only within the limits of the same cortical zones, but within different zones (Bianki and Shramm, 1988; Shramm and Kharitonov, 1988). It is widely accepted that the positive and negative components of the TCR have an independent genesis, being generated in different cortical layers, as a result of transcallosal excitation coming along different systems of callosal fibres with different conduction rates. The negative components recorded on the cortical surface reflect mainly the development of excitatory processes in the superficial cortical layers and/or inhibitory processes in the deep layers (see review: Shramm, 1980a). According to Curtis's conceptions (1940), there is a direct relation between the density of callosal connections and the amplitude of the TCR.

A specially designed technique of multiple topographic recording of evoked potentials (EPs) was worked out (Bianki and Filippova, 1976a,b; Bianki, 1979a; Bianki and Bozhko, 1989). The peculiarity of this technique was successive recording of TCRs from many points on the cortical surface, at equal distances (1 mm) from one another. The experiments were, as a rule, performed on adult cats of both sexes, which were immobilized or anaesthesized. As models, homotopical and heterotopical TCRs were used (Bianki, 1989). The model for homotopical TCRs involved successive recording of transcallosal potentials from points symmetrical to the stimulated ones. The stimulating and recording electrodes were always located symmetrically to each other, and shifted along the surface of the cortical zone under investigation. A pairwise comparison was made of transcallosal potentials from symmetrical cortical points. In this case, one hemisphere was held to be dominant when its TCRs had a greater amplitude, and were recorded from a greater area. In other words, that hemisphere was considered dominant, for its homotopical stream of excitation, which received the more information from the symmetrical points of the opposite hemisphere. The model for heterotopical TCR convergence involved the recording electrode being fixed in the focus of maximal activity (FMAs)[8]. This model made it possible to characterize convergence of excitation within each hemisphere. The hemisphere in which TCRs of greater amplitude were recorded during stimulation of the opposite hemisphere, and in which there was convergence from a greater area of stimulation was held to be the dominant one. In other words, the hemisphere that received a greater stream of excitation was recognized as the dominant one for convergence. As an additional criterion, during the investigation of heterotopical TCRs, the value of the so-called “effective stimulation zones” was used. A pairwise comparison was made of stimulation points in the opposite hemispheres which proved effective for appearance of the TCR in one recording site of the zone under investigation in the contralateral hemisphere (Bianki and Shramm, 1982). It should be emphasized that the stimulated and receiving hemispheres were changed in each experiment, and functional interhemispheric asymmetry was determined on the basis of comparison of TCRs in both hemispheres.

In earlier studies, experimental data were obtained testifying to the asymmetry of streams of transcallosal excitation (Shramm, 1980b; Bianki, 1979a, 1989, 1993; Bianki *et al.,* 1978, 1989b). The essential point is that asymmetry of transcallosal excitation was more strongly expressed in the main cortical projection zones, as compared to the association areas (Bozhko, 1987). It is also important that in the primary cortical projection regions (visual, auditory, somatosensory cortex) species-specific asymmetry was right-sided. In the parietal association cortex, right-sided asymmetry for homotopical TCR was observed with respect to the negative component, whereas in the sensorimotor association cortex the asymmetry of both TCR components was left-sided. Now let us focus on the character of sexual dimorphism of functional interhemispheric asymmetry in different cortical regions.

3.1.1. Visual Cortex

Sexual dimorphism in functional interhemispheric asymmetry in the visual cortex of cats was studied during TCR recording from 120–150 symmetrical points in Fields 17, 18, and 19 (Bozhko, 1988), defined according to the atlas of Otsuko and Hassler (1962). Let us note once more that, during the investigation of a mixed sample, right-sided functional interhemispheric asymmetry of both homotopic TCR components was found in the cats’ visual cortex.

During analysis of animal groups divided according to their sex, certain sex differences in interhemispheric asymmetry of homotopic TCRs were revealed. Most males studied appeared to possess right hemispheric dominance for the amplitude of both components of the homotopic transcallosal potentials. Unlike this, in the female group no single-hemisphere direction of asymmetry for homotopical TCRs could be found. Nevertheless, individual interhemispheric asymmetry was observed.

The averaged maps for the distribution of transcallosal potentials in the visual cortex of the left and right hemispheres in males and females (Figure 17) give a graphic representation of the sexual dimorphism of homotopic TCRs. It can be seen that in males the interhemispheric asymmetry of the above potentials is of a qualitative type, for which the

FMAs of both EP components are located in the right, dominant hemisphere (Figure 17, A). It should be noted that females were characterized by interhemispheric differences with less contrast: FMAs could be distinguished in both hemispheres, interhemispheric asymmetry belonging to the qualitative-topographic type, in which FMAs in the two hemispheres could differ in magnitude and location (Figure 17, B).

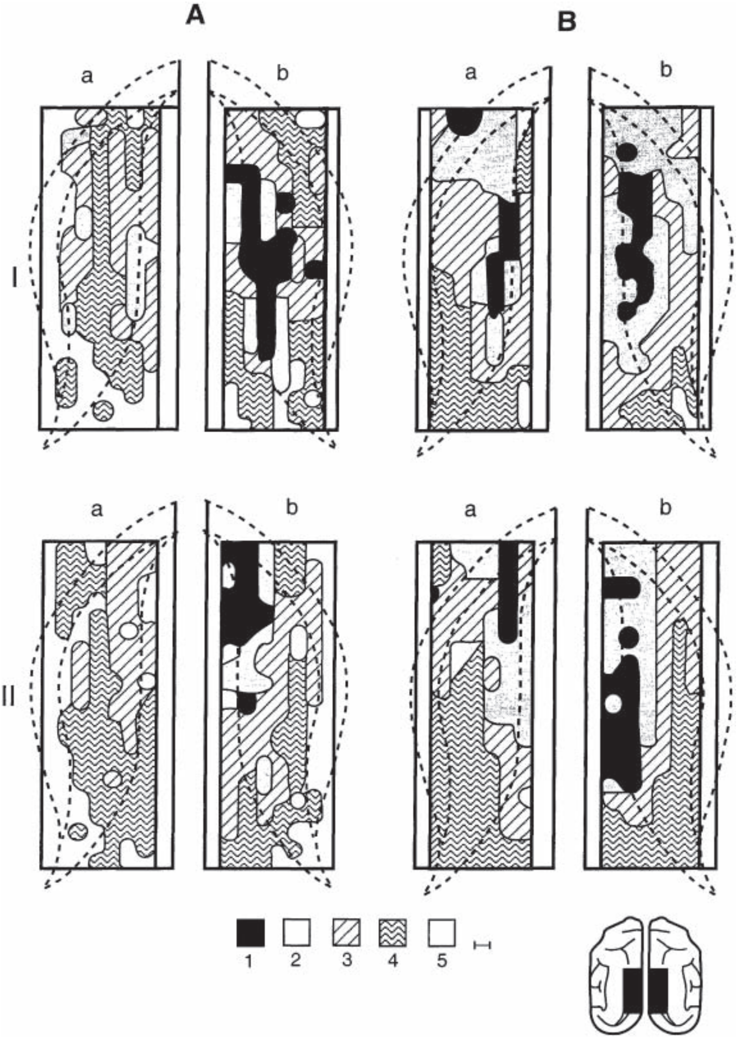

Figure 17: Sex differences of interhemispheric asymmetry of homotopical transcallosal responses in the cat's visual cortex (averaged data from 12 animals of each sex). **A, B**–averaged maps of the distribution of positive **(I)** and negative **(II)** TCR components in the visual cortex of the left **(a)** and the right **(b)** hemisphere of males **(A)** and females **(B)**. **1–4,**–classes of the ranged amplitude of potentials; **5**–absence of EPs. **Scale:** 1 mm. **Insert:** The black colour marks the area of topographical TCR recording.

Similar regularities were also found when interhemispheric differences between heterotopical TCRs were studied. In most males, functional interhemispheric asymmetry was found in the amplitude of both components of heterotopical responses. Most individuals with significant differences between the magnitudes of potentials appeared to possess right hemisphere dominance for the amplitude of both positive and negative components. At the same time, it should be noted that this regularity was characteristic only of the male group, whereas in the female group no single-hemisphere direction of asymmetry could be revealed, in just the same way as in the case of homotopic TCRs.

As mentioned above, an additional criterion of interhemispheric differences used during the study of heterotopical TCR consisted in comparing the areas of the effective stimulation zones in the opposite hemispheres. The number of points during whose stimulation negative and positive components of heterotopical TCRs appeared in the opposite hemisphere, was found to be greater in the left than in the right hemisphere in most of the males studied. In the left hemisphere of the males the number of effective stimulation points for positive and negative components of heterotopical TCRs was, on average, 28±7 and 38±8, whereas in the right hemisphere it was smaller; 15±4 and 21±7 respectively. Similar interhemispheric differences were also revealed in females. In their left hemisphere the average number of effective stimulation points was 25±5 and 21±4, that in the right hemisphere was 21±4 and 19±4 respectively.

In addition to the sex differences of interhemispheric asymmetry of homo- and heterotopical TCRs, described above, it was found, in males, that individual interhemispheric asymmetry was greater than that in females. Thus, in comparing the coefficient of asymmetry[9] for the positive and negative heterotopical TCR components in the male group (K_{as}=0.333±0.081 and K_{as}=0.362±0.077 respectively) and in females (K_{as}=0.180± 0.040 and K_{as}=0.210±0.050) it was found that both measures were significantly greater in males than in females. For homotopical positive TCRs a similar regularity was observed, the coefficients of asymmetry in males (K_{as}=0.519±0.087) being greater than those in females (K_{as}=0.361±0.074). Unlike this, for the negative TCR component, sex differences in average asymmetry coefficient were observed only at trend levels.

Thus, in males, right hemisphere dominance for the magnitude of homo- and heterotopical TCRs in the visual cortex was found, whereas in females no species-specific asymmetry of these potentials could be revealed, only individual asymmetry being observed. Consequently, the direction of right hemisphere species-specific functional interhemispheric asymmetry was shown by males. It was also established that individual interhemispheric asymmetry of TCRs in the visual area of the neocortex was greater in males, compared to females.

3.1.2. Auditory Cortex

Sex differences of functional interhemispheric asymmetry in the auditory cortex of cats were studied (Bianki and Bozhko, 1987), with TCRs recorded from 150–170 points in zones AI, AII, EP, defined according to the schematic map of Woolsey (1964).

It should be recollected that, after studying a mixed sample, right hemisphere functional interhemispheric asymmetry in the auditory cortex of cats was described for both the positive and negative components of homotopical TCRs.

From analysis of the experimental evidence, it appeared that functional interhemispheric asymmetry of homotopical TCRs in the auditory cortex has certain peculiarities associated with the sex of the animal. In the male group, no unidirectional asymmetry could be revealed. Only individual asymmetry was found. In contrast to this, in the female group, functional interhemispheric asymmetry was revealed for both the positive and negative components of the TCR, the right hemisphere being dominant in all the animals.

Interhemispheric asymmetry also appeared to be characteristically of greater magnitude in females compared to males (Figure 18). In particular, analysis of individual data has shown that, in most females, asymmetry belonged to the qualitative type, in which the FMA zones were located in the dominant hemisphere. In males however, the qualitative-topographical type of asymmetry prevailed, in which the size and location of the foci represented in both hemispheres were different.

In the averaged maps of response distribution (Figure 18, A) it can be seen that high amplitude potentials (amplitude ranges 1 and 2) were recorded mostly from a greater area in the right auditory cortex in females, compared to males. It should be emphasized that

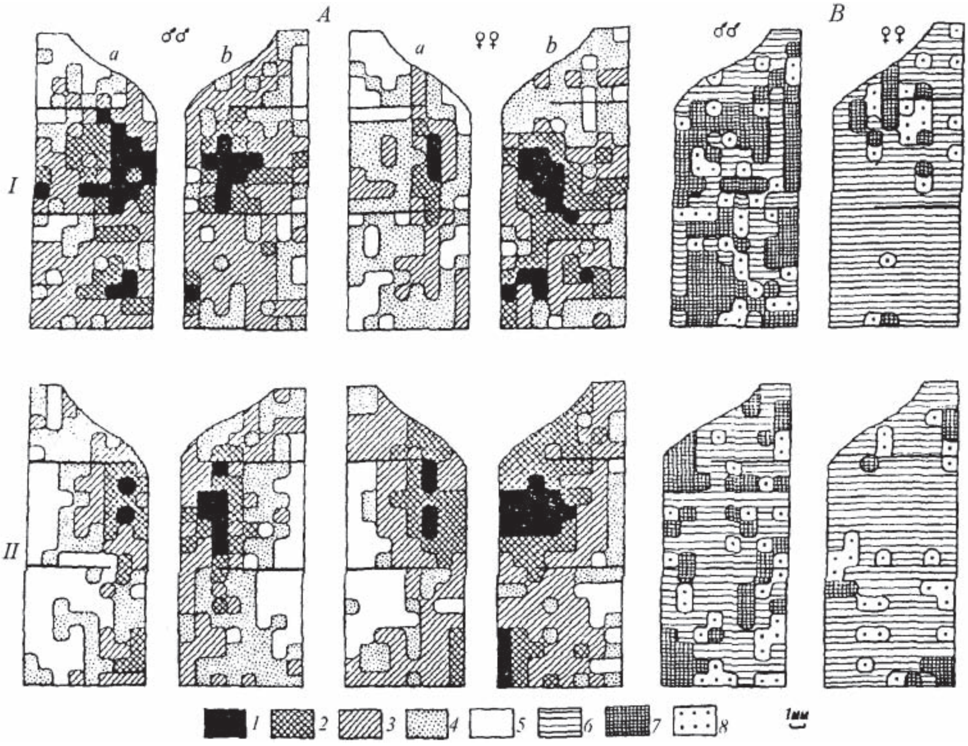

Figure 18: Interhemispheric asymmetry of transcallosal potentials in the auditory cortex of male and female cats (averaged data). **A**–averaged maps of positive **(I)** and negative **(II)** component distribution, **1–4** are ranges of amplitude potentials (decreasing from 1 to 4), **5** is the absence of evoked potentials. **B**–hemisphere mosaicism of interhemispheric TCR asymmetry. **6**–zones of direct dominance, i.e. the prevalence of the TCR amplitude in the right hemisphere; **7**–zones of inverse dominance, i.e. the prevalence of theTCR amplitude in the left hemisphere. **8**–zones in which no asymmetry was observed. **Scale:** 1 mm.

the asymmetry of potentials in females was also characterized by a less-fragmented mosaic, i.e. the responses prevailed in magnitude over a greater area in the right hemisphere (Figure 18, B).

In the female group the average individual coefficients of asymmetry were also greater, compared to those in males (K_{as}=0.6360±0.070 [females] and K_{as}=0.310±0.060 [males] for the positive components, and K_{as}=0.260±0.040 [females] and K_{as}=0.180± 0.040 [males] for the negative components).

Thus, in females right hemisphere dominance was established for the magnitude of homotopical TCRs in the auditory cortex, while in males only the individual form of interhemispheric asymmetry could be found. Consequently, the right hemisphere direction of species-specific interhemispheric asymmetry in the auditory cortex, as distinguished from the visual one, was identified not in males but in females. Moreover, individual asymmetry of interhemispheric TCRs was more strongly expressed in females, compared to males. As for the males, they happened to possess a more fragmented mosaic than the females.

3.1.3. Somatosensory Cortex

Sex specificity of functional interhemispheric asymmetry in the somatosensory cortex of cats was studied (the primary somatosensory zone in Fields 1, 2, 3a, 3b), potentials being recorded from 60–75 symmetrical points in the posterior and lateral sigmoid gyri (according to the map of Hassler and Muhs-Clement, 1964) (Bozhko, 1989).

It was pointed out above that, during the investigation of a mixed sample of animals, right-sided functional interhemispheric asymmetry of both components of the homotopic TCR was found in the cats' somatosensory cortex.

After processing the experimental results obtained from groups of males and females, certain sex differences in functional interhemispheric asymmetry of homotopical TCRs were found. TCR asymmetry was found for both components of TCRs, in most of the males investigated, their right hemisphere dominating for asymmetry of the amplitude of responses. In females, asymmetry was found in a lesser number of individuals, and a unihemispheric direction of asymmetry was not revealed. Only individual asymmetry was observed.

The averaged maps of homotopical TCR distribution in the somatosensory cortex of the right and the left hemispheres of males and females illustrate the above sex differences (Figure 19). Males can be seen to possess a more strongly expressed *species-specific* interhemispheric asymmetry: The positive response component is characterized by a qualitative type of asymmetry (Figure 19, I), while the negative one is again characterized by a greater magnitude of FMA in the right hemisphere (Figure 19, II). Unlike this, females showed interhemispheric differences with a lesser degree of contrast (Figure 19, B).

From analysis of *individual* and functional interhemispheric asymmetry, it was seen that they have greater magnitudes in the group of females, compared to males. For the positive component of homotopical TCRs, the above regularity was statistically significant: In females, K_{as}=0.530±0.129, in males, K_{as}=0.450±0.076. For the negative TCR component, a similar tendency was observed at trend level: In females, K_{as}=0.480±0.131, in males, K_{as}=0.440±0.012.

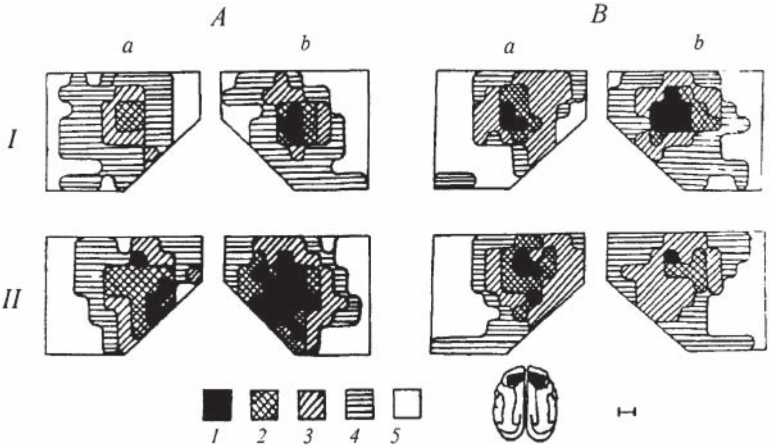

Figure 19: Sex differences of the interhemispheric asymmetry of homotopical transcallosal responses in the somatosensory area of the cat's neocortex (averaged data from 12 animals of each sex). **A, B**– averaged maps of the distribution of positive **(I)** and negative **(II)** TCR components in the somatosensory cortex of the left **(a)** and the right **(b)** hemisphere of males **(A)** and females **(B)**. **1–4**,- classes of the ranged amplitude of potentials; **5**–absence of EPs. **Scale:** 1 mm. **Insert:** The black colour marks the area of topographical TCR recording.

Somewhat different regularities were found when functional interhemispheric asymmetry of heterotopical TCRs was studied. Interhemispheric asymmetry for both components of heterotopical TCRs was found in most animals from the mixed sample. However no prevalent excess in the number of individuals with a definite hemispheric dominance for magnitude of TCR could be found. Asymmetry of heterotopical potentials was found in most males for the magnitudes of both TCR components, the right hemisphere being dominant. In females, interhemispheric asymmetry was found in a lesser number of individuals, and was not directed to any particular hemisphere.

As in the case of the analysis of interhemispheric asymmetry of heterotopical TCRs in other cortical areas, an additional criterion for assessment of interhemispheric differences was a comparative characteristic–the size of the area of somatosensory cortex whose stimulation proved effective for the appearance of potentials in certain points of the opposite hemispheres. Both in males and females the relative area of effective stimulation sites in the left hemisphere was greater than that in the right one. In males, positive and negative components of heterotopical TCRs arose in a point of the right hemisphere, when 38±7 and 37±7 points (respectively) in the left somatosensory cortex were stimulated. If the stimulating electrode was in the right hemisphere, the number of effective stimulation points was, on the average, 27±5 and 25±3 respectively. In females, these relations were 32±5 and 30±5 when the left hemisphere was stimulated, and 23±5 and 25±5 when the right hemisphere was stimulated. In females and in males the areas of effective stimulation sites were greater in the left hemisphere, compared to the right one. At the same time, it should be noted that in males, compared to females, interhemispheric differences were more strongly expressed.

Data on the greater expression of functional interhemispheric asymmetry in males were also obtained by calculation of individual asymmetry coefficients. The values of this parameter for the positive and negative components of heterotopical TCRs in the male groups (K_{as}=0.390±0.066, and K_{as}=0.440±0.053, respectively) were greater than those of females (K_{as}=0.280±0.058 and K_{as}=0.420±0.081). Consequently, interhemispheric asymmetry of heterotopical TCRs was greater in males than in females.

Thus, in males, right hemisphere dominance was found for the magnitude of homotopical and heterotopical TCRs in the somatosensory cortex, while in females no species-specific asymmetry, but only individual asymmetry, was observed. Consequently, in this case, in the same way as in the visual cortex, the overall right hemisphere direction of asymmetry was produced by asymmetry in males. Individual interhemispheric asymmetry for homotopical TCRs was also found to be greater in females, that for heterotopical TCRs being stronger in males.

3.1.4. Parietal Cortex

Sexual dimorphism in functional interhemispheric asymmetry was studied in the parietal cortex with TCR recording from 120–150 symmetrical points in Fields 5a, 5b, and 7 (defined according to the map of Hassler and Muhs-Clement, 1964) (Bozhko, 1990).

Earlier it has been pointed out that in the parietal association cortex, when a sample of cats of both sexes was studied, right-sided functional interhemispheric asymmetry was found for the negative component of homotopical TCRs.

First of all, it should be noted that, in the parietal cortex, functional interhemispheric asymmetry of homotopical TCRs was found in most males and females. Nevertheless, its right hemisphere direction could not be revealed in either males or females. As expected, although species-specific asymmetry was absent, individual asymmetry was observed. Comparison between the average values of individual coefficients of interhemispheric asymmetry in groups of animals of different sexes showed that functional interhemispheric asymmetry had a greater magnitude in females than in males. In females, the average values of asymmetry coefficients for the positive and negative TCR components were as follows: K_{as}=0.370±0.090 and K_{as}=0.400±0.090, respectively. In males the corresponding values were K_{as}=0.330±0.080 and K_{as}=0.330±0.010.

The averaged maps of TCR distribution in the parietal cortices of the left and the right hemisphere reflect sex peculiarities of functional interhemispheric asymmetry (Figure 20). It can be seen that interhemispheric differences between TCR magnitudes in males (Figure 20, A) are expressed somewhat less strongly than in females (Figure 20, B). It should also be noted that the most distinct sex differences were found for the negative TCR component (Figure 20, A, B, II).

In the parietal association cortical area, interhemispheric asymmetry of heterotopical TCRs was found in half the animals of the sample studied. At the same time, no species-specific functional interhemispheric asymmetry could be revealed, either in the sample as a whole, or in groups of different sexes. However, individual asymmetry could be observed. When the individual coefficients of asymmetry of the positive and negative components of heterotopical TCRs were compared they were found to be greater in the females (K_{as}=0.310±0.090 and K_{as}=0.400±0.110, respectively) as compared to the corresponding values in males (K_{as}=0.260±0.060 and K_{as}=0.300±0.080).

Using the additional criterion of functional interhemispheric asymmetry, i.e. comparing the area of the effective stimulation zones in both hemispheres, showed that in the left parietal cortex of females the number of points of effective stimulation for positive and negative

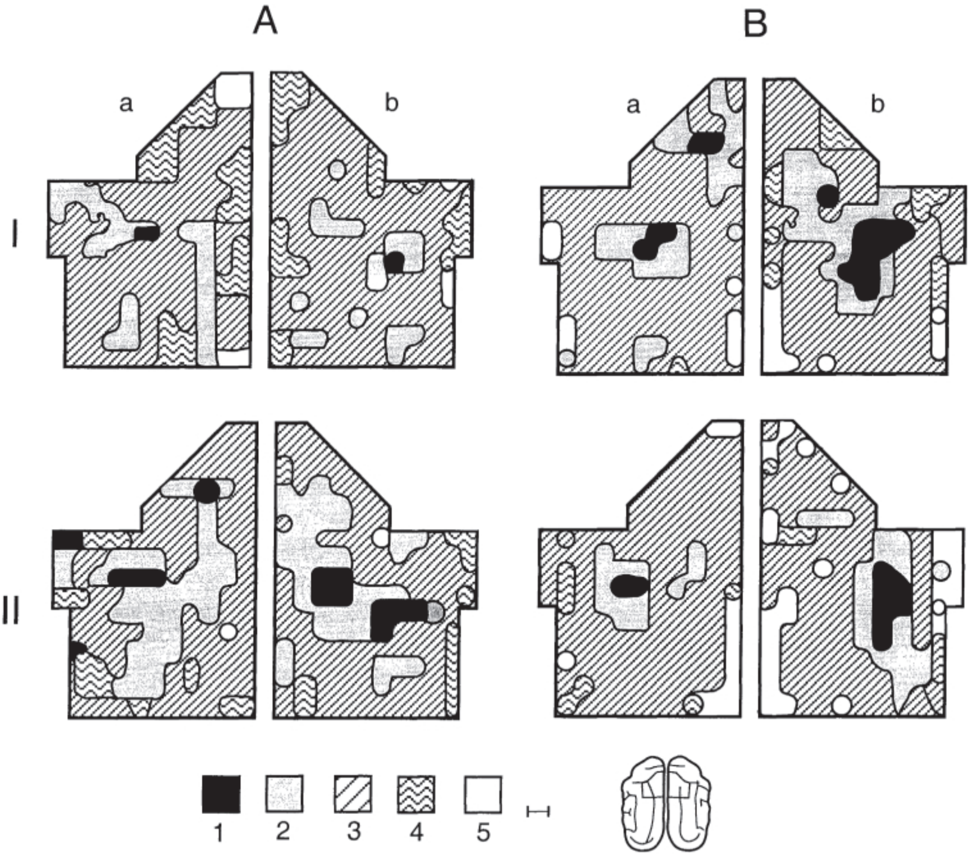

Figure 20: Sex differences in the interhemispheric asymmetry of transcallosal responses in the cat's parietal association cortex (averaged data from 12 individuals of each sex). **A, B**–averaged maps of the distribution of positive **(I)** and negative **(II)** TCR components in the parietal association cortex of the left **(a)** and the right **(b)** hemisphere of males **(A)** and females **(B)**. **1–4,** I–II–classes of the ranged amplitude of potentials; **5**–absence of EPs. **Scale:** 1 mm. **Insert:** The black colour marks the area of topographical TCR recording.

TCR components was, on average, 14±4 and 12±4 respectively, whereas in the parietal cortex of the right hemisphere it was greater, 24±3 and 21±4 respectively. In the male parietal cortex, no interhemispheric differences could be found when this criterion was used: In the left hemisphere, the average number of effective stimulation points for the positive and negative TCR components was 19±5 and 20±4, while in their right hemisphere it was 17±4 and 18±4 respectively. These data can be considered as evidence of greater asymmetry of heterotopical TCRs in the parietal cortex of females, compared to males.

Thus, in the parietal cortex of both males and females only the individual form of functional interhemispheric asymmetry was found for indices of homotopical and heterotopical TCRs, in spite of the fact that, when a mixed sample was studied, right hemisphere asymmetry of the negative homotopical TCR component has been described previously for the parietal cortex. It should also be noted that the magnitude of the individual functional interhemispheric asymmetry in females surpassed that in males.

3.1.5. Sensorimotor Cortex

Sexual dimorphism of functional interhemispheric asymmetry in the sensorimotor cortex was studied, with TCRs recorded from 60–70 points in Fields 4 and 6 (according to the map of Hassler and Muhs-Clement, 1964) (Bozhko, 1990).

In earlier studies of functional interhemispheric asymmetry in the sensorimotor cortex, in a mixed sample, left-sided asymmetry of the positive and negative TCRs was shown. It was established that the characteristics of homotopical TCRs in the sensorimotor cortex depend strongly upon the animal's sex. In particular, a significant prevalence of individuals with left hemisphere dominance for the magnitude of the positive component of the TCR was found only in the male group. Unlike this, in females, interhemispheric asymmetry was found in a smaller number of individuals, and was not species-specific. Individual functional interhemispheric asymmetry appeared to be greater in females than in males. In the females, the coefficient of asymmetry for the positive and the negative component of homotopical TCRs (K_{as}=0.440±0.080 and K_{as}=0.330±0.090) was greater as compared to the males (K_{as}=0.290±0.070 and K_{as}=0.260±0.060).

A graphic idea of sex differences in interhemispheric asymmetry of homotopical TCRs in the sensorimotor cortex is provided by the averaged maps of their distribution in right and left hemispheres (Figure 21). In the male left hemisphere, high-amplitude responses of greater size were recorded, which was testified to by a greater area of cortical sites occupied by the 1st and the 2nd ranges of TCR amplitude in this hemisphere, as compared to the right hemisphere (Figure 21, A). It can also be seen that interhemispheric differences for the positive TCR component were more strongly expressed, the asymmetry being of a qualitative type (Figure 21, A, I). Unlike this, a lesser expression of interhemispheric differences could be observed in females (Figure 21, B).

During analysis of heterotopical TCRs further proof of the existence of sex differences in functional interhemispheric asymmetry was obtained. Left-hemisphere dominance for the magnitude of the positive TCR component was shown in a mixed sample of animals. This picture was observed solely in males, whereas in females only individual asymmetry was found. At the same time, in most males, right hemisphere dominance for the negative component of the TCR was revealed, whereas in females, again, only individual asymmetry was observed. During the investigation of functional interhemispheric asymmetry in animals of different sexes, it was established that it was characteristically of greater magnitude in females than in males. In females, the average values of asymmetry coefficients for the positive and the negative components of heterotopical TCRs were: K_{as}=0.460± 0.00 and K_{as}=0.320±0.080. In males the corresponding values were: K_{as}=0.390± 0.080 and K_{as}=0.260±0.060 respectively.

Comparison of the asymmetry of areas of effective stimulation zones in the two hemispheres showed that interhemispheric differences in this property of heterotopical TCRs are revealed in most females, the above zones occupying a greater area in the right than in the left hemisphere. Unlike this, in males, asymmetry of effective stimulation zones was found in a smaller number of individuals, the resulting asymmetry having no unihemispheric direction. In females, in the sensorimotor cortex of the left hemisphere, the numbers of effective stimulation points for the positive and the negative components of heterotopical TCRs were 14±3 and 18±3, whereas in the right hemisphere they were more numerous, 19±2 and 23±2 respectively. In males, the average numbers of effective stimulation points for the positive and the negative components of heterotopical TCRs

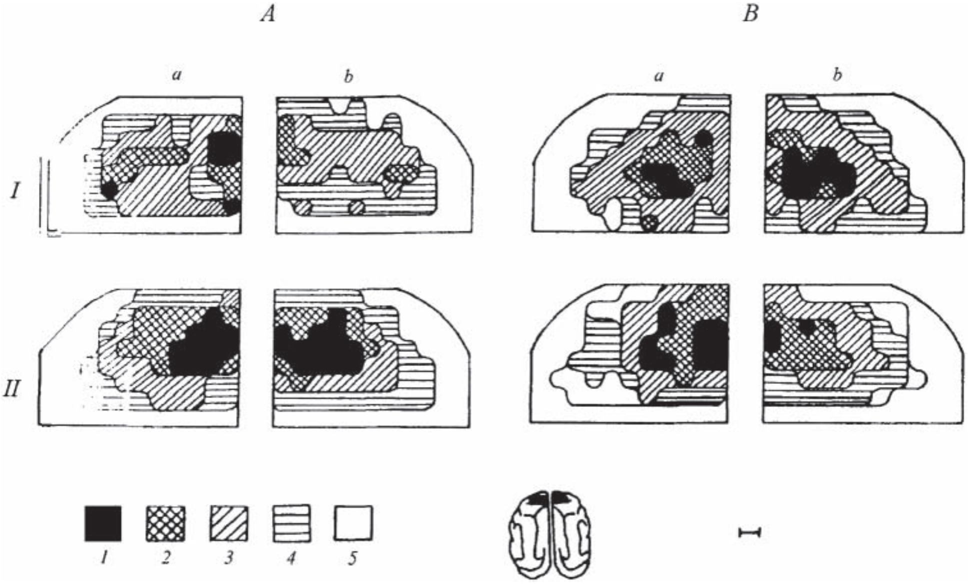

Figure 21: Sex differences in the interhemispheric asymmetry of homotopical transcallosal responses in the cat's sensorimotor cortex (averaged data from 12 animals of each sex). **A, B**–averaged maps of the distribution of positive **(I)** and negative **(II)** TCR components in the sensorimotor cortex of the left **(a)** and the right **(b)** hemisphere of males **(A)** and females **(B)**. **1–4**–classes of the ranged amplitude of potentials; **5**–absence of EPs. **Scale:** 1 mm. **Insert:** The black colour marks the area of topographical TCR recording.

in the left hemisphere were 12±2 and 25±5, and in the right hemisphere the corresponding values were 12±2 and 23±3. These data show the presence of greater asymmetry of heterotopical transcallosal influences in the sensorimotor complex of females, compared to that of males.

Thus, left hemisphere dominance was found in the sensorimotor cortex of males for the magnitude of the positive component of homotopical TCRs, and right hemisphere dominance for the magnitude of the negative component of heterotopical TCRs. In females, only individual interhemispheric asymmetry was observed. These data are somehow different from those obtained from study of a mixed sample of animals, where left hemisphere dominance was found for both components of homotopical TCRs. It should also be noted that the magnitude of individual functional interhemispheric asymmetry was greater in females than in males.

3.1.6. Summary

Summing up the experimental data described above, it should be pointed out that they prove the existence of sexual dimorphism in functional interhemispheric asymmetry of homotopical transcallosal connections, in the primary projection and association cortical areas investigated. Special attention should be directed to the specific character of functional interhemispheric asymmetry in homotopical TCRs in males and females: In males, more often than in females, it was possible to find the species-specific form of interhemispheric asymmetry, irrespective of which hemisphere, left or right, was dominant. The only exception was the homotopical TCRs in the auditory cortex. At the same time, in females, a greater magnitude of individual functional interhemispheric TCR asymmetry was observed, as a rule, in all cortical areas studied, except the visual one. These results can be assessed by using the concepts of penetrance of asymmetry (the frequency of manifestation of a characteristic) and the expression of it (the degree of the expression of the characteristic) (Bianki *et al.,* 1991a). In general, the above facts agree with data showing the greater lateralization of the male brain, and of the symmetrical, bilateral character of the female brain. It can also be observed that the greater magnitude of individual asymmetry in females, as compared to males, without its having any rigid direction, may be the result of its hormonal dependence. For instance, this dependence is revealed during pregnancy (Bianki *et al.,* 1987) or when sex hormones are introduced (Camp *et al.,* 1984; Filippova *et al.,* 1989). The rest of the factual material presented above is better discussed together with the data on interzonal transcallosal connections.

3.2. INTERZONAL AND TRANSCALLOSAL CONNECTIONS

In one of the works on TCR investigation, it was shown that, in a site not symmetrical to the stimulated one, EPs are formed by the interaction of several streams of excitation, spreading both in the stimulated and in the receiving hemisphere (Bianki *et al.,* 1978). Later this proposition was repeatedly supported, elaborated, and developed (Bozhko, 1987). It was also established that transcallosal EPs were formed similarly, not only within the limits of symmetrical cytoarchitectonic areas, but also heterotopically, that is, for interhemispheric EPs, by the transcallosal interaction of different zones (Bianki and Shramm, 1988; Shramm and Kharitonov, 1988).

Functional and morphological connections between different formations and cortical areas are, as a rule, bilateral. In the opinion of the V.L.Ezrokhi and L.S.Grechushnikova (1979), symmetrical points in the cortex of the opposite hemispheres possess neuronal modules organized in similar ways, connected by means of transcallosal projections. Owing to those connections, reverberation of impulses between two definite points of similar areas in the opposite hemispheres can occur. According to the conceptions of J.C.Eccles (1989), each cortical module is connected with several groups of modules in the same hemisphere, and with mirror-image foci in the opposite hemisphere. In their turn, the latter, by means of commissural and associative connections, project back to the initial modules. Owing to the above process, a substrate is created for interhemispheric and intrahemispheric reverberation of excitation. Some authors have also described reciprocal interactions between isolated symmetrical neurones in opposite hemispheres (Kuraev, 1982). Consequently, between different cortical sites in opposite hemispheres, there are mutual direct and inverse functional connections.

We have investigated sex differences of inverse connections in the association neocortex. In the cerebral hemispheres of the cat brain, two association areas are usually distinguished: parietal and frontal. The most developed part of the frontal area is the sensorimotor cortex (Batuev, 1981). Therefore the specificity of direct and inverse connections of the parietal and sensorimotor cortices with primary projection cortical areas (visual and auditory) were studied.

Functional interhemispheric asymmetry was, as a rule, calculated statistically, using pairwise comparison of individual values of the amplitude parameters for the symmetrical positive-negative interzonal TCRs. In a number of cases, averaged TCR parameters were used. Sometimes a statistical comparison between the average parameters of right and left hemispheres was carried out. To identify functional interhemispheric asymmetry, negative-positive potentials were not taken into account in most cases, since, firstly, their number was, as a rule, smaller and, secondly, in this case the direction of asymmetry could not be inverse (Bianki *et al.,* 1991a, 1993).

3.2.1. Parietal Cortex

Visual-parietal TCRs were studied under the conditions of electrical stimulation in the rostral part of Field 19, with multiple topographical EP recording from the parietal cortex of the opposite hemisphere (Fields 5 and 7) (Bianki and Shramm, 1988; Bianki, 1989). The resulting TCRs were, as a rule, positive-negative, but sometimes also negative-positive.

Earlier, using a mixed sample of animals, it was shown that visual-parietal TCRs were characterized by a right-hemisphere direction of asymmetry. During the pairwise comparison of the interzonal visual-parietal TCRs, interhemispheric asymmetry appeared to be present in most of the animals under investigation, the amplitude of the positive and the negative component being greater in the right hemisphere. The average amplitude of the negative TCR phase was also greater in the right hemisphere.

On comparing individual data, no significant sex differences in functional interhemispheric asymmetry could be found in the visual-parietal interzonal TCRs. During the pairwise comparison of the amplitudes of TCRs with a positive-negative configuration, 10 out of 13 females with functional interhemispheric asymmetry appeared to possess right hemisphere dominance for the magnitude of the negative component of interzonal responses, this being found for the positive phase in 8 out of 13 female cats. In males, a similar regularity of EP distribution was observed: Nine out of 14 animals possessed asymmetry, the amplitude of the negative TCR component being greater in the right hemisphere. The right hemisphere was also dominant for the positive component in 9 out of 14 asymmetric animals. Consequently, from this analysis, both males and females were observed to possess a noticeable tendency for right hemisphere dominance.

More distinct results were obtained from comparing the average values of TCR amplitudes in the opposite hemispheres of males and females. In males, the magnitude of the average amplitude of both components of visual-parietal TCRs was greater in the right hemisphere ($p<0.05$), while in females the values of TCR amplitudes in opposite hemispheres did not differ significantly ($p>0.05$). In females the average amplitude of visual-parietal TCRs was greater than in males (18.6±1.8 mV and 13.7±1.5 mV), yet in males the amplitude of the negative TCR component was greater than in females (16.0±0.1 mV and 13.6±0.9 mV). Finally, the latencies of visual-parietal TCRs were greater in males than in females: 3.67±.02 ms and 2.7±.15 ms respectively. At the same time, in the male right hemisphere, TCR latencies were significantly greater than those in the left hemisphere: 4.46±.22 ms and 2.51±.12 ms respectively.

Thus, in males, the direction of asymmetry of visual-parietal functional connections favours mainly the right-hemisphere, whereas in females only the individual form of interhemispheric asymmetry could be found. These data testify, first, to the fact that lateralization of visual-parietal functional connections is more strongly expressed in males than in females, and, second, to the fact that the results of investigating a mixed sample of animals in this case are determined mainly by males.

The auditory-parietal TCRs were studied by placing the stimulating electrode in the rostral part of Field AI in the auditory cortex, with multiple topographical TCR recording from the parietal cortex of the opposite hemisphere (Fields 5 and 7) (Shramm and Kharitonov, 1988; Bianki, 1989). The TCRs recorded were usually positive-negative, but negative-positive potentials also occurred.

The study of a mixed sample showed that during stimulation of auditory zone AI the asymmetry of auditory-parietal TCRs, though observed in most animals investigated, was individual, since dominance of right or left hemisphere was approximately equiprobable.

However, it should be noted that, in the animal group under investigation, some peculiarities, associated with sex, were found in the interhemispheric distribution of the interzonal auditory-parietal TCRs. Pairwise comparison between the amplitudes of positive-negative TCRs showed that, in most males with pronounced asymmetry, the right hemisphere was dominant ($p<0.05$). At the same time, in most females left-sided asymmetry was observed ($p<0.05$). In both cases, these differences concerned the interhemispheric distribution of the positive component of heterotopical auditory-parietal interzonal TCRs.

Let us focus on the results of comparison between the average amplitudes of auditory-parietal TCRs (Figure 22). In males, the average amplitude of the positive TCR phases in the left hemisphere is greater than in the right: 20.85±1.25 mV and 12.35±1.8 mV respectively. In females, the average amplitude of the negative component is greater in the right hemisphere than in the left: 19.76±2.40 mV and 12.80±3.08 mV respectively. Finally, in the female right hemisphere the TCR latency was greater than that in the left one (4.02±0.12 ms and 3.3±.2 ms respectively). In males, the latencies of responses in opposite hemispheres did not differ significantly.

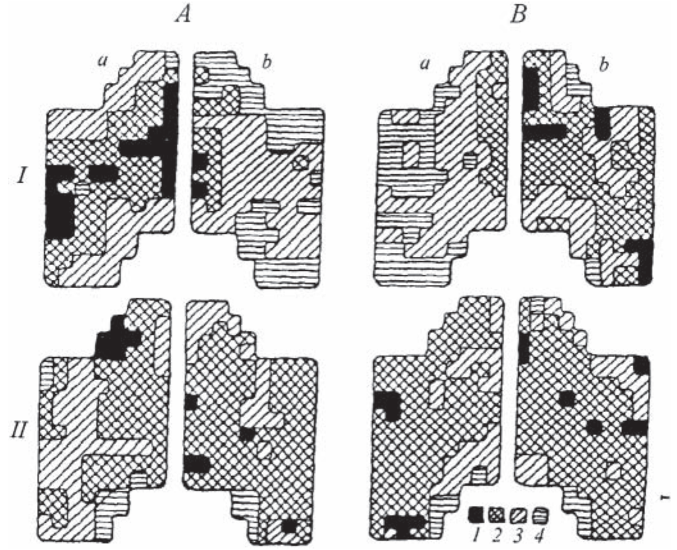

Figure 22: Maps of the distribution of positive-negative interzonal auditory-parietal TCRs in animals of different sexes. **A, B**–averaged maps of the distribution of positive **(I)** and negative **(II)** TCR components in the auditory-parietal cortex of the left **(a)** and the right **(b)** hemisphere of males **(A)** and females **(B)**. **1–4** classes of the ranged amplitude of potentials. **Scale:** 1 mm. **Insert:** For location of recording area, see insert in Figure 20.

Thus, during the investigation of a sample of animals of both sexes, the absence of functional interhemispheric asymmetry directed towards a single hemisphere may be partially accounted for by differences in directional dominance in interzonal parietal-auditory TCRs in animals of different sexes. Indeed, if the females showed left, and the males showed right hemisphere dominance, in the mixed sample these differences were sure to be equalized, which was shown in the above experiments.

Parietal-visual TCRs were studied in the following way: The stimulating electrode was fixed on the surface of the parietal cortex in the area of the focus of maximum activity in Field 5. Multiple topographic recording of interzonal TCRs was performed from the visual cortex of the opposite hemisphere (Bianki *et al.,* 1994).

The parietal-visual interzonal TCRs were mainly positive-negative, but potentials of a negative-positive configuration also occurred. It should be noted that parietal-visual TCRs with initial negativity were noticeably different in their magnitude between animals of different sexes: In males, these responses were smaller, the summated amplitude of their phases rarely exceeding 4–5 mV, whereas in females the above potentials were two- or threefold greater. Sex differences in the parameters of the focus of maximum activity were also observed: In females, the FMA was not greater in area for the positive-negative responses, and was usually localized on the boundary with the parietal cortical areas; in the case of negative-positive FMA responses were localized in the middle of Field 18. In males the localization of TCRs of maximum magnitude was similar, but FMAs were characterized by greater fragmentation, in the case of positive-negative TCRs. They were also greater than those in females, and were localized not only on the boundary with the parietal cortex, but also in the medial sites of Field 18.

Let us emphasize that, when studying a mixed sample, it was possible to establish right hemisphere dominance for the magnitude of the amplitude of positive-negative parietal-visual interzonal TCRs. Functional interhemispheric asymmetry of parietal-visual TCRs was characteristic of the overwhelming number of animals. It should be noted that in 25% (approx.) of cases this asymmetry was qualitative, i.e. the above interzonal EPs could be recorded only in one of the hemispheres. This asymmetry occurred with special frequency in females.

For parietal-visual interzonal TCRs, lateralization of functional interhemispheric asymmetry in animals of different sexes could be revealed on comparing the average values of positive-negative EP parameters in the right and in the left hemisphere, and also during the pairwise comparison of symmetrical TCRs in the averaged maps. Animals of both sexes were characterized by right hemisphere dominance for both components of positive-negative parietal-visual TCRs (Figure 23).

It was also shown that in males the magnitude of the TCR latency with initial positivity, was greater in the right hemisphere (2.0±0.1 ms and 1.8±0.1 ms, in right and in left hemispheres, respectively), while in females it was greater in the left hemisphere (1.7± 0.08 ms and 2.2±0.1 ms in the right and in the left hemisphere respectively). In females the latencies of negative-positive TCRs in the right (2.8±0.1 ms) and left (1.4±0.1 ms) hemispheres were significantly different.

Thus, according to the above data, in the case of parietal-visual interhemispheric TCRs, the direction of species-specific functional interhemispheric asymmetry established for the mixed sample coincided with that of both males and females.

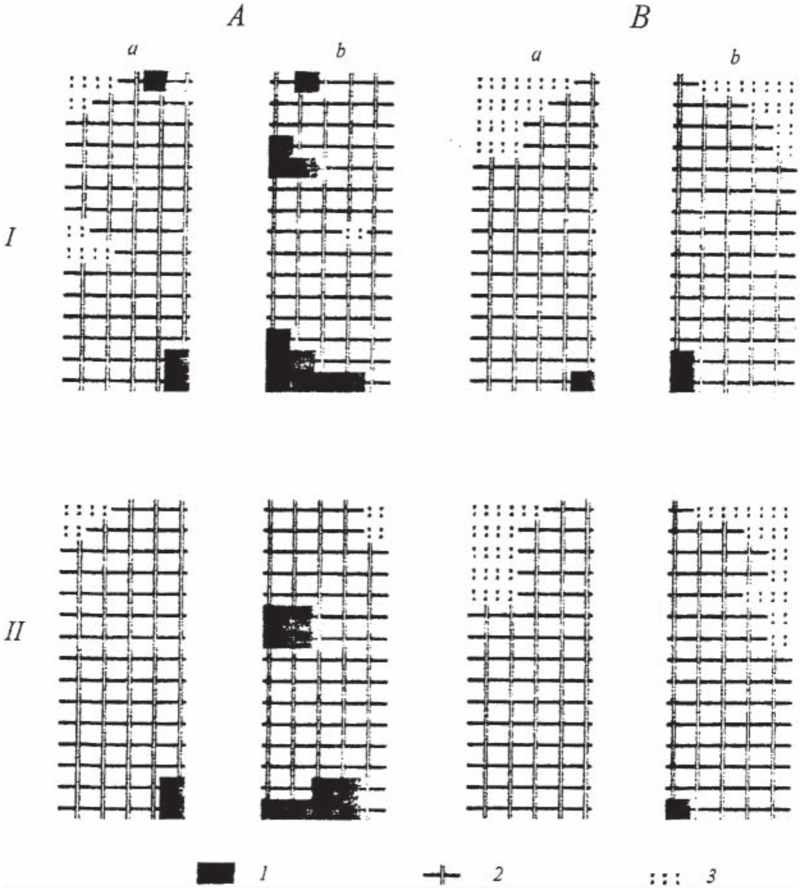

Figure 23: The maps of the distribution of parietal-visual positive-negative TCRs in cats of different sexes. **1**–maximum activity focus, **2**–extrafocal sites of TCR distribution, **3**–zones of TCR absence. **A, B**–averaged maps of the distribution of positive **(I)** and negative **(II)** TCR components in the parietal-visual cortex of the left **(a)** and the right **(b)** hemisphere of males **(A)** and females **(B)**.

Parietal-auditory TCRs were recorded with the stimulating electrode localized on the parietal cortex surface, in the area of the FM A in Field 5. Multiple topographic TCR recording was performed from the auditory cortex of the opposite hemisphere (Bianki *et al.,* 1994).

In the above experiments, together with the prevailing positive-negative potentials, negative-positive ones were also recorded. It should be noted that the magnitude of positive-negative interzonal parietal-auditory TCRs in males was only one half to one third of that in females, whereas the area of their recording in the males' auditory cortex was two or three times greater than that in females. The areas of parietal-auditory TCR recording for responses of opposite phases in males were approximately equal. However, in females the area for positive-negative TCRs was considerably greater than that for negative-positive ones. The FM A was fragmented in animals of both sexes, but in males its summated area exceeded that in females, in which the focus was usually represented by one or two points.

On the basis of studying a mixed sample of animals only individual asymmetry was found for parietal-auditory interzonal potentials. As was the case with parietal-visual TCRs, in the auditory cortex, individual asymmetry was characteristic of practically all animals studied. In this case, a qualitative form of functional interhemispheric asymmetry was found, which was characterized by the appearance of parietal-auditory TCRs only in one hemisphere. The number of such animals was as much as one third of all the sample investigated, the majority of them being females. The frequency of individuals in which right or left hemisphere dominance appeared was approximately equal.

At the same time, after pairwise comparison of averaged parietal-auditory TCRs (Figure 24) it was found that positive-negative potentials in males were characterized by dominance of the left hemisphere, those in females by that of the right.

From comparison of the average values of TCR parameters it follows that positive-negative TCRs in animals of both sexes are characterized by a longer latency in the left hemisphere (2.4±0.1 ms and 3.6±0.1 ms in males, 2.1±0.1 ms and 2.5±0.1 ms in females, in the right and in the left hemisphere respectively). A greater value of the latency was also observed in negative-positive parietal-auditory TCRs in the males' left hemisphere

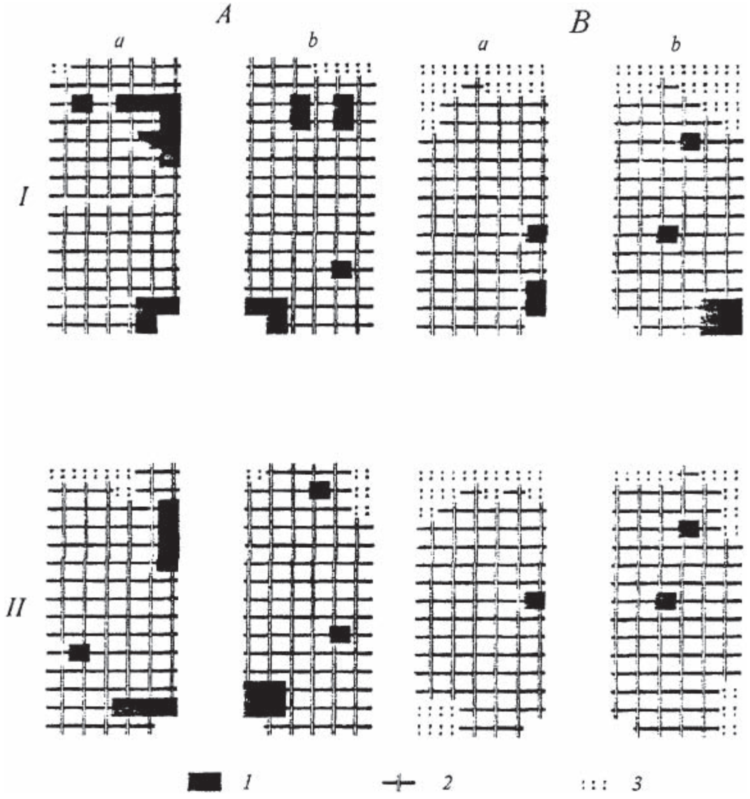

Figure 24: Maps of the distribution of parietal-auditory positive-negative TCRs in cats of different sexes. **1**–the focus of maximum activity, **2**–extrafocal sites of TCR distribution, **3**–zones of TCR absence. **A, B**–averaged maps of the distribution of positive (**I**) and negative (**II**) TCR components in the parietal auditory cortex of the left (**a**) and the right (**b**) hemisphere of males (**A**) and females (**B**).

(1.0±0.1 ms and 1.9±0.1 ms, for the right and the left hemisphere). It should be noted that there was a higher average amplitude of positive-negative TCRs in the females' right hemisphere (15.0±1.1 mV for the right, and 8.0±0.5 mV for the left hemisphere with respect to the positive TCR component; 16.3±1.3 mV and 6.0±0.4 mV with respect to the negative component):

Thus, in the above case of parietal-auditory TCRs, individual functional interhemispheric asymmetry found during the investigation of the mixed sample, seemed to be the result of the equalizing of the left and right hemisphere asymmetry observed separately in groups of males and females.

3.2.2. Sensorimotor Cortex

Visual-motor interzonal TCRs were studied by electrical stimulation of the rostral part of Field 19 in the visual cortex with multiple topographical recording of potentials in Field 4 and 6 in the sensorimotor cortex of the opposite hemisphere (Bianki, 1989; Bianki and Bozhko, 1989). Positive-negative and negative-positive TCRs were observed, the former prevailing.

When studying a mixed sample of animals, and pairwise EP recording, only the individual form of functional interhemispheric asymmetry was found. However,when the average data were compared, right hemisphere dominance was revealed for the amplitude of both components of the interzonal visual-motor TCRs.

No significant sex differences in interhemispheric EP asymmetry in the cats studied were observed when the visual cortex was stimulated. It was shown that, for the magnitude of the positive TCR component, in 6 out of 9 females possessing asymmetry, the left hemisphere dominated ($p>0.05$); for the negative phase, in 7 females out of 10, the left hemisphere was also dominant ($p>0.05$). In males, a similar regularity of EP distribution was observed: In 10 out of 18 asymmetrical animals, the amplitude of the positive response components was greater in the right hemisphere ($p>0.05$). In 9 out of 19 males with pronounced asymmetry for the negative TCR component, the right hemisphere dominated($p>0.05$). Thus it is possible to speak only of a tendency for left hemisphere dominance in females.

Consequently, on the basis of studying visual-motor interzonal TCRs, again, no unidirectional functional interhemispheric asymmetry was found in a mixed group of animals, as in males and females considered separately.

Auditory-motor interzonal TCRs appeared during electrical stimulation of the rostrocaudal part of Field AI in the auditory complex of the opposite hemisphere (Bianki, 1989; Bianki *et al.,* 1989a). As in all the above instances, positive-negative and negative-positive TCRs were recorded. However, in this case, negative-positive responses prevailed. Earlier an admission was made that in visual-motor TCRs, initial excitation and late inhibition prevailed in magnitude. This out-of-phase character of callosal streams flowing to the sensorimotor cortex from different projection areas seems to be able to promote the different timing of the integrated signals passing into the integrative-triggering zone MI.

In a mixed sample of animals, left hemisphere dominance was found during the pairwise comparison of the amplitude of symmetrical interzonal auditory-motor TCRs. Similar results were also obtained for the average amplitude parameters.

During stimulation of the auditory cortex, some peculiarities associated with the animal's sex were found, with respect to the interhemispheric distribution of interzonal TCRs.

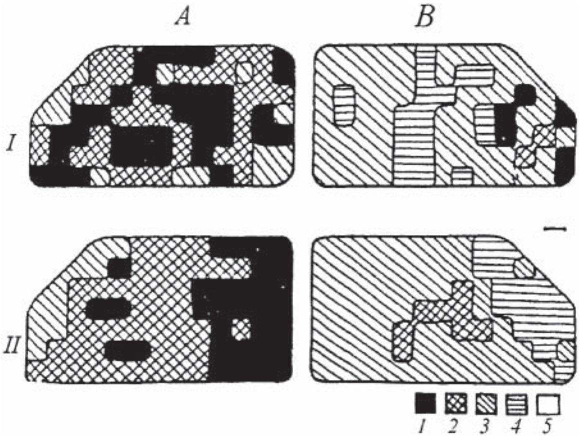

Figure 25: Interhemispheric asymmetry of positive-negative auditory-motor TCRs in females. Individual data. **A, B**–averaged maps of the distribution of positive **(I)** and negative **(II)** TCR components in the auditory-motor cortex on the left **(A)**, and on the right **(B)**. **1–4**–classes of ranging of EP potentials; **5**–absence of EPs. For location of recording area, see insert in Figure 21.

Thus, in 10 out of 11 females studied, there was left hemisphere dominance for both components of auditory-motor TCRs ($p<0.01$). At the same time, for males, left or right hemisphere dominance appeared to be equiprobable: For the positive phase, in 8 out of 20 asymmetrical males, the right hemisphere dominated, in 12 animals it was the left hemisphere ($p>0.05$). For the negative component, the number of right- and left-hemispheric males was 8 and 10 (respectively) out of 20 asymmetric individuals ($p>0.05$). A good example may be supplied by individual data characterizing left hemisphere dominance for the amplitudes of both components of positive-negative auditory-motor TCRs in females (Figure 25). Consequently, left hemisphere dominance in auditory-motor interzonal TCRs, established during the investigation of a mixed sample, is mainly determined by females.

Motor-visual interzonal TCRs were studied with the stimulation electrode localized on the surface of the sensorimotor cortex in the focus of maximum activity (the lateral side of Field 6, 2–3 mm more lateral than the *sulcus cruciatus*) and with multiple topographical EP recording from the visual area in the cortex of the contralateral hemisphere (Bianki et al., 1989a).

As the result of the experiments performed, visual-motor TCRs were found to occur more frequently in males than in females. Their configuration could be both positive-negative and negative-positive. Some sex differences in EPs were also observed. Thus, for positive-negative TCRs, the latency in males was somewhat shorter than in females (1.5±0.1 ms and 2.0±0.1 ms respectively), whereas the amplitude of the TCR components in males was smaller than in females (9.0±0.3 mV and 12.6±0.7 mV for the positive phase, and 18.0±0.7 mV for the negative phase respectively). For negative-positive TCRs, the latency in males and females did not differ significantly, whereas the amplitude of response was somewhat higher in females: 5.5±0.3 mV and 8.0±0.2 mV for the negative phase, and 5.5±0.2 mV and 9.5±0.2 mV for the positive phase in males and females respectively. Sexual dimorphism was also observed in the site of the FMA. Thus, in positive-negative TCRs, the FMA in males was closer to the rostral pole of the visual cortex, whereas in females it was localized in the central part of the visual cortex.

Processing of results was performed on a mixed sample, and on male and female samples separately. After pairwise comparison of positive-negative TCRs, only the individual form of interhemispheric asymmetry was found in animals from a mixed sample and in males, whereas, in females, right hemisphere dominance for the negative TCR component was observed. However pairwise comparison of the average parameters of TCR components showed that the right hemisphere was dominant, both in animals from a mixed sample, and in males and females in separate samples. In addition, right hemisphere dominance was also observed in all the cases for the negative-positive EPs.

Thus, for motor-visual interzonal TCRs, coincidence in the direction of functional interhemispheric asymmetry was observed during the study both of a mixed sample and in separate samples of males and females. In all the cases asymmetry was right-sided.

Motor-auditory TCRs were studied with the stimulating electrode fixed on the surface of the sensorimotor cortex in the FM A in the lateral site of Field 6, 2–3 mm more lateral than the *sulcus cruciatus,* and with multiple topographic EP recording in the auditory cortex of the opposite hemisphere (Bianki and Bozhko, 1989). In the same way as with EP recording in the visual cortex, TCRs could be of two configurations: positive-negative and negative-positive. As for positive-negative TCRs, their latency was shorter in males than in females: 2.3±0.1 ms and 3.1±0.1 ms respectively. In the distribution of negative-positive TCRs across the cortical surface, a certain fragmentation was observed in males; TCRs were located in the rostral pole of the auditory fields and the FMA was also fragmented. At the same time, positive-negative TCRs occupied 65–80% of the area and were characterized by a spacious focus, whose area was as great as 40–50% of the whole recording surface. But the TCR amplitude in females was usually smaller than in males.

From the results obtained in the study of functional interhemispheric asymmetry in motor-auditory interzonal TCRs (Table 14), it follows that during the pairwise comparison of averaged data for positive-negative TCRs, the individual form of asymmetry was found in the mixed sample, while in males dominance of the left hemisphere, and in females that of the right was observed. It should also be pointed out that, for the negative-positive TCRs, right hemisphere asymmetry was observed both in males and in females.

Table 14. Functional interhemi spheric asymmetry of motor- visual and motor- auditory transcallosal connections according to the scores of positive-negative transcallosal EPs

Recording zone	*Sex*	*The number s of animal*	*Positive EP component*			*Negative EP component*		
			The number with FMAs	*The dominant hemisphere*		*The number with FMAs*	*The dominant hemisphere*	
				Right	*Left*		*Right*	*Left*
visual	males	14	14**	8 SD	6	14**	8 SD	6
	females	9	9**	6 SD	3	9**	7*SD	2
	together	23	23**	14 SD	9	23**	15 SD	8
auditory	males	14	14**	5	9 SD	13**	5	8 SD
	females	9	9**	6 SD	3	9**	6 SD	3
	together	23	23**	11	12	22**	11	11

Note: Significant differences in animals of both sexes have been noted, revealed during statistical comparison of individual data in samples of males and females, * – $p<0.05$; ** – $p<0.01$; SD– significant dominance according to averaged maps.

From the above it follows that individual form of asymmetry found in the mixed population must, to some extent, have been the result of the interference of right- and left hemisphere asymmetry, which was found when males and females were studied separately.

3.2.3. Summary and Discussion

Now let us turn to the joint discussion of experimental data obtained from studying both intracallosal and interzonal transcallosal connections (Table 15). The first remark is methodological. Even a cursory look at the above data draws attention to the possible disparity between the conclusions drawn from the study of a mixed sample and single-sex groups. Only in some cases (15%) did the results of the study of a mixed sample and single-sex groups coincide, when, for instance, parietal-visual and motor-visual connections were studied. Sometimes the results obtained from a mixed sample were determined by males (31%): visual-parietal connections, homotopical connection in the visual, somatosensory, sensorimotor cortices. In other cases females exceeded males (15%); auditory-motor connections, homotopical connections in the auditory cortex. Finally, in most of the cases studied (39%), the results of the investigation of a mixed sample are determined by the interference of the characteristics of interhemispheric asymmetry observed in males and females: auditory-parietal, parietal-auditory, visuo-motor, motor-auditory connections, homotopical connections in the parietal cortex. These data point to an urgent necessity of taking the sex factor into account when studying the peculiarities of the lateral specialization of functions. Disregard of this may result in inadequate conclusions.

Now let us consider transcallosal connections between the visual and auditory cortices and the association cortical areas. For convenience, let us conditionally refer to visuoparietal and auditory-motor connections as "direct" and parietal-visual, parietal-auditory, and motor-auditory ones as "inverse".

Table 15. Lateralization of transcallosal connections

Cortical areas and their connections	*The dominant hemisphere*		
	Both sexes	*Males*	*Females*
		Intrazonal connections	
Visual	Right	Right	IA
Auditory	Right	IA	Right
Somatosensory	Right	Right	IA
Parietal	Right	IA	IA
Sensorimotor	Left	Left	IA
		Interzonal connections	
Visuo-parietal	Right	Right	IA
Audio-parietal	IA	Right	Left
Parieto-visual	Right	Right	Right
Parieto-auditory	IA	Left	Right
Visuo-motor	Right	IA	IA
Audio-motor	Left	IA	Left
Motor-visual	Right	Right	Right
Motor-auditory	IA	Left	Right

Note: IA–individual asymmetry.

"Inverse" connections to the visual cortex from areas of association cortex, both in males and females, were characterized by right hemisphere dominance (Table 15, Figure 26). This regularity was typical of parietal-visual (males, females) and motor-visual connections (males, females). In addition, right-sided dominance was also inherent in homotopical TCRs in the males' visual cortex. The same lateralization was characteristic of ascending influences reaching the visual cortex (Bianki, 1989). It is natural to suggest that this single-hemisphere, right-sided dominance indicates functional (and maybe structural) right hemisphere asymmetry inherent in the visual cortex. It could also be suggested that such relatively rigid lateralization of streams of interhemispheric excitation in the visual cortex seems to be optimal for processing sensory visual information arriving simultaneously. Underlying this, however, is mainly unilateral right hemisphere reverberation of excitation in the visual cortex. Since the right hemisphere asymmetry of transcallosal connections in the visual and parietal cortices occurred more often in males than in females (Table 15), parallel processing of visual information by males could be suggested. This suggests a greater lateralization of the male brain as compared to females, when carrying out visual functions.

Of special interest is the consideration of "direct" and "inverse" connections between the auditory cortex and the association cortical areas. For parietal-auditory and motor-auditory "inverse" connections, left hemisphere dominance in males, and right hemisphere dominance in females was established (Table 15). Right hemisphere dominance in

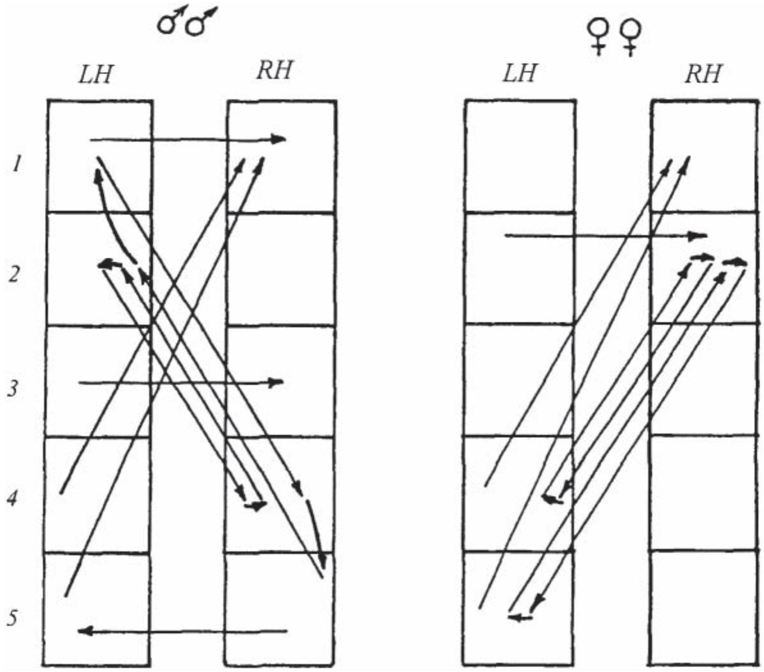

Figure 26: The scheme of the interhemispheric asymmetry of transcallosal connections in different areas of the cerebral hemispheres. **LH**–left hemisphere, **RH**–right hemisphere. **1**–visual, **2**–auditory, **3**–somatosensory, **4**–parietal, **5**–sensorimotor cortex. **Horizontal arrows** mark homotopical connections, **slanting lines**–interzonal heterotopical connections. Explanations are in the text.

females in carrying out homotopical interhemispheric relations was shown on the same illustrative material. As opposed to this, auditory-parietal TCRs in males were characterized by right hemisphere dominance, auditory-parietal and auditory-motor ones in females, by left hemisphere dominance. The above attribution of "direct" and "inverse" interhemispheric connections to the opposite hemispheres may facilitate the possibility of interhemispheric interzonal reverberation, which seems to be conducive to processing of the incoming successive auditory sensory information. Lateralization of interzonal connections in the auditory and associative cortical areas occurred somewhat more frequently in females than in males (Table 15). Consequently, successive processing of auditory information may prevail in females. This also points to a greater brain lateralization in females when they carry out auditory functions, compared to males.

It should be noted that interzonal transcallosal connections in primary projection and association cortical areas (Figure 26) are represented by slanting lines only for convenience, whereas in reality they are the result of the interaction of homotopical transcallosal and intrahemispheric influences. It should also be pointed out that, for the sake of brevity, only lateralized functional connections are represented in the scheme, whereas additionally, there are also other connections determining the individual form of asymmetry.

Even a cursory glance at the above scheme is sufficient to obtain an impression of a great differentiation of the males' brain, compared to that of females. Both interzonal heterotopical and intrazonal homotopical transcallosal connections in males are considerably more numerous than in females. After further consideration of the scheme, both general and specific characteristics of transcallosal interhemispheric connections in animals of both sexes can be distinguished.

The majority of functional interhemispheric connections in visual and association cortical areas coincide in males and females (Figure 26). In both cases, they have a right-sided lateralization, and consist of parietal-visual and motor-visual streams. However, in males, in addition to these, there are also "direct" visual-parietal functional connections, spreading from the left visual cortex to the right parietal area. Homotopical transcallosal connections in the visual cortex also possess right-sided lateralization.

It should be emphasized that a great variety of sex specificity is observed when functional interhemispheric connections in the auditory and association cortical zones are considered. More essential is the fact that the auditory cortex possesses a left-sided specialization in males, and a right-sided one in females. In females reciprocal interhemispheric connections ("direct" and "inverse") are observed between the left parietal and the right auditory zones. In males, more complicated connections are observed: The left auditory cortex is connected with the contralateral sensorimotor cortex by reciprocal interhemispheric relations. In the auditory cortex of females, as compared to males, right-sided homotopical transcallosal relations are observed.

Let us also point out that lateralization of homotopical transcallosal connections is more strongly expressed in males than in females. In addition to the above visual right-sided homotopical connections, males also possess right-sided homotopical ones in the somatosensory cortex and left-sided homotopical connections in the sensorimotor cortex. In female's only right-sided transcallosal connections in the auditory cortex are observed.

Thus, the general impression of the male brain's greater differentiation compared to female's, in the structure of its transcallosal connections, is supplemented by one more piece of evidence: The sex specificity of the brain is, to a certain degree, determined by the transcallosal connections in the auditory cortex, and first of all, by their lateralization. In males, left-sided lateralization and reverberatory circuits connect the left auditory cortex with the right parietal and sensorimotor areas. In females, right-sided lateralization of the auditory cortex is observed, with reverberatory circuits uniting the right auditory cortex with the left parietal and sensorimotor areas. To a certain extent, mirror-image differences between sexes seem to be observed in functional/structural relationships.

Finally, the more strongly expressed and right-sided auditory cortex lateralization in females appears to be somehow conditioned by the biological specificity of reproductive behaviour. The overwhelming majority of cats, while suckling kittens, lie on their right side (a personal observation of N.N.Sokolova). This creates better conditions for the function of the left ear (the right ear being somewhat screened by the substrate) and thereby for the right hemisphere. Similar logistics were used by L.J.Rogers and J.M.Anson (1979) to explain the formation of lateralization in chickens during embryonic development. Earlier it was also shown that, in cats during pregnancy, there is an increased role of the right auditory cortex and left hemisphere association zones in the organization of functional interhemispheric asymmetry, and in the change in the mosaicism of interhemispheric influences (Bianki *et al.,* 1992). Lateralization of the auditory cortex in females seems to be the result of unequal conditions under which the two sides of the auditory system function, and is realized according to the dominanta mechanism, formed with the participation of nervous and hormonal factors.

Let us draw some conclusions. In males and females intra- and interzonal TCRs may be somewhat different in their temporal and amplitude parameters, the area and localization of the recording zone, the magnitude, location, and degree of fragmentation of the FMA. In studying functional interhemispheric asymmetry of TCRs, it is necessary to use single-sex samples, and to make differentiated conclusions, since study of a mixed sample in a number of cases may produce inadequate results. In males and females, afferent intra- and interzonal transcallosal connections in the visual cortex are mainly characterized by right hemisphere asymmetry. This circumstance is supposed to create the optimal conditions for simultaneous information processing, which is underlain by spread of excitation along the reverberatory circuits in the visual cortex. This property is especially distinct in males. In females and males, intra- and interzonal transcallosal connections in the association and auditory cortical zones differ considerably. In males, they are characterized by left, in females by right hemisphere dominance. Owing to this, optimal conditions are supposed to be created for successive auditory information processing, which is underlain by excitation moving along the association-auditory reverberatory circuits. This peculiarity is more inherent in females than in males. In the auditory cortex, functional interhemispheric asymmetry (both quantitative and qualitative) is more strongly expressed in females, that in the visual cortex, in males. On the whole, the male brain seems to be more differentiated than the female brain in the development of transcallosal connections.

3.3. COMPARISON OF CORRESPONDING HEMISPHERES BETWEEN SEXES

Data were presented earlier in this chapter concerning some regularities of sexual dimorphism in the functional interhemispheric asymmetry of intra- and interzonal transcallosal potentials. Below, characteristics of transcallosal reactions in each hemisphere will be compared between male and female cats, i.e. the male left hemisphere is compared with the female left hemisphere, and the male right hemisphere with the female right hemisphere (Bozhko, 1990).

The study was performed in acute experiments on immobilized animals. Homotopical and heterotopical TCRs (in the convergence model) were recorded in primary projection areas (visual, auditory, somatosensory) and in association (parietal, sensorimotor) areas of the cortex. The technique of multiple topographical TCR recording was used. A comparison was made of the average values of positive-negative TCR parameters in foci of maximum activity, for each animal from a mixed sample.

First of all, let us focus on the comparative characteristics of the *left* hemisphere. The amplitude characteristics of homotopical TCR components in the primary projection areas of the left hemisphere cortex possessed a certain sex specificity (Table 16). Thus, in the visual cortex, with respect to the positive component, and in the auditory cortex,with respect to both TCR components, greater amplitudes were observed in females as compared to males. In the somatosensory cortex no significant sex differences in the TCR amplitude were found. Regional peculiarities of the amplitude characteristics of homotopical TCRs were revealed in association cortical areas: In the parietal cortex, the amplitudes of the positive TCR component were greater in females, the negative ones, in males. In the sensorimotor cortex no significant differences in the TCR amplitude could be revealed (Table 16, A).

Sex specificity was also found for such a parameter as the recording area of homotopical TCRs in the left hemisphere. It was established that in the visual cortex of females both components of transcallosal potentials were recorded in a greater area than in males. In the auditory and sensorimotor cortex a similar regularity was observed for the negative TCR component. In contrast to this this, the negative TCR component in the males' sensorimotor cortex was recorded from a greater area than in the females', while in the parietal cortex no significant differences could be revealed (Table 16, A).

Sex differences were also found during analysis of the temporal parameters of homotopical TCRs in the primary projection and association areas of the left neocortex. In the visual cortex, greater latencies of the maximal positive and negative components were noted in females compared to males, while in the somatosensory area the duration of potentials in females surpassed that in males. In the parietal and the sensorimotor cortex, the values of all the temporal parameters of TCRs also appeared to be greater in females compared to males (Table 16, B).

During investigation of heterotopical intrazonal TCRs, sex differences were also revealed in the left hemisphere. It should be recollected that a convergence model was used. In this case, not only did the zones of effective stimulation appear to be different: The magnitude of the latter in females was greater than that in males in the visual, parietal and sensorimotor cortex (Table 16, C).

On the basis of the above data, it can be suggested that homotopical TCRs in the left hemisphere were, as a rule, characterized by greater amplitude and time parameters, and were recorded in a greater cortical area in females, compared to males. Moreover, heterotopical intrazonal TCRs in some isolated points of the left neocortical areas under investigation arose, when a greater area of the same cortical zone in the opposite hemisphere were stimulated in females, as compared to males.

Table 16. Parameters and properties of intrazonal TCRs in different areas of the left neocortex in cats of both sexes

A. Amplitude parameters and topographical properties of homotopical TCRs

Recording areas	*Sex*	*The amplitude of components, μV*		*The relative area of component recording, %*	
		negative	*positive*	*negative*	*positive*
Visual	Males	37.6 ± 1.92	41.1 ± 2.69	19 ± 3	20 ± 3
	Females	51.8 ± 2.83**	52.2 ± 4.18	34 ± 3	37 ± 5**
Auditory	Males	78.3 ± 3.66	80.0 ± 4.28	44 ± 5	39 ± 5
	Females	78.7 ± 4.17	100.9 ± 6.51*	39 ± 5	45 ± 5*
Somatosensory	Males	43.7 ± 3.05	52.9 ± 4.41	20 ± 3	23 ± 2
	Females	41.0 ± 3.55	46.4 ± 4.55	20 ± 5	28 ± 5*
Parietal	Males	80.9 ± 5.20	108.9 ± 5.51	39 ± 7	41 ± 6
	Females	84.8 ± 3.67*	72.3 ± 3.22**	43 ± 5	41 ± 6
Sensorimotor	Males	45.7 ± 3.03	109.8 ± 6.36	45 ± 5	52 ± 5
	Females	55.1 ± 3.34	101.3 ± 5.40	42 ± 5	42 ± 5**

B. Temporal parameters of homotopical TCRs

Recording areas	*Sex*	*The latent period, ms*			*The duration of potential, ms*
		of response	*maximum component*		
			positive	*negative*	
Visual	Males	3.1 ± 0.11	6.5 ± 0.26	19.4 ± 0.86	29.9 ± 1.14
	Females	3.9 ± 0.24	7.5 ± 0.41**	19.8 ± 1.13**	33.0 ± 1.51
Auditory	Males	3.8 ± 0.16	16.8 ± 0.67	39.5 ± 1.57	59.0 ± 2.06
	Females	3.6 ± 0.15	15.6 ± 0.55	36.2 ± 0.94	19.8 ± 2.07
Somatosensory	Males	3.8 ± 0.19	8.9 ± 0.40	31.9 ± 1.09	42.8 ± 1.86
	Females	3.7 ± 0.16	11.3 ± 0.59	27.7 ± 1.18	54.0 ± 2.10*
Parietal	Males	6.6 ± 0.40	15.0 ± 0.49	36.6 ± 0.83	53.7 ± 1.22
	Females	10.5 ± 0.38**	20.5 ± 0.62**	44.6 ± 1.05**	61.1 ± 1.44**
Sensorimotor	Males	8.2 ± 0.31	15.2 ± 0.41	33.4 ± 0.58	50.8 ± 0.80
	Females	12.4 ± 0.44**	23.4 ± 0.91**	60.0 ± 1.76**	78.3 ± 2.08**

C. The relative area of effective stimulation zones for components of heterotopical TCRs, %

Recording areas	*Sex*	*Components*	
		positive	*negative*
Visual	Males	10 ± 3	
	Females	14 ± 3*	
Auditory	Males		9 ± 2
	Females		13 ± 3
Somatosensory	Males		
	Females		
Parietal	Males	14 ± 3	15 ± 3
	Females	20 ± 2*	18 ± 3*
Sensorimotor	Males	20 ± 3	
	Females	32 ± 3*	

Note: Significant differences in animals of both sexes have been noted, revealed during the statistical comparison of individual data in samples of males and females, * – $p<0.05$; ** – $p<0.01$.

Let us now present the comparative characteristics of TCRs in the *right* hemisphere. The amplitude characteristics of homotopical TCRs in the primary projection cortical zones of the right hemisphere were characterized by some sex peculiarities (Table 17, A). Thus, in the visual, and the somatosensory cortex, both TCR components had a greater amplitude in females than in males, whereas in the auditory cortex this regularity was observed only for the positive component. In the association cortical areas (parietal, sensorimotor) the amplitude of the positive TCR component was also greater in females, whereas the amplitude of the negative TCR component in the parietal cortex was, on the contrary, greater in males (Table 17, A). From comparing these data with the corresponding indices for the left hemisphere, it follows that the females' advantage over males for the amplitude parameters of homotopical TCRs is found in a greater number of cases in the right hemisphere, except for the auditory cortical area, in which females surpassed males for the positive TCR component in the left hemisphere.

Sex specificity was also found for the parameter of the area of homotopical TCR recording in the right hemisphere. In females, in the primary projection cortical areas (visual, auditory), transcallosal potentials were recorded in a larger area compared to males. In contrast to this, in males, in the association cortical areas of the right hemisphere, homotopical TCRs were recorded in a larger area than in females (Table 17, A). Comparing these facts with the corresponding data obtained from studying the left hemisphere, the advantage of males and sometimes females for the above parameter appeared to be found more frequently in the right than in the left hemisphere. It should be also noted that there is some specificity in the auditory cortex of the right hemisphere, in which the females' advantage was revealed not just for the negative TCR component (as it was in the left hemisphere) but for both components.

Sex differences were also revealed for the temporal parameters of homotopical TCRs in the right hemisphere. Processing of the experimental material showed that in the primary projection cortical zones (visual, somatosensory cortex) and in the association zones (parietal, sensorimotor cortex) the values of all the temporal parameters analysed (the latency of response, the latency of maxima of the positive and negative components, the duration of the potential) were greater in females than in males. In the auditory cortex of females, the latencies of potentials and the maximum of the positive component were greater than in that of males (Table 17, B). Comparison of these data with the results of studying similar parameters in the left hemisphere points to these measure being more commonly greater in the right hemisphere in females than in male, for the temporal parameters of TCRs, as compared to the left hemisphere. It should also be noted that the values of the temporal parameters of the TCR in the auditory cortex of the right hemisphere in females surpassed those in the males' left hemisphere for both TCR components.

Finally, in the case of heterotopical TCRs, in the right hemisphere an advantage was also found for females over males for the magnitude of effective stimulation zones (visual, auditory, parietal, and sensorimotor cortex) (Table 17, C).

Thus, it may be suggested that homotopical TCRs in the right hemisphere in the projection cortical zones of females possess greater measures of amplitude and temporal parameters, and of the the recording area than those in males. In the association neocortical areas, the positive component and the temporal parameters of homotopical TCRs are also greater in females, whereas the amplitude of the negative component in the parietal cortex, and the area of potential recording in the association areas is greater in males. In females,

Table 17. Parameters and properties of intrazonal TCRs in different neocortical areas of the right hemisphere in cats of both sexes

A. Amplitude parameters and topographical properties of homotopical TCRs

Recording areas	*Sex*	*The amplitude of components, (V)*		*The relative area of component recording, %*	
		positive	*negative*	*positive*	*negative*
Visual	Males	53.2 ± 3.92	5.8 ± 4.18	25 ± 4	28 ± 5
	Females	69.9 ± 3.74**	56.8 ± 7.00	37 ± 4**	39 ± 5**
Auditory	Males	70.1 ± 4.01	104.0 ± 5.30	40 ± 5	45 ± 5
	Females	99.5 ± 6.27**	109.9 ± 7.48	51 ± 6**	53 ± 4*
Somatosensory	Males	55.8 ± 3.56	52.9 ± 4.72	27 ± 2	32 ± 3
	Females	72.8 ± 3.44	72.9 ± 4.02**	27 ± 5	30 ± 5
Parietal	Males	83.6 ± 5.18	104.2 ± 5.74	39 ± 6	45 ± 8
	Females	90.7 ± 5.29*	78.7 ± 4.37**	35 ± 7*	33 ± 8**
Sensorimotor	Males	35.9 ± 2.32	121.0 ± 6.42	37 ± 5	53 ± 5
	Females	75.2 ± 6.92**	120.3 ± 6.76	35 ± 7	40 ± 7**

B. The temporal parameters of homotopical TCRs

Recording areas	*Sex*	*The latent period, ms*			*The duration of potential, ms*
		of response	*maximum component*		
			positive	*negative*	
Visual	Males	2.8 ± 0.11	6.0 ± 0.28	16.3 ± 0.69	29.1 ± 1.27
	Females	4.4 ± 0.27**	9.3 ± 0.58**	22.4 ± 1.08**	37.1 ± 1.50**
Auditory	Males	3.0 ± 0.12	14.7 ± 0.63	36.2 ± 1.50	51.8 ± 1.91
	Females	3.1 ± 0.18*	15.6 ± 0.67**	35.7 ± 1.05	52.1 ± 2.07
Somatosensory	Males	3.7 ± 0.19	8.6 ± 0.36	31.5 ± 1.19	53.5 ± 2.36
	Females	4.1 ± 0.27*	12.7 ± 0.60**	34.9 ± 1.49*	74.3 ± 2.17**
Parietal	Males	6.9 ± 0.37	14.7 ± 0.71	38.8 ± 1.08	54.4 ± 1.21
	Females	9.9 ± 0.35**	20.3 ± 0.68**	44.9 ± 0.95	62.4 ± 1.37**
Sensorimotor	Males	7.4 ± 0.32	14.2 ± 0.41	33.4 ± 0.48	58.6 ± 0.84
	Females	12.7 ± 0.63**	24.8 ± 1.17*	57.3 ± 2.30**	76.8 ± 2.84**

C. The relative area of effective stimulation zones for components of heterotopical TCRs, %

Recording areas	*Sex*	*Components*	
		positive	*negative*
Visual	Males		25.5 ± 5
	Females		14 ± 3
Auditory	Males	9 ± 3	15 ± 5
	Females	13 ± 3**	24 ± **
Somatosensory	Males	38 ± 7	37 ± 3
	Females	32 ± 5*	30 ± 5
Parietal	Males	16 ± 4	17 ± 3
	Females	12 ± 3**	10 ± 3**
Sensorimotor	Males	20 ± 3	37 ± 5
	Females	23 ± 5	30 ± 5*

Note: The asterisks mark the significant predominance ($p<0.05$) of asymmetrical individuals among males compared to females. I–positive-negative TCRs, II–negative-positive TCRs, LP–latent period.

heterotopical TCRs in the auditory cortex arise during the stimulation of a greater area in the corresponding zone of the opposite hemisphere, whereas in males a greater area of effective stimulation zones was found in the somatosensory, visual, and association cortical zones.

Now let us turn to discussion of the above factual material. Sex specificity was shown to be present during the function of both left and right hemisphere, yet it is important that in the latter case it is more frequent, and somewhat more strongly expressed and variable.

As a rule, in both cerebral hemispheres, the amplitude parameters and the area of homotopical TCR recording is greater in females than in males. The above peculiarity is revealed more often during right than left hemisphere function. The TCR amplitude is known to reflect, to a certain degree, the density of callosal projections, whereas the registration area of these projections is an index of the development of interhemispheric connections within the limits of the cortical areas studied. Consequently, it can be suggested that the brain of females is supplied with more functional transcallosal connections than that of males. On this basis, a relative bilaterality or symmetry of the cerebral hemispheres of females can be supposed, as compared to the male brain. On the contrary, the male brain can be thought of as more asymmetrical, i.e. relatively more lateralized.

In the literature, some indirect support of the above can be found. Thus, there is evidence that, in women, the corpus callosum is thicker, especially in the occipital regions, as compared to men (McGlone, 1980). However, in subsequent studies, this conclusion was disputed, although the existence of sex differences in the corpus callosum was not denied at the microlevel (Peters, 1988). The thalamic commissure (massa intermedia) in women was found to be more developed than in men, agenesis of this commissure and other brain commissures, and the grey commissure occurring more often in men (McGlone, 1980). Other indirect evidence for the prevalent bilaterality of the female neocortex may be data showing greater coherence of EEG oscillations in symmetrical sites of the cortex (McGlone, 1980; Butler, 1984; Otmakhova, 1987); also in women, when different functional loads are addressed to the different hemispheres, interhemispheric asymmetry was unidirectional (i.e. the same hemisphere was always dominant) (Bryden, 1982; Kimura and Harshman, 1984; Otmakhova, 1987). Functional specialization was thus weaker.

At the same time, the literature contains data pointing to the primary role of the right hemisphere in determining sex differences. Thus, N.A.Otmakhova (1987), analysing the relative changes in EEG power in each hemisphere when subjects performed tasks of processing information of different modalities, observed a greater expression of differences between men and women in EEG reactions of the right hemisphere. It should be noted that gonadectomy in adult rats, resulting in changes in the contents of steroid sex hormones, leads to modulation of functional interhemispheric asymmetry of behavioural reactions in animals of both sexes, due mainly to an influence on the right hemisphere (Filippova *et al.,* 1989).

The data obtained point to the fact that the values of the temporal parameters of homotopical TCRs (the response latency, the latencies of the maxima of positive and negative components, and the general duration of potentials) during both left and right hemisphere function in females were greater than in males. This regularity is almost twice as frequent during TCR recording in the right hemisphere than in the left. These data testify to the fact that the processing of transcallosal signals by females starts later and is carried out more slowly than when it is done by males. In other words, the male brain works faster, more dynamically than the female brain, this being especially characteristic of the right hemisphere.

The amplitudes of heterotopical TCRs in the left hemisphere of females were found to exceed those in males, while in the right they could be greater in males or in females. This points to a denser distribution of callosal fibers in the left hemisphere in females, and in the right hemisphere in animals of both sexes. Consequently it indicates greater convergence of excitation in the left hemisphere in males and females.

Comparison of the regional specificity of the amplitude parameters of homotopical TCRs in animals of both sexes suggests that the advantage in females is usually found in the primary projection cortical zones, while that of males was found in the association areas. This regularity is more often observed in the right than in the left hemisphere. The association neocortical zones are known to be richer in transcallosal connections compared to the projection ones. These data can be considered as an indication of the existence of differences in the balance of transcallosal activity in the projection and association cortical zones between males and females.

On the basis of the above facts obtained from comparing reactions in the same hemisphere between animals of the two sexes, the following conclusions can be drawn. The female brain is more bilateral, symmetrical, whereas the male brain is more asymmetric, lateralized. The cerebral hemispheres of males function more dynamically than those of females. Under such conditions, sex differences are more evident during right than during left hemisphere function. Sex peculiarities of the female brain are determined mainly by transcallosal connections in the primary projection cortical zones, those of the male brain can be found in those in the association cortical zones.

3.4. THE DYNAMICS OF TRANSCALLOSAL RESPONSE PROCESSING

In the previous chapter, it was emphasized that dynamic aspects were one of the most important properties of functional interhemispheric asymmetry. Here attention will be concentrated on the analysis of dynamics of asymmetry. Unlike the above data, TCRs were analysed more fractionally (not at *two* time intervals, corresponding to the positive and negative TCR components, but at four intervals). They were also more fully analysed (potentials being taken into account of any configuration, not only positive-negative ones, and over the whole site under investigation, not just in the focus of maximum activity). In addition, the work was carried out on rats rather than cats (Bianki and Makarova, 1994; Makarova and Bianki, 1994).

First of all, results will be presented of transcallosal signal processing on a mixed animal sample. The technique of multiple topographical recording of homotopical TCRs on the dorsolateral surface of both cerebral hemispheres was used. In anaesthesized Wistar rats TCRs were recorded in the visual, auditory, parietal, and motor cortical areas (Zilles, 1985). Functional interhemispheric asymmetry was analysed by comparing the amplitude and temporal parameters of TCRs. Taking into account the variability of the form and the components constituting the responses recorded, interhemispheric differences were estimated with respect to the latencies of the first component, and also with respect to the latencies and amplitudes of the maxima of the positive and negative components, at four specially-chosen time intervals: 7–14 (I), 17–27 (II), 31–46 (III), and 53–92 ms (IV).

The treatment of the data obtained was based on morphological facts on the structural diversity of the corpus callosum, in terms of homotopical, discrete and layer-wise principles of the construction of callosal connections (Killackey, 1982; Olavarria and Van Sluyters, 1985; Bianki, 1989), and also on modern concepts of the genesis of TCRs. It should be recollected that, according to widespread opinion, the positive and negative TCR components possess an independent genesis, and arise in different cortical layers, as a result of the income of transcallosal excitation along different systems of callosal fibers possessing unequal velocities of conduction (Purpura *et al.,* 1960; Grafstein, 1963). The negative TCR components recorded on the cortical surface represent mainly the result of the development of excitatory processes in superficial layers, the positive ones reflecting mainly inhibitory processes in the surface cortical layers and/or activation in the deep layers (Killam and Killam, 1960; Grafstein, 1963; Mareš *et al.,* 1980). The temporal parameters of TCR components correlate with the rate of the conduction along the fibre systems of the corpus callosum, the TCR amplitude serving as an index of the density of callosal afferents in each brain site, or the effectiveness of callosal connections (Purpura *et al.,* 1960; Grafstein, 1963; Mareš *et al.,* 1980).

Taking the above into account, let us consider first the temporal dynamics of interhemispheric asymmetry of homotopical transcallosal influences (Figure 27). Judging by the latencies of the positive and negative TCR components, transcallosal influences reached the visual, parietal, auditory, and motor cortical zones in the right hemisphere faster, along systems of fibres with the highest rates of conduction (Figure 27,I,a). In interval I (Figure 27,I,b) greater amplitudes of the negative component were noted on the right, those of the positive component, on the left, which may reflect the prevalence of excitatory processes in the right hemisphere, while inhibitory processes prevail in the left. Judging by the temporal parameters of the negative component, conduction was faster when directed towards the parietal cortical area in the right, and towards the auditory cortical area in the left hemisphere.

In interval II (Figure 27,II,a) the excitatory processes were already more strongly expressed in the left parietal cortical zone, those of inhibition, in the right hemisphere. Conduction of transcallosal influences acting on the negative component, was faster towards the left parietal cortex, that acting on the positive one, towards the right motor area. In interval III (Figure 27,II,b) excitation could prevail in both the left and right hemisphere: The visual cortical zone in the left hemisphere, and the auditory area in the right hemisphere dominated with respect to the amplitude of the negative component. At the same time, judging by the temporal parameters of the negative component, transcallosal influences reached the right hemisphere before they approached the left, in all recording zones under study except the auditory one.

And, finally, in interval IV (Figure 27,III), activation processes prevailed again over the whole area of the cortex of the right hemisphere for indices of the amplitude-time response parameters, and transcallosal influences were conducted faster to the right than to the left hemisphere, whereas processes of inhibition were more strongly expressed in the visual cortical zone of the left hemisphere, and in the auditory area of the right hemisphere cortex.

Thus, on the whole, the temporal dynamics of functional interhemispheric asymmetry of homotopical transcallosal influences was characterized by three consecutive phases of hemispheric dominance (Figure 27, the Roman figures). In addition, the pattern of

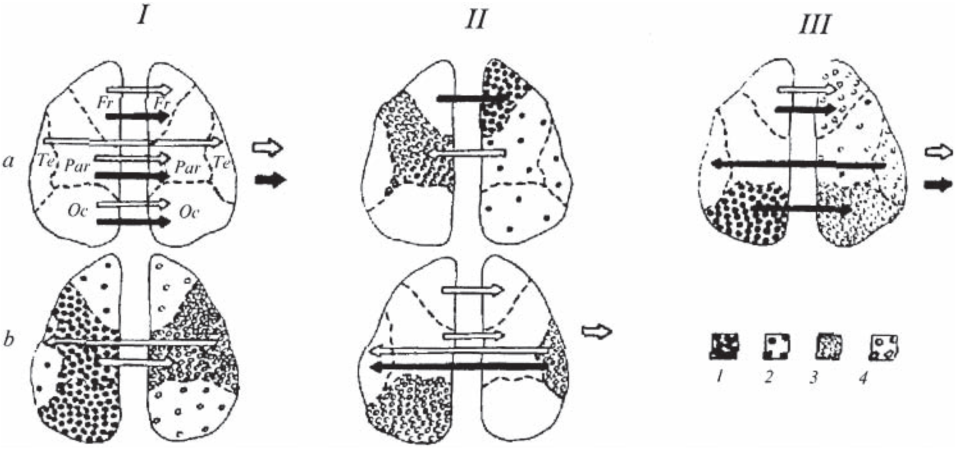

Figure 27: The pattern of dynamics of the interhemispheric asymmetry of homotopical transcallosal influences in the rat's neocortex in the process of TCR development. Schematized brain: to the left–the left hemisphere, to the right–the right hemisphere. **I**–**III**–phases of hemispheric dominance: **I,a**–with respect to the latency of the first component; **I,b**–with respect to the amplitude-time parameters of the first component peak, **II,a**–with respect to those of the second component peak, **II,b**–with respect to those of the third component peak, **III**–with respect to the fourth component peak. **Thin arrows** indicate the asymmetry of time parameters in the cortical zone under investigation, **thick arrows**–asymmetry for the whole recording area. Arrows pointing to the right indicate right hemisphere asymmetry, those pointing to the left indicate left hemisphere asymmetry. The **black arrows** indicate positive components, the **white arrows** indicate negative components. **1**–asymmetry of the amplitude parameters of the positive components of the cortical zones under investigation, **2**–of the whole recording zone, **3**–asymmetry of the amplitude of the negative components of the cortical zone under investigation. **4**–of the whole recording area. **Oc**–visual, **Par**–parietal, **Te**–auditory, **Fr**–motor cortex. The boundaries of zones are marked by broken lines.

asymmetry, as far as activation of transcallosal influences was concerned, developed according to the principle of right-left-right shift, the pattern of inhibitory influences following the opposite shift in the direction of asymmetry, namely left-right-left.

The above dynamics testify to the fact that the right hemisphere acts more diffusely, the left one, comparatively focally. Indeed, phases I and III of right hemisphere asymmetry, as regards activating influences, had a polyzonal origin, arising with the participation of the visual, auditory, parietal, and motor cortical zones. The same holds for the conduction time for transcallosal influences: It was shorter for the majority of the cortical zones investigated in the right hemisphere, compared to the left. A different picture was observed during the second, left hemisphere phase of asymmetry: Activating influences prevailed only in the parietal or visual cortical zones, and the time taken to conduct transcallosal influences into the auditory or parietal cortical zones in this hemisphere was shorter. The peculiarities revealed for the function of each hemisphere seem to be determined by the dynamics of inhibitory transcallosal influences. It should be noted that, in the literature, there are data showing a greater concentration and effectiveness of receptors binding GAB A in the cortex of the left hemisphere of rats as compared to the right (Guarneri *et al.,* 1988).

Thus, the above data allowed us to characterize the dynamics of interhemispheric asymmetry in processing transcallosal signals. First, a relatively diffuse evaluation of information takes place in the right hemisphere, bringing into action mainly the sensory cortical areas. Then, in the left hemisphere, which functions relatively focally, information processing is carried out with the association functions prevailing. After this, the right hemisphere starts working again, its function being relatively diffuse, and the sensory cortical areas are activated again. It may be supposed that, underlying the dominance of one hemisphere, and its inversion, are the mechanisms of the physiological dominanta (Bianki, 1989, 1993).

Now let us turn to consideration of sex differences in the dynamics of functional interhemispheric asymmetry of homotopical TCRs, in the processing of the transcallosal signal. First of all, let us compare the temporal dynamics of functional interhemispheric asymmetry of homotopical transcallosal influences in animals of different sexes.

Judging by the latency of the positive and negative components, it may be suggested that, in female rats, transcallosal excitation flows into most of the cortical sites investigated in the right hemisphere (Figure 28,B,1). In males, right-sided asymmetry occurs only as regards positive components, whereas left-sided asymmetry was registered in the auditory cortex for the negative component (Figure 28,A,1). In interval I, in males, the conduction time for transcallosal influences to most of the regions investigated in the right cortex was shorter, with respect to both TCR components (Figure 28,A,2). At the same time, in females, right hemisphere dominance was weaker, and was observed only for the negative components in the parietal and auditory cortices (Figure 28,B,2). In interval II, in both males and females, the asymmetry of both components varied in direction, depending on the recording zone (Figure 28,A,3; B,3). In interval III, judging by the latency for development, as far as the maximum of the positive component, in males, transcallosal influences reached most of the areas investigated earlier in the left hemisphere (Figure 28,A,4). At the same time, in females, conduction of transcallosal influences was faster towards the right hemisphere, judging by the negative TCR components (Figure 28,B,4). On the other hand, the direction of asymmetry of the negative component in males and the positive components in females varied, according to the recording area. In interval IV, in females, both components of transcallosal influences reached the right neocortex faster (Figure 28,B,5). In males, however, the direction of asymmetry over the whole recording area was summarily right-sided for its positive component, but left-sided for its negative one (Figure 28,A,5).

Using TCR amplitude parameters as an index of temporal dynamics of functional interhemispheric asymmetry in transcallosal influences, the results, in animals of different sexes were as follows: In interval I, judging by the amplitude of the negative component, activation processes prevailed over the greater cortical area in the right hemisphere in females, and mainly in the auditory cortex of this hemisphere in males (Figure 28,A,2; B,2). At the same time, judging by the amplitude of the positive component, inhibitory processes were more strongly expressed in the left hemisphere of females, compared to males. Thus, in females, left-sided asymmetry was observed in both parietal and visual zones, whereas in males it was the case only in the parietal region. Alongside this, in the visual cortical area, an opposite right-sided asymmetry was observed in males. In interval III, activation processes in males were shifted from the left into the right hemisphere (Figure 28,A,4). In females, excitation prevailed in the visual and motor zones of the left hemisphere (Figure 28,B,4). And finally, in interval IV, in females, activation was again more strongly expressed over a greater area in the right hemisphere cortex, whereas depression prevailed in the visual cortex of the left hemisphere (Figure 28,B,5). At the

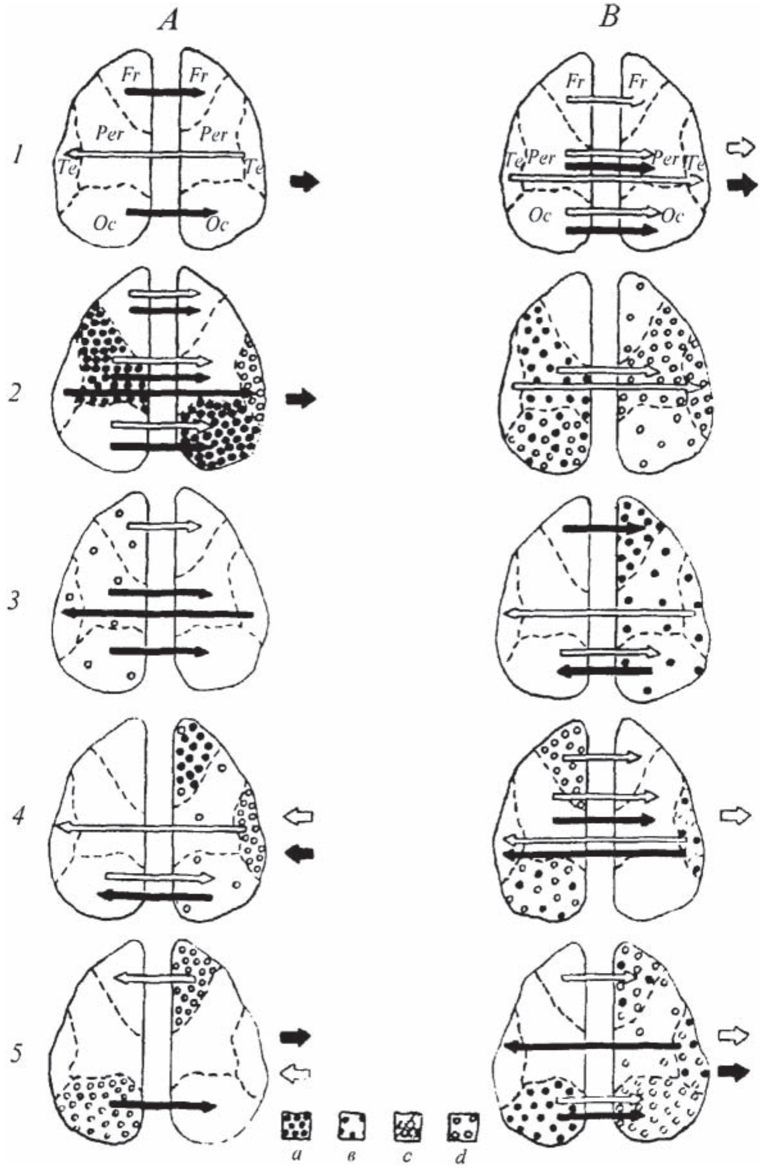

Figure 28: Comparative characteristic of the dynamics of interhemispheric asymmetry of transcallosal influences in different cortical zones of both hemispheres in male **(A)** and female **(B)** rats in the process of TCR development. **1–5**–phases of hemisphere dominance, 1–with respect to the latency of the first component, 2–with respect to the amplitude-time parameters of the first component peak, 3–those of the second component peak, 4–those of the third component peak, 5–those of the fourth component peak, **a**–hemispheric dominance for the amplitude parameters of the positive components in the zone under investigation, **b**–over the whole recording territory, **c**–for the negative components in the zone under investigation, **d**–over the whole recording territory. **Thin arrows** indicate the asymmetry of time parameters of the cortical zone under investigation, **thick arrows**– asymmetry for the whole recording area. Arrows pointing to the right indicate right hemisphere asymmetry, those pointing to the left indicate left hemisphere asymmetry. The **black arrows** indicate positive components, the **white arrows** indicate negative components. **Oc**–visual, **Par**–parietal, **Te**–auditory, **Fr**–motor cortex. The boundaries of zones are marked by broken lines.

same time, in males, the activation level was higher in the motor cortex of the right hemisphere and in the visual cortical area of the left hemisphere (Figure 28,A,5).

Thus, the general regularity of the above dynamics of the asymmetry of transcallosal influences could be manifest by the same regional pattern, and a unidirectional character of asymmetry in animals of different sexes, all the changes in asymmetry being of one type. For instance, functional interhemispheric asymmetry of the temporal parameters of the positive components, and the amplitude parameters of the negative ones, in animals of both sexes corresponded to the rule of the right-left-right shift.

It should be emphasized that sex differences in functional interhemispheric asymmetry were manifest by its zonal specificity, or in the opposite direction of asymmetry in the time periods analysed. Changes in asymmetry between individuals of different sexes could be characterized by the approximately mirror-image patterns of hemispheric dominance. Thus, for instance, functional interhemispheric asymmetry of the temporal parameters of the negative TCR components are referred to as the right-left-right shift in females, and the left-right-left shift in males. Opposite sequences of asymmetry were also observed in animals of different sexes with respect to measures of the duration of transcallosal influence on visual, auditory, and motor cortices, and with respect to the magnitude of callosal influences in the visual and motor neocortical zones.

On the whole, the specificity of the temporal dynamics of asymmetry of transcallosal influence revealed in males and females may be supposed to be determined by the existing differences in transcallosal information processing in animals of different sexes. The right hemisphere in females may function more diffusely than in males, at least at the initial and final stages of transcallosal signal processing. Thus, the right hemisphere of females receives relatively stronger transcallosal activating influences in most cortical zones investigated, in intervals I, IV (Figure 28,B,2; B,5). In principle, the same also holds for their conduction latency. A different picture could be observed only at the intermediate stages of transcallosal information processing, so that, in a number of cases, right-sided asymmetry in males appeared to be more strongly expressed than in females. In addition, left hemisphere dominance was found over a relatively greater area of the cortical zones investigated in males, compared to females (Figure 28, A,1,4,5).

Thus, general and sex-specific characteristics of the dynamics of interhemispheric TCR asymmetry were described above. In males, for some indices, a left-right-left shift is revealed, whereas in females a right-left-right shift of hemispheric dominance is found. The data obtained testify to the fact that in males, compared to females, the left hemisphere takes a relatively greater part in processing the transcallosal signal, whereas in females it is the right hemisphere. Moreover, the male brain seems to work more focally, while the female brain appears to be relatively more diffuse.

Now let us focus on the more detailed characteristic of the single hemispheres in male and female rats when processing the transcallosal signal. As a result of the summated analysis of the temporal parameters of TCRs, sex differences were found in the conduction time for transcallosal influences mediated by the positive and negative components in the left hemisphere. Thus, the latency of positive and negative TCR components I, II and IV and negative components I, II, III differed considerably in the left hemisphere in animals of different sexes. Moreover, in the right hemisphere, sex differences in the temporal parameters of the positive components were found only in interval IV, those in negative ones, only in intervals I, II and IV. These sex differences were characterized by a certain dynamics, depending on the time interval analysed. The latencies of responses, beginning both with positive and negative components, are significantly shorter in males than in females. In a similar way, the latencies of the maxima of positive component III and negative components I, III were shorter in males, compared to females. However the opposite correlation of the time parameters in individuals of different sexes were observed in intervals I, IV for the positive components and II, IV for the negative ones.

Let us consider the regional specificity of sex differences in the temporal parameters of TCRs in the two hemispheres. It can be seen that, in the left hemisphere, sex differences in the average values of the temporal parameters of positive components of TCRs were, as a rule, revealed in the parietal, auditory, and frontal cortical zones (Figure 29,A), the negative ones in the frontal and auditory areas (Figure 29,B). They were observed much more rarely in the visual cortex of this hemisphere. At the same time, in the right hemisphere, sex differences for both TCR components occurred frequently in the auditory cortex, more rarely in the visual and motor, and most rarely, in the parietal cortex (Figure 29,A,B). In the time intervals studied, conduction of transcallosal influences into the deep layers of the above cortical zones in the right hemisphere and into the surface zones of the left one is usually faster in males than in females, judging by the temporal parameters of the positive and negative TCR components respectively. However, the conduction time of transcallosal influence into the deep cortical layers of the left hemisphere, and the superficial layers of the right one during the time intervals analysed could be shorter either in males or in females, with equal probability.

Proportions between the cortical areas are characterized by equally large values for the temporal parameters of TCR components in males and females in the two hemispheres (Figure 29). It can be seen that in females, larger values of temporal parameters for both positive and negative TCR components were recorded over a comparatively greater cortical area than in males. In this case, sex differences were revealed in a somewhat greater recording area in the left than in the right hemisphere, in the interval corresponding to the latency of both components (Figure 29, A, 1), and in intervals I, II, with respect to the positive components (Figure 29, A,2,3). At the same time, sex differences in the negative components were found over a comparatively greater recording area in the right hemisphere than in the left, in intervals I-III (Figure 29, 2–5)

Thus, the above data indicate the specificity of functional organization of homotopical callosal neocortical connections in the left and right hemispheres in individuals of different sexes. In treating the results obtained, we adhered to the view that the temporal parameters of positive and negative TCR components correlate with the rate of conduction of excitation via fibres of the corpus callosum afferent to the deep and surface cortical zones respectively (Grafstein, 1963; Mares *et al.,* 1980). Transcallosal influences arriving via the system of the corpus callosum fibres with the greatest rates of conduction (judging by latency I of the positive and negative TCR components) appeared to influence a greater part of the area of all the left hemisphere cortex investigated in males than in females. On the contrary, in the right hemisphere, the corresponding sex differences are not observed. A greater expression of sex differences in the left, as compared to the right hemisphere was also observed for the temporal parameters of the positive TCR components. However, for the negative TCR components, sex differences in the temporal parameters could be more distinct in the right than in the left hemisphere. Conduction of transcallosal influences into the deep layers of the right and the superficial layers of the left hemisphere was found to be faster in males than in females.

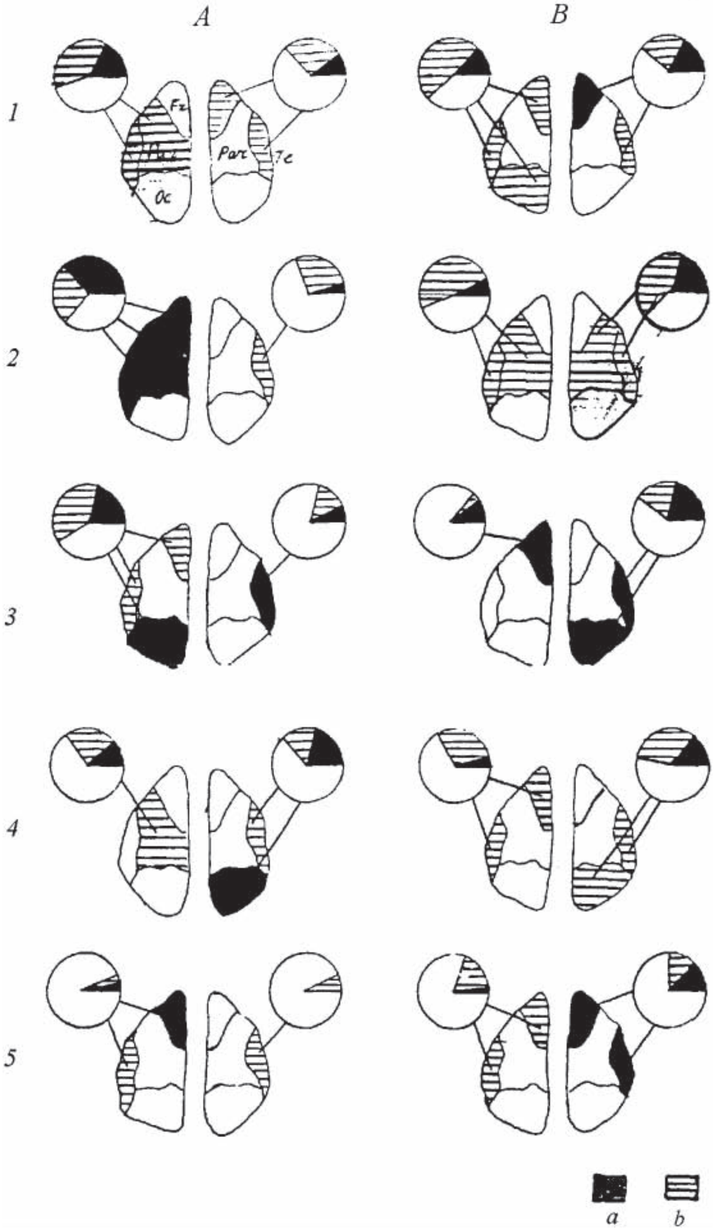

Figure 29: Sex differences in the temporal parameters of homotopical TCR components in different cortical zones in the rat's left and right hemisphere. **A**–positive TCR components, **B**–negative TCR components. The left hemisphere is on the left. The right one is on the right. **1**–the latency (conduction time) of the 1st TCR component, **2**–latency of the maximum of the 1st component, **3**–latency the maximum of the IInd component, **4**–latency of the maximum of the IIIrd component, **5**–latency of the maximum of the IVth component. In the schemes of the brain: **Fr**–frontal, **Par**–parietal, **Te**–auditory, **Oc**–visual cortical zone; **a**–higher mean values of the conduction rate parameters in females, b–in males. In the **circular diagrams**: **a**–the cortical territory in which the time TCR latency parameters are considerably greater in males, **b** in females.

It would be reasonable to compare the above evidence for the existence of sexual dimorphism in functional homotopical transcallosal connections with data in the published literature on anatomic and ultrastructural peculiarities of the corpus callosum structure in rats (Berrebi *et al.,* 1988; Juraska and Kopcik, 1988). Thus, differences in the area of a cross-section of the corpus callosum were found in rats of different sexes, most distinctly in the rostral parts connecting the frontal neocortical regions, and also in the occipital parts, probably connecting the visual and auditory cortical zones (Berrebi *et al.,* 1988). The areas of the cross-sections of this commissure at different rostro-caudal levels were significantly greater in males than in females. The differences may be determined by a relatively greater percentage of myelinated axons and of fine, nonmyelinated fibres contained in the corpus callosum in males than in females (Juraska and Kopcik, 1988). Consequently, faster operation of the male as compared to the female brain for a number of temporal parameters of TCRs may be determined, at least partially, by the above morphological peculiarities.

Taking into account the relatively more diffuse character of right hemisphere function and the comparatively focal left hemisphere activity (Bianki, 1989; 1993), it seems reasonable to consider some interzonal differences in the functional organization of callosal connections with respect to the indices of temporal parameters of TCRs in males and females. From the data obtained it was apparent that, from the interzonal differences between the temporal parameters of positive and negative TCR components in males, regional specificity is more distinct in the right hemisphere. The essential point is that, on the whole, sex differences in the functional organization of callosal connections in both hemispheres consisted of their having comparatively greater zonal specificity in males compared to females (in the left hemisphere for the negative TCR components, in the right for positive TCR components). Thus, the male brain seems to be more specialized than the female brain. The greater specialization of the male brain is maintained by both hemispheres, or, to be more exact, specialization of the left hemisphere may be maintained by the superficial cortical layers, that of the right hemisphere, by its deep layers. It should be emphasized that there are also facts suggesting that the male brain is more specialized not only for quantitative but also for qualitative indices.

On the basis of corresponding calculations it was found that in males the latency for interaction between the visual cortex and the auditory zone differed from that between the visual cortex and the parietal zone, and also differed from the latency of its interaction with the motor zone. It also differed from the latency of interaction between the parietal and the motor zones. In females, the latency of the auditory zone interaction with the parietal one differed from that of its interaction with the motor zone.

To conclude, let us focus on the sex peculiarities of the amplitude parameters of positive and negative homotopical TCR components. Analysis of the summary amplitude parameters recorded in the visual, auditory, parietal, and motor neocortical zones suggests that the amplitude of the positive components are greater in males than in females in the left hemisphere in intervals II and III. At the same time, the negative components were marked by greater sex differences in the right hemisphere. In intervals II and IV, the average values of the amplitude of the negative TCR components were higher in females, those in interval III, in males.

After investigating the zonal peculiarities of sex differences in the homotopical TCR parameters in both hemispheres, it was established that the greater size of the amplitude parameters of the positive component in the left hemisphere in males, compared to females is mainly determined by the parietal and frontal cortical areas (Figure 30,A). Alongside this, in females, the amplitudes of the positive components in this hemisphere surpassed those in males in the auditory and visual zones. At the same time, a greater amplitude of the negative components could be observed in each of the right cortical zones studied in females, compared to males, in intervals II and IV. In interval III, however, the amplitude of the negative component was higher in males compared to females. In addition, the amplitude of positive and negative components, characterized by greater magnitudes in females than in males, were also recorded simultaneously in relatively greater recording areas (Figure 30, diagrams). The inverse proportions of the amplitude parameters in animals of different sexes were recorded only in the left hemisphere for the 1st negative component, in the right one, for the 1st positive and the IIIrd negative components (Fig. 30,A,1; B,1,3). Sex differences were found over a comparatively greater recording area in the left hemisphere for the positive component in intervals I and II and over comparatively greater areas in the right hemisphere in intervals I, II, V, for the negative potential components.

Taking into account the fact that the amplitudes of positive and negative TCR components recorded from the cortical surface reflect the effectiveness of depressing or activating callosal influences respectively, the following can be suggested. Judging by the amplitudes of positive TCR components, the processes of inhibition in the superficial cortical layers of the left hemisphere (mainly in the parietal and frontal zones) are more strongly expressed in males than in females. Alongside this, in the right hemisphere, more powerful processes of activation are observed in females, compared to males, in all cortical areas investigated. In addition, in males, the areas to which depressing transcallosal influences spread appeared also to be greater on the surface of the left hemisphere, while in females the sites of activating callosal influences in the cortical layers were greater in the right hemisphere. Consequently, greater development in males (compared to females) of inhibitory processes in the cortical layers of the left hemisphere may be one of the causes determining a comparatively high level of the specialization of this hemisphere in males. On the other hand, the female right hemisphere, provided with comparatively more highly-developed callosal activating influences than in the male, seems to be characterized by relatively lesser specialization. The results obtained agree with the concept of a more focal character of the left hemisphere cortex, and a more diffuse character of right hemisphere activity.

Let us summarize the studies on the dynamics of transcallosal signal processing in male and female rats. The dynamics of hemispheric dominance in males and females are, to a certain degree, the opposite of one another. During transcallosal signal processing, a left-right-left shift may occur in males, whereas in females a right-left-right shift is observed. The male brain works more dynamically than that of females. Males are noted for a greater conduction velocity of transcallosal excitation, which is characteristic of excitation flowing into the surface layers of the left hemisphere, and into the deep layers of the right hemisphere, as compared to females. During the processing of the transcallosal signal in males, the left hemisphere plays a relatively greater role, whereas in females it is the right hemisphere. The male brain is more specialized than that of females. The advantage of brain specialization in males is determined mainly by the function of the

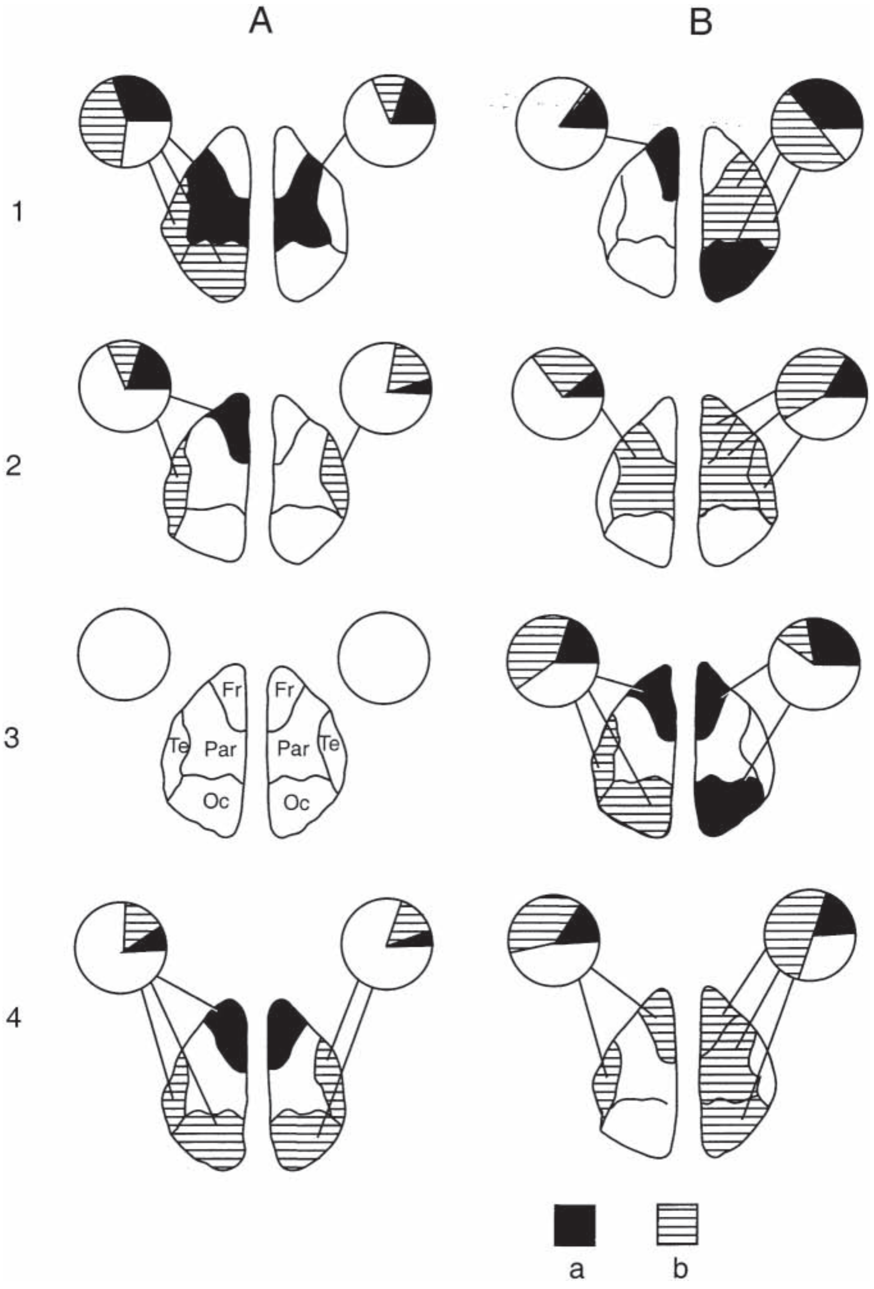

Figure 30: Sex differences of the amplitude parameters of the homotopical TCR components in different zones of the right and the left hemisphere in rats. **A**-positive TCR components, **B**-negative TCR components **1**–the maximum amplitude of the 1st TCR component, **2**–that of the IInd component, **3**–that of the IIIrd component, **4**–that of the IVth component; **a**–prevalence of the mean values of the corresponding amplitude parameters in males, **b** in females. Schematized brains: **Fr**–frontal, **Par**–parietal, **Te**–auditory, **Oc**–visual cortical zone; **a**–the prevalence of the mean values of the corresponding parameters in females, **b**–in males. In the **circular diagrams: a**–the cortical territory in which the TCR latency parameters are considerably greater in males, **b**–in females.

surface layers of the left hemisphere, and by the deep cortical layers of the right hemisphere. The processes of inhibition appear to be more strongly expressed in the left hemisphere of males, those of excitation, in the right hemisphere of females. These peculiarities seem to determine a relatively focal character of brain function in males, and a comparatively diffuse action of the female brain.

Thus, the relatively greater specialization of the male brain, compared to the female one, is maintained mainly by the specialization of their left hemisphere, a greater rate of conduction of transcallosal excitation into the left hemisphere, and stronger processes of inhibition in the cortex of the left hemisphere.

3.5. PATTERNS OF ASYMMETRY

Mosaicism, or partialness, is one of the main properties of functional interhemispheric asymmetry (Bianki, 1989, 1993). In the dominant hemisphere, greater areas of direct dominance are always interspersed with relatively small island-like zones of inverse dominance, i.e. sites in which the opposite hemisphere dominates. In addition to this, unidirectional asymmetry is expressed differently at different cortical points. Below, the patterns of interhemispheric asymmetry of homotopical TCRs will be considered in greater detail. In this case, in contrast to most of the above experiments, not only was quantitative dominance of positive-negative potentials taken into account, but also that of negative-positive potentials. Special attention was paid to distinguishing the sex specificity of *patterns* of interhemispheric asymmetry (Bianki *et al.,* 1991, 1993).

The experiments were performed on lightly anaesthesized cats, under the conditions of polyzonal TCR recording. Homotopical TCRs in one animal were successively recorded, first from parietal fields 5 and 7, and visual fields 17, 18, 19 in the left hemisphere cortex, then from the auditory area (fields AI, AII, EP) in the left hemisphere, from the visual and parietal areas of the right hemisphere, from the somatosensory (SI) and sensorimotor (fields 4 and 6) areas in the right hemisphere cortex, and, finally, from areas SI and MI in the left hemisphere. One half of the experiments was carried out with such a randomly chosen, but consistantly-used sequence of stimulation and recording homotopical TCRs, the other half, with the opposite sequence.

As mentioned above, in addition to positive-negative TCRs, negative-positive ones were also recorded. Transcallosal potentials with initial negativity were described in earlier studies (Chang, 1953). Their genesis was initially associated with the physical spread of the electric current via cortical structures (Chang, 1953; Grafstein, 1959), and therefore was not analysed. However, later, TCRs with an initial negative component were consistently seen in the auditory cortex of dogs (Gmyria and Vasechko, 1971), in the rat cingulate gyrus (Jones and Powell, 1968), and in the cat sensorimotor and parietal cortices (Bianki *et al.,* 1988, 1989). Comparative analysis of positive-negative and negative-positive TCRs, recorded layer-by-layer in the MI zone, suggested that negative-positive responses arise in those cortical points where deep layer activitation is comparatively weak. Indeed, in the sensorimotor cortex, callosal terminals possess maximum density in the deep layers of Field 4, and in the more superficial layers of Field 6 (Marsala and Luttenberg, 1962). Opposite patterns of TCRs in MI were accounted for earlier in terms of such a structure of the callosal system in the sensorimotor cortex (Shramm, 1980a,b). Admittedly, the terminals of positive-negative transcallosal fibres are also known to be localized mainly in the surface cortical layers (Otellin and Meshkenaite, 1984), and it is only with certain caution that the appearance of TCRs of different types can be associated with the structural peculiarities of callosal projections in different cortical areas. Nevertheless, it seems probable that TCR configuration also reflects the functional peculiarities of the callosal stream, though it certainly depends on the structure of interhemispheric connections.

First of all, let us point to some sex peculiarities of homotopical positive-negative TCRs. The average coefficients of asymmetry for each hemisphere as a whole were calculated by means of the formula: K=(A-B)/(A+B), where A was the corresponding index in the right, B, in the left hemisphere. For males, the coefficient was negative (equal to -0.03, indicating left hemisphere asymmetry) for both TCR phases, while for females the coefficient of was positive (equal to +0.005 for the, positive and +0.03 for the negative TCR component), indicating right hemisphere asymmetry. Hence two conclusions follow. First, in females, the right hemisphere dominates on the whole, in males, the left hemisphere. Second, the magnitude of interhemispheric asymmetry in females appears to be lower, approximately by an order of magnitude, than that in males (at least for the positive TCR component). What is the relative abundance of the transcallosal potentials of the two types in animals of different sexes? Positive-negative TCRs appeared to prevail in all individuals. In males, the number of positive-negative TCRs was twice as many as in females, and three times as many as that of the negative-positive ones in males.

The study of the temporal and amplitude parameters of negative and positive TCRs also revealed their sex specificity. The latencies of positive-negative transcallosal potentials were longer, and also the amplitudes of their components were larger than the corresponding parameters of negative-positive TCRs, by two fold or more. The amplitudes of positive-negative TCRs in the primary projection cortical areas were smaller than in the association areas, while, among the primary projection zones, minimal values of the amplitude parameters were found in the auditory cortical fields. Such differences were not typical of negative-positive responses, and in all the cortical sites studied, the amplitudes of negative-positive potentials were approximately equal. It should be emphasized that the amplitude characteristics of positive-negative TCRs were, as a rule, greater in females than in males, except in the sensorimotor cortical area, where the proportion of the amplitudes of TCRs of this type, in males and females was the opposite.

When the spatial FMAs of TCRs with opposite phases were considered in different cytoarchitectonic areas, the FMAs of the positive-negative and negative-positive responses appeared never to coincide. On the contrary, they were localized in different sites of the zones. The focus of positive-negative TCRs was, as a rule, registered in the sites immediately adjoining the sagittal sinus, or in medial sites of the areas under investigation. At the same time, the focus of negative-positive TCRs was observed in more lateral sites of the given zone. For instance, in the parietal cortex, the FMA of the positive-negative TCRs was localized in Field 5, that of negative-positive ones, in Field 7 in the suprasylvian gyrus.

In maps of the FMA of TCRs with opposite phases, attention is drawn (in relation to localization in animals of different sexes–Figure 31), to the fact that, in males, in all the

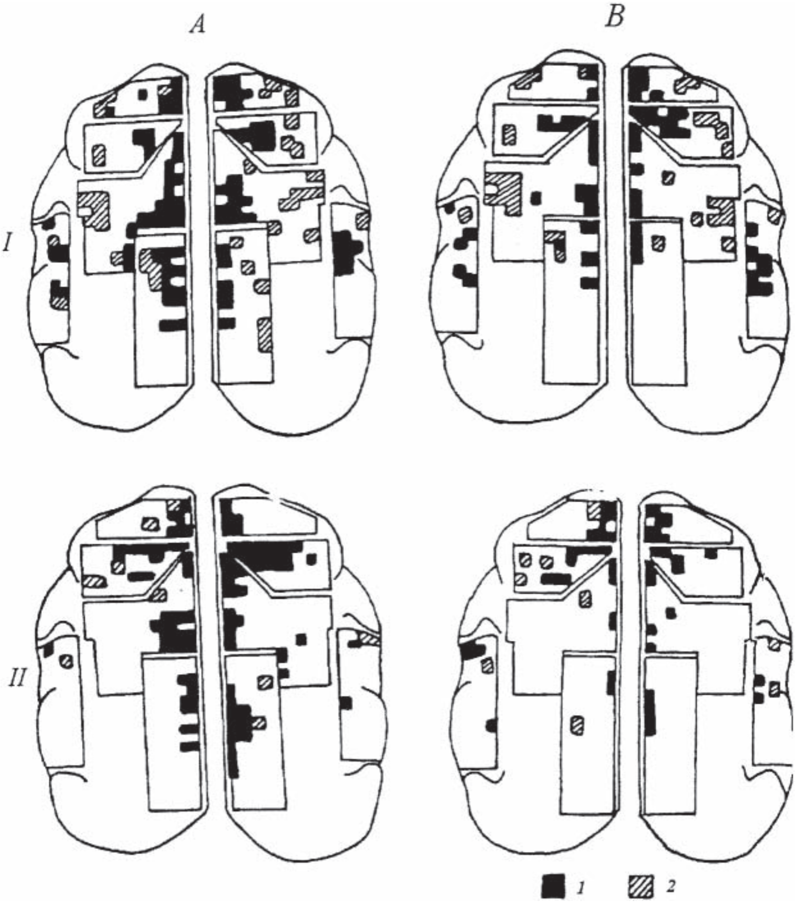

Figure 31: Topography of the maximum activity foci of TCRs of opposite phase in animals of different sexes. **I**–topography of maximum activity foci in males, **II**–in females. **A**–positive, **B**–negative TCR component. **1**–foci of positive-negative TCRs, **2**–foci of negative-positive TCRs. The left hemisphere is to the left, the right one is to the right. In the schemes of the brain:

cortical areas investigated, the FMAs of negative-positive TCRs were localized in both hemispheres, were relatively more fragmented, and had an area comparable with that for positive-negative TCRs. At the same time, in females, in most cases, the foci of negative-positive TCRs were localized only in one hemisphere, and were comparatively small.

In each cortical area investigated, the FMAs of positive-negative TCRs were more-or-less surrounded or, more commonly, supplemented by foci of negative-positive responses (Figure 31). A similar picture–positive-negative TCRs in the centre, surrounded by peripheral sites with opposite phases–was also revealed when the whole hemisphere was considered. An impression thus arises that the main stream of transcallosal impulses, represented by high-amplitude positive-negative responses, and localized in the area of the maximal accumulation of homotopical callosal connections is, as it were, emphasized, "singled out", and contrasted by means of low amplitude negative-positive potentials with opposite phases. In one of the earlier studies, arguments were presented in favour of the idea that, during transcallosal stimulation, a focus of increased excitability is formed in the cats' sensorimotor cortex, which possesses dominant properties (Bianki, 1979a). The opposite-phase "surrounds" of such a focus must be conducive to its being "singled out".

Of special interest is the different timing in the formation of opposite-phase TCRs. The earlier appearance of negative-positive potentials may be taken as evidence that the transcallosal activation of the cortical sites surrounding the focus "pretunes" or "primes" the dominant centre (focus). The different timing of these complementary transcallosal streams seems to promote a fuller involvement of focal structures in processing of the transcallosal signal. It should also be noted that the main stream (the central one, represented by positive-negative TCRs) and the supplementary stream (the peripheral one, mediated by negative-positive TCRs) of transcallosal impulses are always in counter-phase: Formation of the negative phase of negative-positive TCRs has a delay matched by the formation of the positive component of positive-negative TCRs. However, the second phase of positive-negative TCRs lags somewhat behind the positive component of negative-positive responses. Assume that the positive and negative EP components reflect inhibitory and excitatory processes developing at different cortical levels. Then, probably, under the influence of the transcallosal stream in the receiving hemisphere, an excited periphery is formed first, which surrounds an inhibited centre, and next, in contrast, the excited centre appears, surrounded by an inhibited periphery. As mentioned above, in females, negative-positive TCRs occur less frequently than in males. Consequently, the brain cortex of males functions with higher contrast than that of females.

Now let us touch upon the asymmetry of positive-negative and negative-positive TCRs, and its manifestation in animals of different sexes. Both negative-positive and positive-negative TCRs were characterized by functional interhemispheric asymmetry (Figure 31). Without dwelling on all the details, the most important characteristics of the asymmetry of negative-positive TCRs should be noted. First of all, there is a weaker expression of the interhemispheric asymmetry of negative-positive EPs, compared to positive-negative ones. In particular, a smaller number of asymmetric individuals was recorded in the visual and somatosensory cortical areas for the negative component, and in the parietal area for the positive one. This could even amount to the absence of asymmetry. In those cases where interhemispheric asymmetry was significant, it was revealed in a smaller number of animals than asymmetry for positive-negative TCRs. When analysing the direction of single-hemisphere dominance, only individual asymmetry was observed, indicating weaker expression of asymmetry for negative-positive TCRs. The weakest asymmetry of transcallosal activity was observed in the association (parietal and sensorimotor) cortical areas.

Attention is also drawn to the effect of the opposite direction of hemispheric dominance of negative-positive TCRs, compared to positive-negative ones, in single cortical areas. Thus, during analysis of the averaged amplitude characteristics, negative-positive TCRs were shown to dominate in the right visual cortex, while positive-negative ones dominated in the left visual cortex. In the auditory fields, on the contrary, positive-negative responses prevailed in the left, negative-positive ones in the right hemisphere. Earlier, a similar opposition of the directions of the asymmetry of opposite-phase patterns of potentials was shown for interzonal heterotopical TCRs in the association cortex. It may be supposed that transcallosal streams of excitation addressed to the visual and auditory cortices are thereby contrasted, and isolated. It may also be possible that, by means of this process, the output characteristics of streams of excitation are contrasted when they become afferent signals for processing in association structures.

Finally, the peculiarities of asymmetry of positive-negative and negative-positive TCR associated with the animal's sex, should be observed. They are manifested in right hemisphere dominance with respect to the magnitude of the positive component of negative-positive TCRs in males, and left hemisphere dominance for the negative component in females in Area S1. They are also shown in the larger amplitude of the negative phase of negative-positive TCRs in the left hemisphere in males, and in the right in females, shown for the auditory cortex. The dominance of parietal TCRs with an initial negative component was established in the right hemisphere in males, but in the left one in females. In this case, in the parietal cortex of males, positive-negative TCRs possessed a greater amplitude in the left, negative-positive ones in the right hemisphere. In females, on the contrary, high amplitude positive-negative TCRs were recorded in the right hemisphere, negative-positive TCRs, in the left one. These data point to the possibility of the existence of functional interhemispheric asymmetry in different directions in animals of different sexes.

The main thing to point out, when considering sex differences of the localization of the FMAs of positive-negative and negative-positive TCRs, consists in a sharper interhemispheric contrast in males compared to females. In the cortex of both cerebral hemispheres, in males, TCRs of opposite phases (positive-negative and negative-positive) are recorded, and become adjacent more frequently in males than in females (Figure 31).

To conclude, let us dwell upon the comparison of the direction of lateralization in the functional interhemispheric asymmetry of positive-negative and negative-positive TCRs, in pairs of different cortical zones in each animal studied. The first conclusion to be drawn, on the basis of analysis of the corresponding averaged schemes (Figure 32), is that, for positive-negative TCRs, differences in the direction of asymmetry are more typical of males, while in females, a uniform direction is more typical (Figure 32, II, III, A, B). In this case, in males, asymmetry in different directions is created mainly between visual and auditory, auditory and somatosensory, visual and sensorimotor, somatosensory and parietal, sensorimotor and parietal cortical zones. In females unidirectional asymmetry was found between visual and parietal, somatosensory and sensorimotor zones. The second conclusion is that for negative-positive TCRs, males are, on the contrary, characterized only by unidirectional asymmetry (somatosensory and sensorimotor, visual and parietal, and also auditory and parietal zones (Figure 32, II, III, C, D). Consequently, in both types of TCR, differences in the direction of asymmetry in males are preserved between somatosensory and parietal, and also visual and auditory zones, while unidirectional asymmetry occurs between somatosensory and sensorimotor cortical zones.

Taking into account the fact that positive-negative TCRs occur much more frequently than negative-positive ones, and that functional interhemispheric asymmetry of positive-negative TCRs was much more strongly expressed than that of negative-positive ones, it can be concluded that the brain cortex in males is functionally more differentiated and constrasted than that in females. This seems to be one of the sex peculiarities of the mosaicism of functional interhemispheric asymmetry.

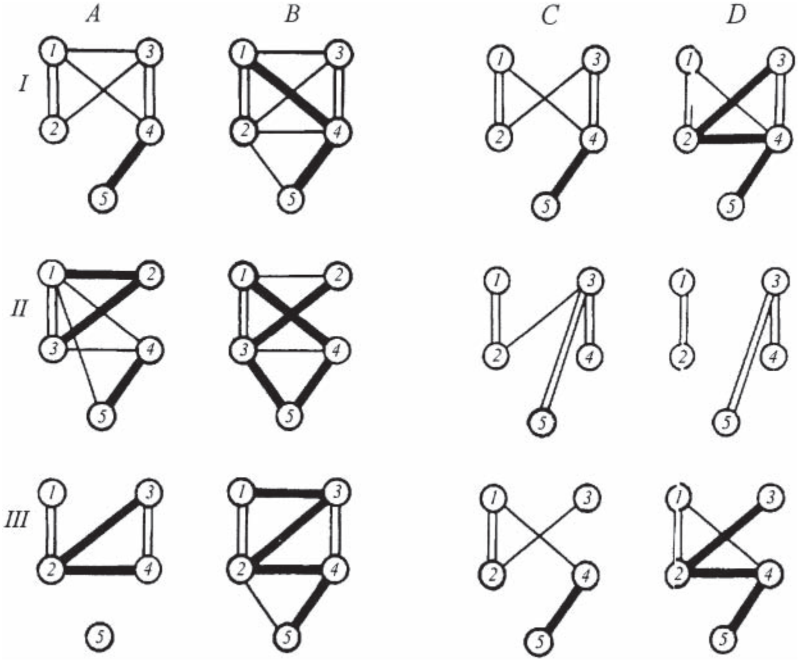

Figure 32: The interaction of the maximum activity foci of the positive-negative and negative-positive TCRs in the association and projection cortical zones. **A, B**–positive-negative TCRs; **C, D**–negative-positive TCRs; **A, C**–positive, **B, D**–negative TCR component. **I**–the whole sample, **II**–females, **III**–males. **1**–sensorimotor, **2**–somatosensory, **3**–parietal, **4**–visual, **5**–auditory cortical zone. The **light lines** indicate unidirectional asymmetry, the **black lines** indicate asymmetry in different directions. The thicker the black lines, the greater the magnitude of asymmetry. The absence of lines between the zones designates the independence of asymmetry formation. $p<0.05$.

The final remark concerns the validity of using a mixed sample to evaluate the patterns of functional interhemispheric asymmetry which really exist. Let us compare the schemes constructed on the basis of studying a mixed sample (Figure 32, I, A-D) with those reflecting the correlations between zones in males and females considered separately (Figure 32, II, III, A-D). Some connections seem to have been contributed to the common schemes by males (4–5, 1–4, 3–4). Other connections characterize both males and females, but they are fewer (1–2, 4–5). However, attention should be drawn to the fact that none of the common schemes can be observed in any mixed sample.

To sum up, functional interhemispheric asymmetry is, as a rule, expressed more strongly in males than in females. However, in animals of different sexes, asymmetry can have not only quantitative but also qualitative differences. In individuals of different sexes it may exhibit different directions, and be formed in different cortical layers (in males, mainly in the surface ones, in females, mainly in the deep ones).

Another conclusion to be drawn from the above facts, which characterizes one of the most important properties of functional interhemispheric asymmetry, is its mosaicism, as follows: Each cerebral hemisphere of males is more differentiated, more specialized, and is functionally more focal than that of females. A more structured nature of the male brain, compared to that of the female one, is manifested, first, in the prevalence in them of differences in the direction of functional connections between different cortical zones and, second, in the presence of a greater number of contrasts in transcallosal potentials.

3.6. PENETRANCE AND EXPRESSION

Usually such terms as "more–less", "more frequently–more rarely", "right-sided–left-sided" etc., are used to compare functional interhemispheric asymmetry in individuals of different sexes. However, this is insufficient, and new comparative characteristics are necessary. In search of these, we fixed our attention on the quantitative indices of phenotypical changeability, which are quite widely used in genetics, i.e. on penetrance and expression (Timofeev-Resovsky and Ivanov, 1966). Penetrance is usually understood as the percentage of individuals distinguished by a given character (out of the general number of individuals), expression being the percentage of individuals in whom the character under discussion is *strongly* expressed, as compared to all individuals in which this character is revealed.

Experiments were performed on lightly anaesthesized cats (Bianki *et al.,* 1991b). Total homotopical TCR recording was performed from the dorsolateral surface of the visual, parietal, auditory, somatosensory, and sensorimotor cortical areas. It should be specially emphasized that only individual asymmetry was studied, i.e. its sign (direction) was not taken into account.

3.6.1. Penetrance of Interhemispheric Asymmetry

In the case of positive-negative TCRs, in all zones, asymmetry was found more frequently in males than in females (Table 18), i.e. penetrance of asymmetry was higher in males. In particular, in the auditory cortex, asymmetry was observed in 100% of the cases in males, and in only in 63% in females. For the negative component, in area SI, asymmetry occurred in 95% of males and in 63% of females. For the negative-positive TCRs asymmetry also occurred more frequently in males. Thus, during the investigation of the auditory cortex, 100% of males but only 53–58% of females appeared to be asymmetric. In studying other cortical zones, a tendency for higher penetrance in males was also observed.

A more frequent appearance of asymmetry among males was observed both for the temporal parameters of TCRs (Table 18) and for the amplitude of responses. The ratio of males to females with asymmetry of positive-negative TCRs in the somatosensory and auditory cortices was 100:63 and 100:79 respectively. Asymmetric males were also found more frequently for measures of the latency of TCR phases in SI.

It should also be noted that penetrance of asymmetry in males was higher for measures of positive-negative responses than for those of negative-positive TCRs (Table 18). For instance, in the somatosensory cortex, during the appearance of positive-negative TCRs, asymmetry for the negative component was observed in 95% of the males, for the negative-positive EPs, in 58%. In the visual area, asymmetry of positive-negative TCRs was also recorded in 95% of the cases, and that of negative-positive ones in only 63%. In females, no such differences were observed in the frequency of appearance of asymmetric individuals between TCRs of opposite phases. Comparing between the number of individuals with left or right hemispheric dominance, asymmetric individuals prevailed significantly in

Table 18. The number of asymmetrical individuals, as a percentage of the general number of the individuals of the given sex investigated for different cortical areas

Parameter	*Somatosensory*		*Visual*		*Auditory*		*Sensorimotor*		*Parietal*	
	males	*females*	*males*	*females*	*males*	*females*	*males*	*females*	*males*	*females*
I: LP TCR	100	63	95	68	100*	79	100	84	100	89
Amplitude of the										
positive phase	79	63	95	84	100*	63	79	79	100	89
negative phase	95*	63	95	89	100*	69	79	74	84	84
Latency of the peak of the										
positive phase	100	58	100	84	89	79	74	74	100	84
negative phase	95*	63	89	84	95	84	79	68	100	84
II: LP TCR	93*	47	79	68	100*	79	79	69	79	74
Amplitude of the										
negative phase	58	50	63	63	100*	58	100	93	79	68
positive phase	68	50	68	68	100*	53	74	80	63	58
Latency of the peak of the										
negative phase	79*	53	79	68	100*	79	84	61	74	68
positive phase	79*	37	74	63	89	79	74*	38	79	79

Note: The asterisks mark the significant predominance ($p<0.05$) of asymmetrical individuals among males compared to females. I–positive-negative TCRs, II–negative-positive TCRs, LP–latent period.

males, for the amplitude of positive-negative TCRs in the somatosensory and auditory cortical areas, showing that the greater penetrance is produced by the prevalence of individuals with right hemisphere dominance among males.

Thus, in all the cases where it was possible to find sex differences in penetrance of asymmetry in the animals studied, penetrance appeared to be higher in males. This was found, as a rule, in the primary projection cortical areas for the indices of positive-negative responses and was mainly maintained by individuals with right hemisphere dominance.

3.6.2. Expression of Interhemispheric Asymmetry

To assess the degree of expression of functional interhemispheric asymmetry in animals of different sexes, coefficients of asymmetry (ranged into four classes) were compared. Expression was determined as the percentage of individuals from the general number in which the K_{as} values were within ranges III and IV.

Greater K_{as} in the areas of TCR recording was shown to occur more frequently in females. Thus, in the case of positive-negative TCRs, expression of asymmetry was greater for the negative component in the somatosensory cortex, and for the negative component in the visual cortex. For negative-positive TCRs greater K_{as} values in recording areas were also found in females for both components in the visual, auditory, and somatosensory cortical areas. In other words, expression of asymmetry of TCRs was greater in females than in males, due mainly to negative-positive responses in the primary projection cortical areas.

Furthermore, it was found that, in the visual cortex, a strong expression of asymmetry of positive-negative potentials occurred more frequently in females than in males. These differences were observed in animals with both left and right hemisphere dominance. In the sensorimotor area expression was higher in females, the positive TCR component being maintained by individuals with the dominance of both hemispheres, that of the negative TCRs, by individuals with left hemisphere dominance.

For negative-positive TCRs in the somatosensory area, asymmetry with a high degree of expression was observed in females for the negative component, due to the individuals with right hemisphere dominance, and for the positive one, due to the individuals with left hemisphere dominance. In the visual cortex, greater expression of asymmetry was also found for both TCR components in females, with left hemisphere dominance. In the left auditory cortex of females, a strong expression of asymmetry in females more frequently than in males.

Consequently, in all those cases when it was possible to find a high expression of interhemispheric asymmetry for the TCR amplitude, this was characteristic of females, and was revealed more frequently for negative-positive potentials.

From analysis of the temporal parameters of TCRs, it appears that the expression of asymmetry of the latencies of positive-negative responses is the same in animals of both sexes. However a prevalence of females was observed with high expression of asymmetry for negative-positive TCRs in the somatosensory cortex, and in the visual and auditory areas. For the latencies of the peaks of the positive and negative components of positive-negative TCRs in the visual cortex high K_{as} values prevailed in females, this being determined by individuals with left hemisphere dominance. Expression of asymmetry was greater in females with respect to the time for development of the maximum of both components of positive-negative TCRs, with dominance of the left hemisphere in the visual cortex, and that of the right hemisphere in the somatosensory cortex. Thus, a common regularity was found: If it was possible to reveal differences in expression of asymmetry, its greater magnitude for all the TCR parameters was observed in females, more often for negative-positive TCRs and, as a rule, in primary projection zones of the cortex.

3.6.3. Discussion

Now let us discuss the above facts. In males, the penetrance of interhemispheric asymmetry was greater than in females. These data may support the widespread point of view that there is greater brain asymmetry in male compared to female individuals.

The second of the above facts throws new light on the relations between brain asymmetry in animals of different sexes. A high degree of asymmetry of TCRs was shown to be present more often in females, i.e. expression of functional interhemispheric asymmetry was higher in females. It should be noted that data on greater K_{as} values in females were also found during analysis of results of isolated recordings of homotopical TCRs in the primary projection and association areas of the cat's cortex, but the frequency of high K_{as} values appearance was not taken into account (Bozhko, 1990).

The main regularity found is as follows: In males, functional interhemispheric asymmetry was revealed fairly frequently, but, at the same time, it was comparatively weakly expressed. In females, on the contrary, together with symmetrical or very weakly asymmetrical individuals, there was a distinct group of individuals with degrees of expression of

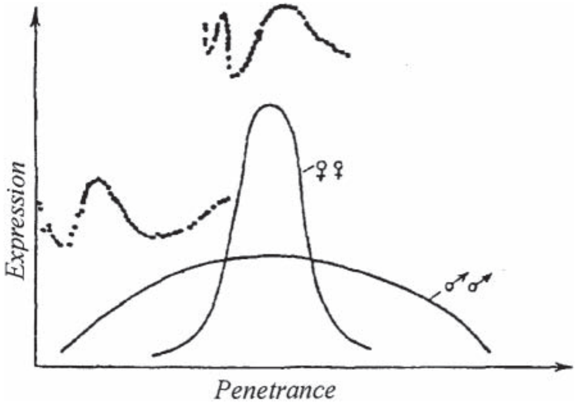

Figure 33: The relation between penetrance and expression in animals of different sexes. For explanations see text.

asymmetry close to maximal (Figure 33). The above regularity may indicate two things: First, in some females, the asymmetry was stronger than that in males. This circumstance may have been conducive to the viewpoint of the female brain being more asymmetric than the male one. However, secondly, the males appeared to be a uniform group in their pattern of functional asymmetry, whereas the females seemed to be a comparatively heterogeneous, more variable group. The varying degree of expression of asymmetry in females may have been determined, to a certain degree, by hormonal factors. In any case, recently the influence of hormones upon interhemispheric asymmetry has been shown to be quite distinct (Diamond *et al.,* 1982; Maggi and Lucchi, 1987; Filippova *et al.,* 1989; Holman and Hutchinson, 1991; Bianki *et al.,* 1992 etc.).

Let us focus on the comparative characteristic of penetrance and expression of functional interhemispheric asymmetry, for TCRs of different types. The greater penetrance of asymmetry in males appeared to be associated mainly with positive-negative TCRs, while the stronger expression of asymmetry, was associated with negative-positive TCRs. Here, at least two points should be noted: First, in animals of both sexes, positive-negative TCRs are more common than negative-positive ones. In males, they are approximately twice as common, in females, three times as common (Bianki *et al.,* 1991b). Consequently, they may be supposed to predominate in the overall picture of asymmetry. Second, positive-negative and negative-positive TCRs are, to a certain degree, the opposite of one other, which may indicate the opposite-phase character of asymmetry, both in males and in females.

Attention is also drawn to the fact that sex differences in penetrance and expression of functional interhemispheric asymmetry were, as a rule, more strongly expressed in the primary projection cortical zones. In those zones, TCRs are determined mainly by the activity of the homotopical callosal system, differences in penetrance and expression being mediated by the callosal functional connections. In contrast, in the association cortical fields, TCRs are of a more complicated nature. Here they are mainly conditioned by the interaction between intra- and interhemispheric projection activity.

Thus, it can be suggested that a higher penetrance of functional interhemispheric activity is inherent in males, occurs, as a rule, in the primary projection cortical zone, is mainly revealed for positive-negative TCRs, and is maintained mostly by individuals with right hemisphere dominance. At the same time, individual functional interhemispheric asymmetry in females is characterized by a greater expression, which is usually found for negative-positive TCRs, and also in the primary projection cortical fields.

3.7. INTRAHEMISPHERIC CONTRAST

As pointed out repeatedly, one of the main properties of functional interhemispheric asymmetry is its mosaicism. Earlier, we repeatedly concentrated our attention on the evidence for greater differentiation, and more prevalent brain specialization in males, compared to females. Males were also observed to possess a more specialized left hemisphere, while in females it was the right one. Here we shall focus specially on the results of studying this problem (Bianki *et al.,* 1994). Certain characteristics of intrahemispheric TCR contrast were subjected to investigation in the primary projection and association areas of the cats' neocortex. Two indices were chosen for such characteristics. It was accepted that mosaicism was characterized by intrahemispheric contrast, that is, heterogeneity of the intrazonal or interhemispheric TCR distribution. Its index was the coefficient of contrast (K_c), which reflected the magnitude of differences in TCR parameters between a given point and those in the adjoining points surrounding it. Another index of intrahemispheric contrast was the gradient of contrast (G_c). It measured the degree of focality, focussing and structuring of the focus of transcallosal activity.

Experiments were performed on lightly anaesthesized cats, using multiple total topographical TCR recording, from different cortical areas. The sequence of TCR recording was as follows. In one half of the experiments, TCRs were recorded first from the parietal and visual, then from the auditory cortex of the left hemisphere, after which recording was carried out from the auditory, visual and parietal cortical areas of the right hemisphere and, finally, from symmetrical areas of the rostral cortical pole in the left hemisphere. In the other half of the experiments, lateralization of TCR recording was in the reverse sequence.

The coefficient of intrahemispheric contrast for the amplitude TCR parameters was calculated according to the formula:

$$K_c = \frac{\sum\left(\frac{A_0 - A_i}{A_o + A_i}\right)}{n} \cdot \frac{A_0}{A_{\max}},$$

where $\mathbf{A_0}$ was the amplitude in the point analysed, $\mathbf{A_i}$–TCR amplitudes in surrounding points shifted by 1 mm from that under investigation; **n**–the number of the possible surrounding points in the rostral, caudal, lateral, and medial directions (for the "medial" points n=4, for the "peripheral" ones, n=3 and for the "corner" ones, n=2); $\mathbf{A_{max}}$ was the maximal TCR amplitude in the area under discussion.

For the temporal parameters of TCRs, K_c was calculated according to the formula:

$$K_c = \frac{\sum(T_0 - T_i)/(T_0 + T_i)}{n} \cdot \frac{A_0}{A_{\max}},$$

where $\mathbf{T_0}$ was the value of the temporal parameter of the TCR in the point analysed; $\mathbf{T_i}$–the value of the same parameter in the surrounding points; $\mathbf{A_0}$ and $\mathbf{A_{max}}$–the corresponding amplitude values, **n**–the number of the possible surrounding points.

The gradient of contrast was calculated as the ratio between the maximal contrast of TCRs in the cortical area investigated and the mean value of K_c of the same zone. The following formula was used:

$$G_c = \frac{K_{c\max}}{K_c},$$

where $\mathbf{G_c}$ was the gradient of contrast, $\mathbf{K_{c\,max}}$ was the magnitude of the maximum TCR contrast in the given cortical area, and $\mathbf{K_c}$ was the average value of the contrast.

First, let us turn to the problem of interhemispheric asymmetry of intrahemispheric contrasts, in animals of different sexes. When the coefficients of contrast in symmetrical points of the opposite hemispheres were compared, interhemispheric asymmetry of K_c was revealed, which may serve as the interhemispheric measure of intrahemispheric heterogeneity of adjoining cortical points, in other word, their “mosaicism”. In this case it is important that TCR contrast was greater in the hemisphere which was dominant with respect to amplitude. Consequently, the dominant hemisphere is characterized not only by a general elevation of its transcallosal activation, but also by an increase in the degree of the functional heterogeneity of its different sites. Here, the more frequent manifestation of interhemispheric asymmetry of contrast coefficients should be emphasized (higher in males compared to females: $p<0.05$). In this sense one can speak of TCRs having higher contrast in males compared to females, on the basis of a greater frequency of appearance of functional interhemispheric asymmetry of intrahemisphere contrast in males.

Alongside the traditional evaluation of functional interhemispheric asymmetry, with respect to the lateralization for each phase of the recorded responses, analysis of contrast was performed in the process of formation of transcallosal response. By the time of appearance of the final phase of TCRs of the negative component of corresponding negative responses, the mean value of contrast was shown to be only half that of the initial stages of transcallosal reaction. This lowering of K_c seems to reflect the gradual equalizing of transcallosal reactions in adjoining points, and is observed both in the right and the left hemisphere. At the same time, lowering of the mean coefficient of contrast is accompanied by the increase in another index–the gradient of contrast. In other words, by the time that the TCR was completed, the differences between the contrast of their focus and the mean contrast of the surrounding cortical sites are intensified. The observed dynamics of the indices of intrahemispheric contrast seems to reflect the transition from a diffuse focus of transcallosal excitation into its complete, structured organization, and thereby the contrast gradient becomes the measure of focal cortical function.

The above dynamics of intrahemispheric TCR contrast is inherent in both hemispheres. At the same time, interhemispheric asymmetry of intrahemispheric contrast (described earlier) allows one to distinguish the role of the left and the right hemisphere at different stages of transcallosal signal processing. In this case it is important to take the following facts into account: In both hemispheres, the dynamics of change in K_c and G_c in animals of different sexes is reciprocal. In graphs of changes in G_c and K_c in animals of different sexes, taking into account the hemisphere dominant for those indices, it can be seen that the curves vary in opposite directions. Thus, in males (Figure 34, I) the coefficient of contrast, at the beginning of TCR formation, was greater in the left hemisphere, then in the right one and, after a second inversion, was dominant again in the left hemisphere; the gradient of contrast, on the contrary, was maximal in the right hemisphere at the initial stages of TCR development, then its maximum passed over to the left side, and appeared to be maximal again in the right hemisphere during the completion of the transcallosal reaction. The mean value of K_c was +1.1±0.3 and that of G_c, -2.9±0.8. A similar pattern of relations of G_c and K_c was also observed in females (Figure 34, II). However, in this case, changes in K_c occurred mainly in the left hemisphere (K_c=-3.96±1.0), those in G_c, in the right (G_c=+1.2±0.6).

After comparing the above absolute values of the summated gradient of contrast in males and females, and taking into account the fact that G_c serves as a measure of focality, it can be suggested that the brain of males is, on the whole, more focal, and that of females, relatively more diffuse. At the same time, in males the left hemisphere was more focal, while in females it was the right.

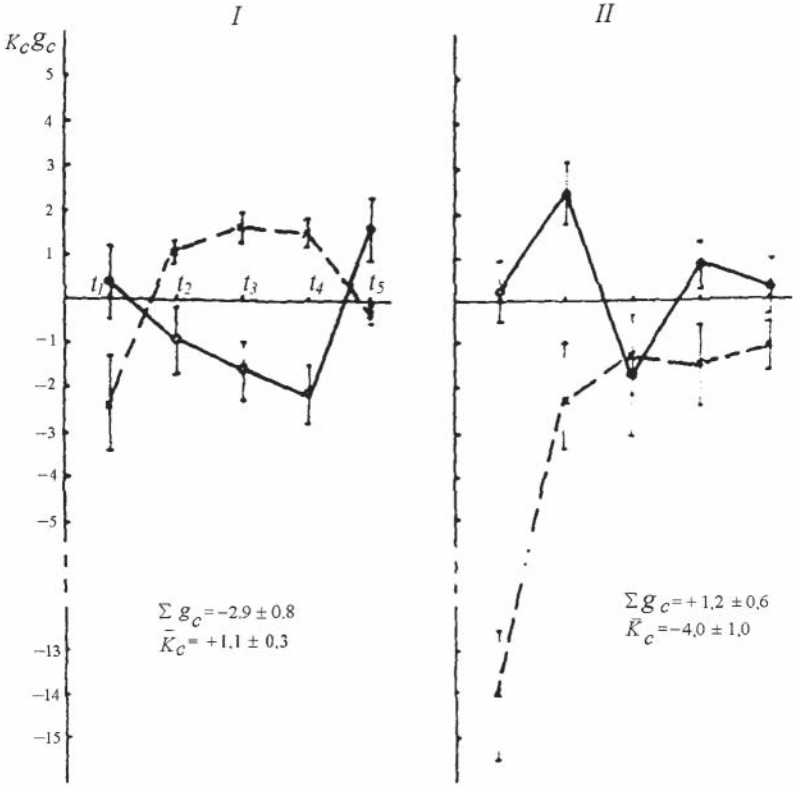

Figure 34: Comparative dynamics of the intrahemispheric coefficient of contrast, and contrast gradient in animals of different sexes. **I**–males, **II**–females. **Solid line**–contrast gradient, **broken line**–contrast coefficient. **Abscissa:** time, **ordinate:** values of the corresponding indices of intrahemispheric contrast, the positive values are in the right hemisphere, the negative ones are in the left hemisphere.

Thus, one more indication is revealed of relative reciprocity of interhemispheric contrast in animals of different sexes, and (which is more important in this case) the curves presented point to the opposite, inverted character of the lateralization of the contrast gradient and the contrast coefficient, or focality. In other words, the hemisphere, dominant for the index of the TCR value, i.e. the hemisphere in which more high amplitude EPs are recorded, also shows a higher contrast. Putting it in another way, in such a dominant hemisphere, the TCR parameters in the neighbouring points are more heterogeneous than those in the opposite hemisphere. In addition, the same hemisphere is less focal–more diffuse–compared to the opposite one, which dominates for the index of the contrast gradient. This in its turn, points to a different character of TCR distribution: a strictly localized focus of maximum activity, in which the TCR value surpasses the relatively low amplitude responses in the surrounding points.

Consequently, analysis of TCR distribution reveals a new characteristic of hemisphere dominance, on the basis of the gradient of contrast (focality). Indeed, as shown earlier, the area of appearance of the TCR is the focus of increased excitability possessing dominant properties (Shramm, 1980b). If two symmetrical foci of TCRs (recorded in the opposite hemispheres) should be compared, it seems possible that two competing characteristics can be distinguished in the dominant hemisphere: On the one hand there is the degree of its activation, or excitability, determined, for instance, by the magnitude of the TCR, and on the other hand (no less important) is the degree of its "structuredness" or focality of symmetrical transcallosally activated (in this case) foci. This measure of focality is the gradient of contrast.

As pointed out repeatedly, in the works on the study of the dominanta (or "dominant focus"), starting with A.A.Ukhtomsky's investigations, one of its main properties is considered to be its dynamism (Ukhtomsky, 1966). In this case a young, developing dominanta is distinguished, then the stage of its maturation follows and, finally, the concluding phase of the dominanta follows, which, in particular, is associated with its reinforcement (the so called endogenous end of the dominanta). Proceeding from this, and also taking into account the fact that the zone of transcallosal excitation possesses the major properties of such a dominant focus, it is natural to draw the following conclusion: The prevalence of high amplitude TCRs may serve as a sign of the leading number of high amplitude TCRs, and a greater area of FMAs in the given hemisphere (and greater as compared to the opposite hemisphere) indicates the reinforcement of the dominanta, at the final stage of its existence. At the same time, the development of a young dominant focus, capable of further evolution may be manifest as a high degree of focality, a strict structuredness of the focus of transcallosal excitation in the opposite hemisphere, the narrowness of FMAs in it and pronounced differences between TCRs in the focus and in the perifocal sites[10].

As shown above, changes in G_c (the main property of TCR focality) in the course of development of transcallosal reactions, are phasic changes of its lateralization. In the graph of changes in TCR focality (Figure 35,V), it can be seen that at the initial stages of transcallosal signal processing (the period corresponding to the latency and the initial negative component of the TCR) the right hemisphere is characterized by a greater G_c. Then, for the period of the formation of positive TCR components, the greater G_c is shifted into the left hemisphere, and, at the initial stage of re-inversion of the dominance of the transcallosal reaction, there is a regrowth of the G_c in the right hemisphere. However, this is a summated curve constructed from animals of both sexes.

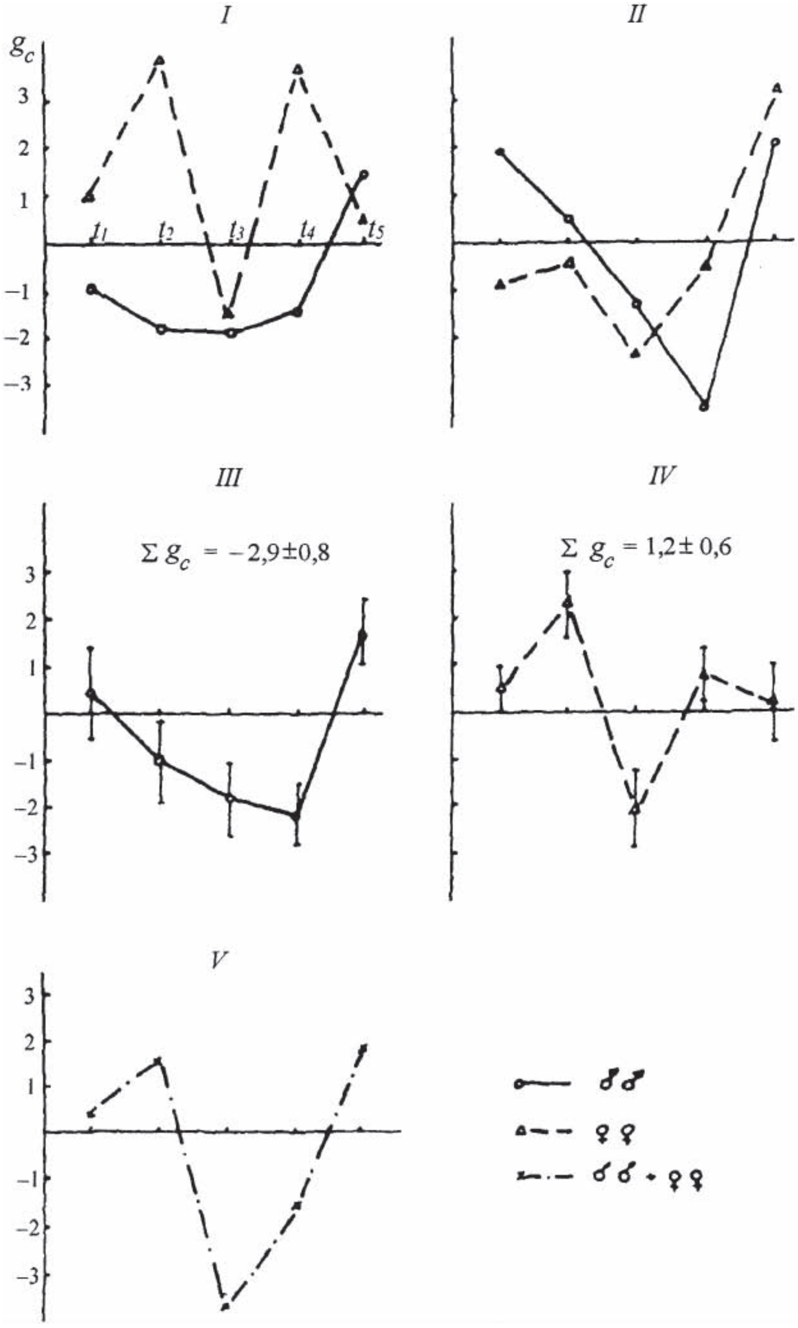

Figure 35: Summated graphs of the change in contrast gradient in the process of TCR formation. **I**–primary projection, **II**–association cortical areas, **III**–dynamics of contrast gradient in males, **IV**–in females, **V**–changes in the contrast gradient in the entire group of animals investigated. **Solid line**–contrast gradient, **broken line**–contrast coefficient. **Abscissa:** time, **ordinate:** values of the corresponding indices of intrahemispheric contrast, the positive values are in the right hemisphere, the negative ones are in the left hemisphere.

At the same time, in males, the main dynamics of change of focality is associated with the left hemisphere (Figure 35, III). In this respect, as well as during the discussion of the frequency of interhemispheric asymmetry of contrast, transcallosal reactions of males may be considered to be more lateralized than those in females. In addition (this being important), the above fact indicates greater "structuredness" or focality of the left hemisphere in males. The hypothesis about the link between diffusion of function and the right hemisphere, and between focality and the left, was advanced earlier by J.Semmes (1968) on the basis of analysis of motor dysfunction in patients–males with left or right hemisphere lesions–and was then supported and developed in experiments on animals (Bianki, 1989, 1993). At the same time, females determined those sites of the summated curve which were associated with the focality of the right hemisphere. Hence it follows that in males the left hemisphere is more focal, whereas in females it is the right.

Different roles for the primary projection areas and association areas in the formation of the summated curve of G_c changes, in animals of different sexes, should also be noted (Figure 35, I, II). From the above analysis it follows that, in females, the prevalence of the right hemisphere in the gradient of contrast was determined mainly by the primary projection zones, whereas this index was considerably lower for the association areas. At the same time, in females, in the primary projection and association fields the values of G_c were greater in the left hemisphere, yet focality in the primary projection cortical areas was somewhat stronger than that in the association areas.

Thus, consideration of the development of intrahemispheric contrast of TCRs judged by the index of contrast gradient allowed us to demonstrate the fluctuation, and dynamism of interhemispheric asymmetry of this type of responses: At the beginning of the reaction, the right hemisphere was more focal, then it was the left one and, finally, the right hemisphere again. This double right-left-right inversion is similar to the right-left gradient of hemisphere dominance during the formation of conditioned reflexes and during extrapolation learning (Bianki, 1985, 1988), and in the course of ontogenesis (Bianki and Makarova, 1994) etc. described above. This fluctuation of dominant focality, in the process of realization of an isolated transcallosal reaction, is one particular case of a general regularity, and one of its neurophysiological mechanisms.

Now let us sum up the results on sex differences in intrahemispheric contrast. We studied intrahemispheric TCR contrast, which assessed the nature of the mosaic, and the heterogeneity of the intrahemispheric distribution of transcallosal potentials. The degree of TCR structuring was measured by the gradient of contrast, which characterized the specialization, structuring and focality of transcallosal activation. The following points were shown: The cortex of both hemispheres in males functions more focally, and is more specialized than that in females. This is indicated by a more frequent manifestation in males of functional interhemispheric asymmetry of intrahemispheric contrast, and also by the greater value of the summated contrast gradient. In males, the left hemisphere is more focal, more specialized, whereas the right is functionally more diffuse. In contrast, in females, the right hemisphere is somewhat more focal, the left one being more diffuse. This is indicated by the dynamics of G_c during transcallosal signal processing: In the process of development of transcallosal reactions, a certain dynamic of the gradient of intrahemispheric contrast is observed: At the beginning of the reaction, the right hemisphere is more focal, then the left one, and then the right one again. In the course of transcallosal signal processing, the cerebral cortex turns, from being functionally relatively heterogeneous, into a formation which (prevalently) is functionally focussed.

3.8. CONCLUSION

From the result of experiments performed mainly on cats (and also some on rats), sexual dimorphism of functional interhemispheric asymmetry was found. It was revealed for amplitude-time parameters of TCRs, the frequency of their occurrence, the area and localization of recording zones, the magnitude, location and fragmentation of FMAs etc.

In most cases, species-specific functional interhemispheric asymmetry appeared to be more strongly expressed in males than in females. This indicates a greater asymmetry of the male brain, and a comparative symmetry of function or bilaterality of the female brain. This picture was observed when studying intrazonal and interzonal transcallosal influences, and when comparing homotopical transcallosal connections in the corresponding hemispheres in the two sexes. It should be noted that, in males, a more strongly expressed species-specific functional interhemispheric asymmetry of homotopical TCRs was observed, whichever hemisphere might be dominant, the right or the left one. The only exception was the auditory cortex. At the same time, in females, a greater magnitude of individual functional interhemispheric asymmetry of homotopical TCRs was found in all the areas except the visual cortex.

The above evidence for the existence of sexual dimorphism in functional interhemispheric asymmetry allows one to pose the methodological question of the validity of studying mixed samples. Indeed, only in some cases was coincidence observed between the results of studying mixed and single-sex samples. Sometimes the results of studying a mixed sample coincided with the data obtained from separate groups males and females. In most cases a mixed sample revealed only the result of the interaction, showing interference of the specific peculiarities of interhemispheric asymmetry seen separately in males and females.

From the results obtained, it appears that, in a number of cases, the male brain is shown as more dynamic, compared to the female brain. For instance, this was observed during the study of homotopical TCRs in corresponding hemispheres in males and females, and the dynamics of transcallosal signal processing etc. In the latter case, the greater dynamics of the male brain function was manifest as a greater velocity of transcallosal conduction in males, which was especially characteristic of the conduction of excitation into the surface cortical layers of the left hemisphere, and into the deep layers of the right hemisphere cortex, compared to the female brain. In a number of cases, the sequence of involvement of the two hemispheres in transcallosal signal processing in animals of different sexes was also different. Thus, in males, the left-right-left gradient was usually observed, whereas in females it was the right-left-right one.

In a number of cases, the cortex of both cerebral hemispheres is more differentiated (and more specialized) in males than in females. This is indicated by data obtained from studying intra- and interzonal transcallosal connections, when corresponding hemispheres are compared in males and females, when patterns of functional interhemispheric asymmetry are studied in males and females, and especially when functional contrast is measured directly in males and females. The sex specificity of the male brain appeared to be determined mainly by transcallosal connections in the association areas of cortex, while in females they were studied in the primary projection cortical zones.

It was possible to establish that in males the main role is, as a rule, played by the left hemisphere, in females, by the right. For instance, this picture was observed when comparing the characteristics of corresponding hemispheres in males and females, when studying the course of transcallosal signal processing, or the interaction of transcallosal and thalamocortical excitation, or in describing functional interhemispheric contrast in individuals of different sexes, and in other cases. In males, the left hemisphere functions more focally, the right one, more diffusely than in females. By contrast, in females, the right hemisphere was somewhat more focal, the left one, relatively more diffuse. The greater specialization of the male brain is determined primarily by the surface cortical layers of the left hemisphere and the deep layers of the right one. Inhibitory processes in the cortex of the left hemisphere turned out to be more strongly expressed in males than in females. By contrast, in females, excitatory processes in the right hemisphere cortex are more developed. This may determine the relative focality of the male brain, and the comparative diffuseness of brain function in females. The modulating and filtering functions of the transcallosal stream of excitation are supposed to be expressed more strongly in males compared to females.

Summing up the above data, the following conclusion can be made. Species-specific interhemispheric asymmetry is more strongly expressed in males in most cortical zones, individual asymmetry is more strongly expressed in females. Unlike this, in the auditory cortex, species-specific asymmetry is greater in females, whereas in the visual cortex it prevails in males. In males, penetrance of asymmetry is stronger, in females expression of asymmetry is greater. The male brain functions more dynamically than that of females. The cortex of both hemispheres in males is more specialized functionally, more differentiated, and more focal than that of females, this being determined by the association and primary projection areas. In males, as a rule, a relatively greater role is played by the left hemisphere, in females, by the right one. In most cases the male left hemisphere functions more focally, the right one, relatively more diffusely. In females, these differences are less strongly expressed.

4 Hormonal Factors

4.1. GENERAL CHARACTERISTICS

The main differences between the male and the female brain are known to be determined by the functional specificity of structures controlling sexual and reproductive functions. In female mammals, the periodic development of the ovum, and ovulation, are regulated by gonadotropic hormones of the pituitary gland, whose cyclic secretion is mediated by the hypothalamus. In males, the capacity for cyclic changes in gonadotropic function is lost during the period of sexual maturation of the brain, under the influence of androgens, at the end of embryonic development, or soon after birth (Savchenko, 1967; Babichev, 1981; Reznikov, 1982). Those hypothalamic nuclei which produce releasing-factors which regulate hormonal secretion via pituitary gland hormones and which control species-specific sexual behaviour, are also characterized by structural sex differences (Gorski *et al.,* 1978; Matsumoto and Arai, 1983; Arai, 1984; Arai *et al.,* 1986). However, sexual dimorphism is not limited to the above fields, but has been observed in some other brain structures (and their functions), which are not immediately related to sexual behaviour and reproduction. Sexual differences have also been observed in functional interhemispheric asymmetry, which has been the focus of repeated attention in the preceding chapters.

Sexual dimorphism in the reactivity of brain structures was observed in a number of studies. The metabolism of glucocorticoids in females is more marked in the hypothalamus (Turner and Weaver, 1985). An increased level of corticosterone under stress was more pronounced in females (Anischenko *et al.,* 1989). In experiments on rats and cats, the development of convulsions under the action of picrotoxin was observed only in females (Pericic, 1986). The number of synapses in the ventromedial nucleus of the rat's hypothalamus is greater in males (Matsumoto and Arai, 1986). Studies on the influence of the environment on hippocampal neurones have established that, in males, the number of neurones increased under conditions of isolation, whereas in females this happened in enriched environment (Juraska *et al.,* 1985). In the latter case, males appeared to possess more dendrites in the distal branches of the neurone, whereas in females this occurred in its proximal branches (Juraska *et al.*, 1989). Unlike males, in females, the neurones of the frontal cortex contain numerous progesterone receptors (Maggi and Lucchi, 1987).

In male rats, right hemisphere lesions gave rise to hyperactivity which was accompanied by a lowered catecholamine level, while in females, on the contrary, reduced catecholamine level was not accompanied by hyperactivity, and was observed after both left and right hemisphere lesion (Lipsey and Robinson, 1986; Starkstein *et al.,* 1989). In males of some song birds, song learning is correlated with the enlargement of the hyperstriatum ventrale, the nucleus controlling vocalization. The number of neurones in the corresponding nucleus was smaller in females than in males (De Voogd and Nottebohm, 1981). In newborn female rats, unlike males, the tail is oriented to the left with regard to the body (Rosen *et al.,* 1983), and only females show asymmetry in absorbing glucose derivatives in the hippocampus. The authors consider tail shift to be the analogue of limb preference, and correlate it with the direction of circling movement. In adult animals, spontaneous rotations, and also those induced by amphetamine, occur in the same direction as that in which the tail of newborns was turned (Ross *et al.,* 1981; Camp *et al.,* 1984; Glick, 1985). Circling movements are known to be connected with asymmetry of the nigrostriatal system: They are directed to the side with lower dopamine content (Glick *et al.,* 1981; Glick and Shapiro, 1985). Circling behaviour and asymmetry in the metabolism of this mediator are more strongly expressed in females, only they show a species-specific direction of asymmetry (Glick, 1985).

It should be emphasized particularly that behavioural and locomotor asymmetries, observed in S.Glick’s laboratory, are, in the opinion of the authors, determined by different dopamine levels in the left and right side of the striatum, i.e. this is asymmetry of subcortical structures. In other studies, anatomical and functional asymmetry was observed mainly at the level of the neocortex. Hence it is suggested that, at least in some cases, the asymmetry of subcortical formations is more strongly expressed in females, whereas cortical asymmetry is stronger in males.

The structural and functional sex differences observed are, as a rule, related to the action of sex hormones. It is accepted that the influence of steroid hormones on the brain should be divided into organizing functions and activating (or, to be more exact, modulating) functions. The former is limited to the critical period of brain differentiation during the prenatal period, goes on continuously, and results in the differentiation of the hypothalamus into the male and the female type. The latter is observed during the period of sexual maturity, is transitory, and determines the sexual and reproductive behaviour of individuals (Ross *et al.,* 1981; Reznikov, 1982; Rosen *et al.,* 1983; Arnold and Breedlove, 1985; Geschwind and Galaburda, 1985).

4.2. THE INFLUENCE OF SEX HORMONES UPON INTERHEMISPHERIC ASYMMETRY DURING THE PRENATAL AND NEONATAL PERIOD

Two experimental models were used mainly: that of emotional resonance, and that of the open field. A detailed description of these can be found in Chapter 2. Earlier it was shown that in both cases (reactions of emotional resonance, and motor and exploratory activity) sexual dimorphism in functional interhemispheric asymmetry was present. The asymmetry could be quantitative (e.g. in males it was greater than in females) or qualitative (e.g. its direction was different in males and females) (Bianki *et al.,* 1985; Filippova, 1985, 1989a,b, 1990).

To investigate the influence of neonatal gonadectomy in male and female rats, sex glands were removed during the first two days after birth (Filippova, 1989a). Testing of interhemispheric differences was performed at an age of 2–3 months. In half the rats, the conditioned reflex of emotional resonance was elaborated, and then its continued presence was tested during left and right hemisphere inactivation. Temporary unilateral cortical inactivation was carried out according to the method of J.Bureš and O.Burešova (1962). The other half of the animals was used for studying interhemispheric asymmetry for control of motor and exploratory activity in the open field.

Establishment of the reaction of emotional resonance, in rats which had been gonadectomized neonatally, was performed under the same experimental conditions as in the intact animals, although it required much more time. In unoperated individuals, a stable reaction was established after 9 experiments on average, while in gonadectomised ones this required 14 experiments. All animals without exception were repeatedly used as "victims". In 32% of the sample, no stable reaction could be formed, which testifies to the lower reactivity of the animals gonadectomized neonatally. However, the average duration of stay in the preferred chamber in gonadectomized male and female rats in whom a reflex could be elaborated with both hemispheres remaining active was practically the same as that in intact animals (Figure 36, I). In other words, gonadectomy seems to have affected the rats' emotionality but not their ability for reflex formation. Both left and right hemispheric inactivation disrupted the reaction of emotional resonance. It should be emphasized that in gonadectomized rats, no interhemispheric asymmetry for this reflex was observed. Comparison with intact animals (see Figure 15A) showed that, while, in the latter, the emotional reaction of avoidance occurred both when the two hemispheres were working concurrently, and during isolated function of the left hemisphere, in rats gonadectomised neonatally, neither of the hemispheres, when acting in isolation, ensured the performance of the reaction investigated.

Exposing neonatally gonadectomised rats to the open field showed, first of all, a considerable decrease in motor activity, both in males and in females with both hemispheres active. The number of the squares crossed in the open field was, on average, half that in intact rats in the first part of the experiment; the same can be said of the exploratory reactions. A distinguishing characteristic of the motor and exploratory activity of the gonadectomised rats was the equalizing of interhemispheric asymmetry. No significant advantage of either right or left hemisphere was observed for control of motor activity during some testing periods, nor during the experiment as a whole (Figure 36, II).

It should also be mentioned that different measures of exploratory reactions (i.e. the number of rearings on hind legs, and peepings in openings) gave results analogous to the dynamics of summated motor activity.

Thus the results obtained from the experiments performed suggest that the interhemispheric asymmetry characteristic of intact rats, for either the reaction of emotional resonance, or for motor and exploratory activity in the open field (see Figure 4), was not observed in neonatally gonadectomized animals.

In further experiments we tried to restore interhemispheric asymmetry (which had been eliminated in rats after early removal of the gonads) by injecting sex hormones into them (Filippova, 1992; Filippova *et al.,* 1989). The experiments were carried out using the method of the open field on rats aged 2–3 months. Sex steroids were injected for two weeks before beginning testing, and also during the experiments: Each male was injected daily

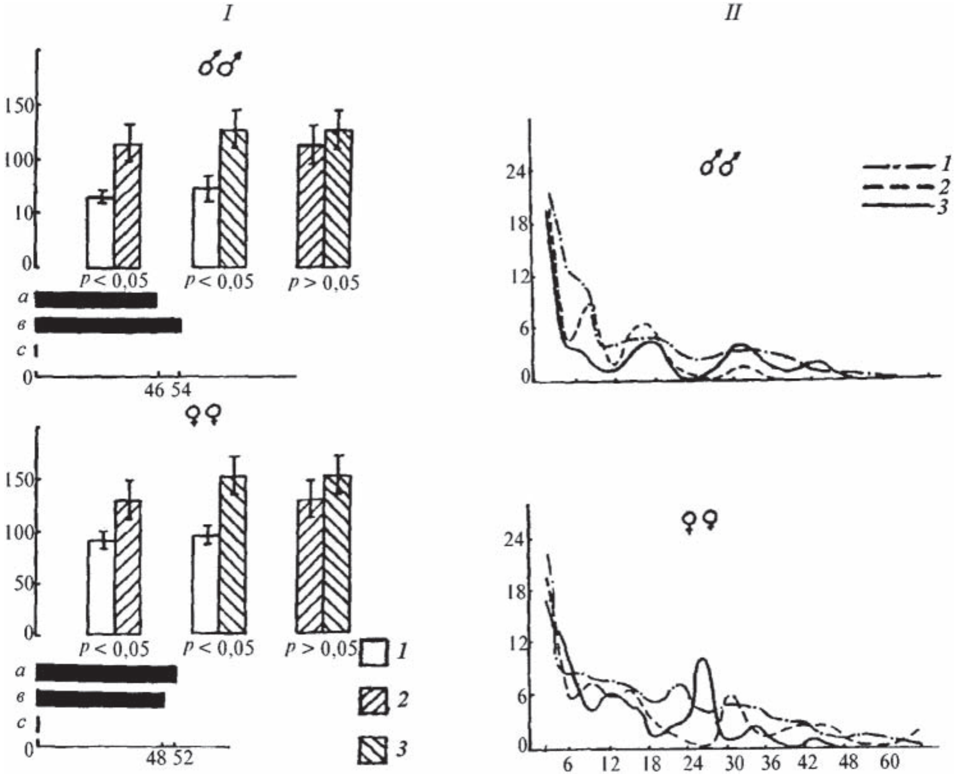

Figure 36: The influence of hemisphere activation on the reaction of "emotional resonance" **(I)** and motor activity in the open field **(II)** in neonatally gonadectomized rats. **I: ordinate:** the period of staying in the preferred chamber, **1**–the norm, **2**–after left, **3**–right hemisphere inactivation, **a**–percentage of individuals with left hemisphere dominance **b**–with right hemisphere dominance **c**–percentage of ambilateral individuals. (See Fig 15A, p. 82, for similar experiments in unoperated rats) **II: abscissa:** time, min, **ordinate:** the number of squares crossed; **1**–the norm, **2**–after left, **3**–right hemisphere inactivation.

with 1 mg of testosterone-propionate, each female with 5 mg of estradiol-dipropionate. After recording the animals' reactions during exposure to the open field, the motor activity of the males appeared to be reduced considerably, compared to the castrated animals which had not received any hormones. The number of the squares crossed in the open field was reduced by 30% during the first minutes of testing with both hemispheres remaining active. In the second half of the experiment the rats often did not move at all (Figure 37). The same could be said of exploratory reactions. In females, estradiol introduction did not result in any considerable change in motor activity: The number of the squares crossed was even somewhat greater, compared to the ovariectomized rats which had not received any sex steroids, and did not change until the end of the experiment; the number of exploratory reactions was somewhat reduced. The essential point is that introduction of sex steroids did not result in restoration of the interhemispheric asymmetry of motor and exploratory activity, which had been eliminated by neonatal gonadectomy. Significant interhemispheric differences were not revealed in either males or females during the whole observation period (Figure 37).

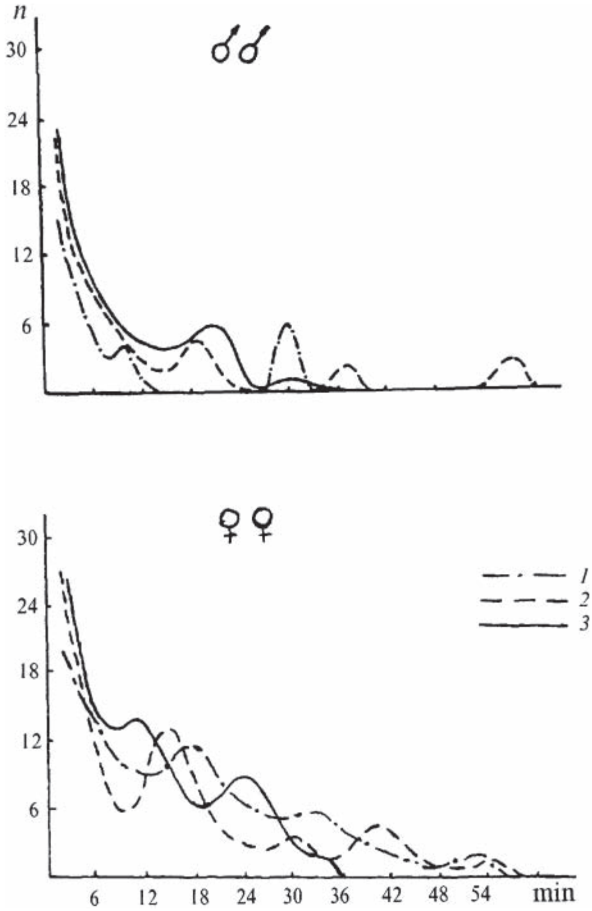

Figure 37: The influence of hemisphere inactivation on motor activity in the open field in neonatally gonadectomized rats with subsequent administration of testosterone-propionate to males, and estradiol-dipropionate to females. **Ordinate:** the number of squares crossed; **abscissa:** time, min; **1**–the norm, **2**–after left, **3**–after right hemisphere inactivation.

Neonatal gonadectomy, and injection of newborn animals with sex steroids, are traditional techniques used in investigating the organizing influence of hormones on the brain. It should be pointed out that, in most previous works, it has been reported that early removal of the gonads, and hormone therapy immediately after birth, are effective with respect to the sexual dimorphism of cerebral functions for which interhemispheric asymmetry has not yet been studied. Thus neonatal orchidectomy, and injection of females with androgens, affected sex differences in maze learning: Intact females made fewer mistakes after reflex reversal, and males learned better as a result of the above actions (Guillamon *et al.,* 1986). The same factors affected the number of synapses in the ventromedial region of the rats' hypothalamus: Castration of males, and injection of females with testosterone immediately after birth resulted in a reduced number of synapses in males, and an increase in females. As a result, the ratio of the number of synapses in males and females was reversed. (Normally the number of synapses tended to be greater in males: Matsumoto and Arai, 1986). Similar data were obtained concerning estrogen receptors: Neonatal castration of males led to an increased in the number of receptors in the preoptic area, the ventromedial and the arcuate nucleus, while androgen administration immediately after birth reduced the number of receptors in the same zones (Kühnemann, 1995). Neonatal injection of female rats with testosterone eliminated sex differences in the size of the hippocampal nucleus and in spatial orientation: These indices became similar to those in males (Roof and Havens, 1992). The above data point to a critical role of androgens in the organization of interhemispheric differences at early stages of ontogeny. In some studies an influence of sex hormones upon interhemispheric asymmetry in females has been demonstrated. Ovariectomy performed immediately after birth changed the sexual dimorphism of interhemispheric asymmetry in the thickness of the rats' cortex: Following ovariectomy, the pattern of interhemispheric asymmetry in females became similar to that in males (Diamond *et al.,* 1982). The neonatal action of androgens reduced the number of progesterone receptors in neurones of the frontal cortex, thus eliminating sex differences (Maggi and Lucchi, 1987). Injecting pregnant female rats with testosterone changed the left-sided tail position only in female progeny (Rosen *et al.,* 1983).

Neonatal removal of gonads, or the action of androgens at the same age, eliminated sexual dimorphism in female rats with respect to parameters of the corpus callosum: In intact animals, the sagittal section of anterior and posterior regions of the corpus callosum in males is larger than in females. The same operation in males was not effective (Titch *et al.,* 1990). Indirectly, the influence of sex hormones upon the development of the corpus callosum is indicated by the increased frequency of agenesis of this commissure in mice, if their intrauterine development coincided with lactation in the pregnant females (Wahlschen, 1982).

Some interesting results were obtained from studying the influence of neonatal castration upon the development of the compact zone of the hypothalamus in the Mongolian gerbil (Holman and Hutchinson, 1991). Sexual dimorphism was observed for this structure: In males, the size of the compact zone is larger, it being responsible for the asymmetric control of vocalization in the supersonic range, characteristic of males: Level of vocalization correlated only with the magnitude of the left compact zone. Orchidectomy immediately after birth caused reduction in the size of nuclei (and of vocalization) to the level of females. The essential point is that, in castrated animals, vocalization correlated with the magnitude of both the right and the left compact zone, i.e. elimination of functional asymmetry was the result of gonadectomy during the neonatal period.

Thus, the above data suggest that neonatal gonadectomy, or androgen injection, usually eliminates sex differences in the parameters of behaviour (or in brain structures) whose asymmetry has not been previously studied (Guillamon *et al.,* 1986; Fitch *et al.,* 1990; Matsumoto and Arai, 1986). The same procedures usually eliminate the sexual dimorphism of structural brain asymmetry (Diamond *et al.,* 1982; Roof and Havens, 1992) or of the simple locomotor response (Rosen *et al.,* 1983). In one case, when functional asymmetry was studied in a complex behavioural act (Holman and Hutchinson, 1991), removal of sex glands during the critical period of brain differentiation eliminated interhemispheric differences, i.e. it disorganized the lateralization of functions.

The above data suggest that the pattern of functional hemispheric specialization is formed mostly at the intrauterine stage, the sex steroids determining the expression and direction of interhemispheric differences. To test this hypothesis we (Filippova, 1992) used the model proposed by van Saal (1983). He, and then other authors, showed that the position of the foetus in the uterus between two foeti of the same, or of the opposite sex, affected the maternal and the aggressive behaviour of mice, and also the rate of sexual maturation of the Mongolian gerbil (Kinsley and Svaare, 1985; Kinsley *et al.,* 1986; Clark and Galef, 1988). The authors consider that the number of male embryos affected the level of the androgens contained in the amniotic fluid, since the testes of the male foetus secrete hormones intensively during the prenatal period.

Taking all the above evidence into consideration, we studied the interhemispheric asymmetry of behaviour in the open field, in rats born in litters with a prevalence of the male or the female sex, and also with an equal number of males and females. In the first two cases, only those litters were used in which individuals of one sex prevailed over those of the others by not less than fourfold. Groups of males and females were formed which had been born in litters with the prevalence of females ("female litters"), with an approximately equal number of brothers and sisters ("neutral litters") and those where males prevailed ("male litters"). It should be noted that each group was made up of five or six litters. At the age of 30 days, the pups were weaned from their mothers and divided according to their sex. In females, the rate of sexual maturation was determined by the time when the vagina opened. Testing rats in the open field was performed at age of 2–3 months. The exposure period was 30 min.

When sexual maturation of the females was being observed it was found that females born in "female litters" had their vagina open on the 55th day, on average, while for those born in "neutral litters" it usually happened on the 63rd day, and for rats from the "male litters" the vagina usually opened on the 72nd day after birth. Thus an inverse proportion between the rate of maturation and the number of males in the litter was observed: The more male pups were developing together *in utero* with the female, the later did the first ovulation occur.

Similar data were obtained earlier from studies of Mongolian gerbils: The presence of males in the litter slowed down females' sexual development (Clark and Galef, 1988). The sex glands of male rats are known to start functioning during the process of embryonic development, testosterone secretion in the embryo exceeding that in the adult individual (Wunder, 1980). This is also the case for humans. Androgen concentration in the amniotic fluid of the litters seems to be different, depending on the number of the male embryos. On the contrary, sexual maturation in female rats occurs mainly in the last third of the first month of their postnatal life, and ends in the first ovulation and the opening of the vagina (Reznikov, 1982). The prerequisite condition for this is the function of the cyclic centre for hypothalamic endocrine regulation, and the formation of hypomalamopituitary interaction (Savchenko, 1967; Babichev, 1984). The fact that the action of androgens during intrauterine development slows down the development of females suggests that the result of this action may be a considerable change in the function of brain structures concerned with reproductive behaviour, and the expression of their function in mature animals.

This suggestion was also confirmed by the study of interhemispheric asymmetry in control of behaviour of rats in the open field. It can be seen that, with both hemispheres active, the number of the squares crossed in the open field was approximately equal in the males of all groups (Figure 38, I). As a rule, reduction of locomotion was observed during the first few minutes, and then a certain increase in locomotion was observed. When the hemispheres were inactivated, in rats from “male litters”, differences in motor performance were observed: With an active right hemisphere, the number of squares crossed was greater than when the left hemisphere was working during some periods of exposure. In other words, the right hemisphere was dominant in the control of motor activity at that time. In the animals from “neutral litters”, the same interhemispheric differences, i.e. right hemisphere dominance, were noted, but for only a short period. In the control of the motor activity of the males born in “female litters” interhemispheric asymmetry was observed during the whole period when the reaction was manifest, but, unlike the rest of the animals, the left rather than the right hemisphere was dominant. Interhemispheric asymmetry in the control of exploratory reactions, while it lasted, coincided in its direction with asymmetry of motor activity.

Thus in males from “male litters” the right hemisphere dominated in carrying out the reactions tested, while in those from “female litters” it was the left one, and in animals from “neutral litters”, interhemispheric asymmetry was not, as a rule, evident. On the basis of data concerning testosterone secretion during the embryonic period, its action in the first case can be said to be maximal, in the second it is claimed to be minimal, in the third it appeared to be intermediate. Thus testosterone seems to exert an inhibitory action upon the left hemisphere of embryonic males. This is also indicated by comparison of motor activity during hemispheric inactivation: The number of the squares crossed in the open field during left hemisphere inactivation and with the right one functioning was approximately the same in the animals from all three groups, whereas motor activity when the left hemisphere was working was considerably lower in the males from “male litters” (Figure 38, I). When females were tested in the open field, changes were recorded in motor activity in the animals which were similar between all groups of females. Interhemispheric activity also did not differ substantially in females born in different litters. During the first minutes of testing, the number of squares crossed was smaller after right than left hemisphere inactivation. Later, in rats from the “male” and “neutral” litters, right hemisphere dominance was observed, while in animals from “female litters” interhemispheric differences were not significant (Figure 38, II). After recording exploratory reactions, the right hemisphere appeared, as a rule, to be dominant in females from all the three groups.

The results obtained from studying male rats should be compared, first of all, to the hypothesis of N.Geschwind (1983, 1984), according to which androgen secreted by the testes of the male embryos exerts an inhibitory action upon the left hemisphere in humans, and disrupts the function of the thymus. As a result, a deficit of left hemisphere functions may arise in boys (in particular left-handedness and speech disruptions), as well as a predisposition towards autoimmune diseases. Our data demonstrate the truth of this supposition: Not only for humans, but also for non-human animals, the prenatal action of increased doses of androgens causes inversion of left hemisphere dominance, owing to the reduced activity of the left hemisphere in males. As mentioned above, in some areas, the thickness of the cortex of the right hemisphere in male rats is greater than that of the left hemisphere cortex (Diamond *et al.,* 1982). In a series of studies (Berrebi *et al.,* 1988; Denenberg *et al.,* 1989; Fitch *et al.,* 1990) the anterior and posterior regions of the corpus callosum showed sexual dimorphism, and were sensitive to the influence of sex hormones. In rats, in the process of development, interhemispheric asymmetry of estrogen receptors

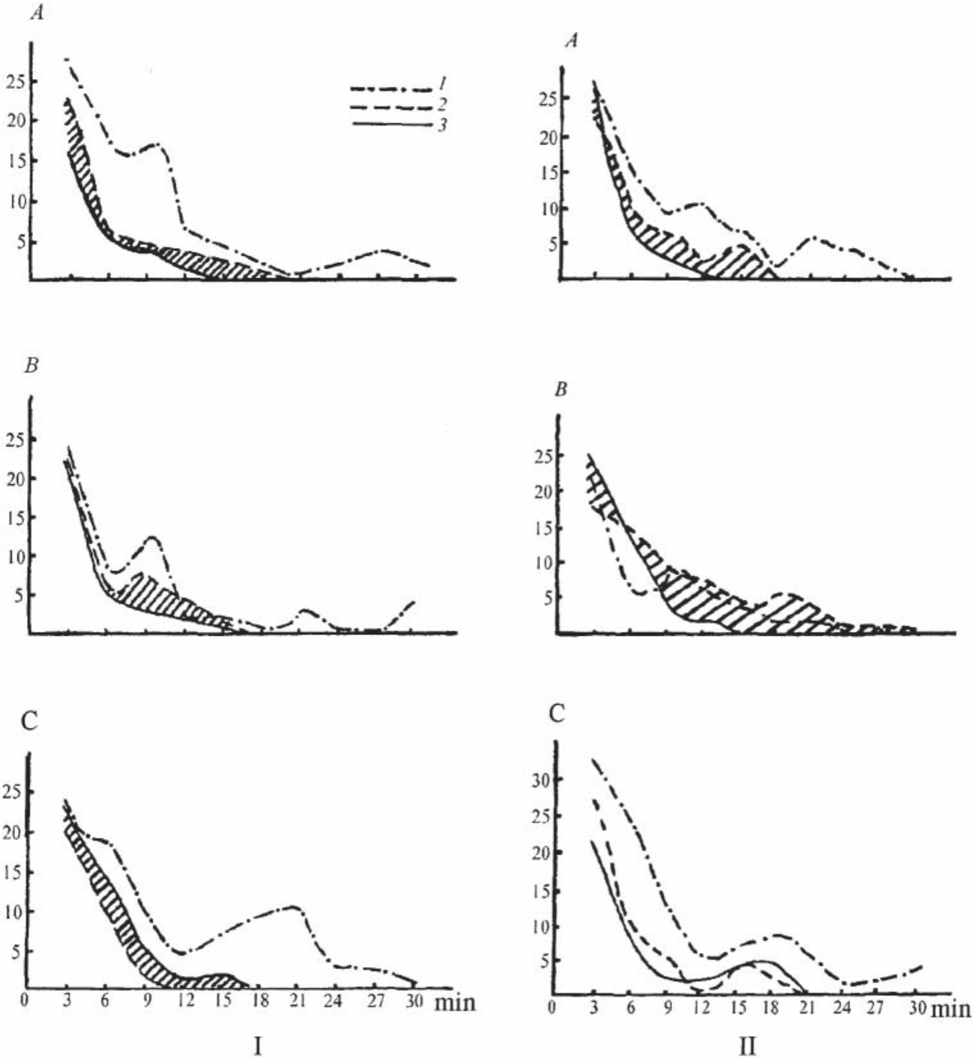

Figure 38: The influence of hemisphere inactivation on motor activity in the open field in male **(I)** and female **(II)** rats from litters with a greater number of males **(A)** and an approximately equal number of males and females **(B)** and with a greater number of females **(C)**. **abscissa:** time, min, **ordinate:** the number of squares crossed; **1**–the norm, **2**–after left, **3**–after right hemisphere inactivation.

has been observed, which is concerned with sex: In males, they are more numerous in the left hemisphere, in females in the right one (Demotes-Mainard *et al.,* 1990; Diamond, 1991). Androgens may exert an inhibitory action upon the left half of the brain, not only in males but also in females. This is indirectly indicated by a number of data on the structural and functional asymmetries described above. Thus in female rats, as distinct from males, left-sided tail orientation was found after birth, and in adult animals a left-sided direction of circling was observed. In the author's opinion both these asymmetries are determined by differences in content or level of metabolism of dopamine between the left and right sides of the nigrostriatal system: Its level is lower in the left side of the striatum (Glick and Shapiro, 1985). It should be noted that these asymmetries are intensified in females born in litters with a prevalence of males (Geschwind and Galaburda, 1985).

In our experiments, a distinct dominance of the right hemisphere in the "male" and "neutral" litters, i.e. in those in which there were more males, was observed in females. In the "female litters" (i.e. in those with few males) weak interhemispheric differences were observed. It can be suggested that, under the above conditions, excess action of testosterone inhibits the activity of the left side of the striatum, which results in the asymmetry of locomotion.

Keeping pregnant rats under stress also appeared to change the position of the tail in newborn animals, and intensifies indices of left-sided circling after amphetamine, and in adult females with this prenatal background, a decrease in the rate of dopamine metabolism in the left striatum has been observed (Fride and Weinstock, 1989). It is considered that keeping pregnant rats under stress affects the level of sex steroids during gestation: In males, demasculinization is observed, and lowered testosterone level. On the contrary, in females, sexual and maternal behaviour is defeminized, and aggression is intensified (Kinsley and Svare, 1985; Hoepfer and Ward, 1988). Both males and females whose mothers have been put under stress during pregnancy have a tendency for homosexual reactions (Ward, 1972; Dahlof *et al.,* 1980; Ward and Weisz, 1980; McLusky and Naftolin, 1981). The above facts do not affect cerebral asymmetry in males. Finally, one more consequence of males prevailing in the litter is a delay in sexual development of females observed earlier (Clark and Galef, 1988). In the studies of D.Nordeen and P.Jahr (1982) hypothalamic functional asymmetry in the regulation of ovulation in female rats was shown: Action of estradiol upon the area of the preoptic and ventro-medial nuclei on the left side in newborn rats caused disruption of ovulation, and made them sterile. This was not the case when this action was right-sided. Sexual development of females from "male litters" may be delayed due to the left-sided action of androgens. However, it should be noted that the prenatal action of testosterone (seen when females are treated with this hormone), changed left-sided tail posture in newborn females to the right-sided one (Rosen *et al.,* 1983), which does not agree with our supposition of the inhibitory action of androgens upon the left side of the brain. The above action may depend on the dose of the hormone. The quantity of androgens formed naturally in the organism (determined, for instance by keeping the mother under stress, or the prevalence of males in the litter) seems to be considerably smaller than in the above experiment. It should also be pointed out that inhibitory left-sided influence of androgens, and interhemispheric asymmetry associated with it, seem to be revealed at the level of the cerebral cortex in males and at the level of subcortical structures in females.

To conclude, we would like to list the main facts obtained from this part of the study. Neonatal gonadectomy in rats of both sexes appeared to result in elimination of functional interhemispheric asymmetry for control of the emotional resonance reaction, and also for motor and exploratory activity in the open field, these being observed in intact adult animals. Subsequent injection of steroid hormones did not result in restoring functional interhemispheric asymmetry for control of motor and exploratory activity in the open field. During the prenatal period, androgens were shown to exert an inhibitory action upon the left hemisphere of embryonic males, and to cause delay in sexual development in adult females.

4.3. THE INFLUENCE OF SEX HORMONES UPON INTERHEMISPHERIC ASYMMETRY IN MATURE ANIMALS

Now let us move on to presenting results obtained from the study of functional interhemispheric asymmetry in rats gonadectomized when they reached adulthood (Filippova, 1989a; Bianki and Filippova, 1992). Removal of sex glands was performed two weeks before the experiments. The experimental results were compared to those obtained from intact animals. As mentioned earlier (sect. 2.14), sexual dimorphism of interhemispheric asymmetry in carrying out the emotional reaction was manifested in different degreees of asymmetry in males and females. When control of behaviour in the open field was tested, sexual dimorphism was revealed as differences in the direction of asymmetry (Bianki and Filippova, 1992).

In elaborating the reaction of emotional resonance, the operated animals appeared to require approximately the same number of experiments for achieving the criterion for establishment of the reflex as did intact ones: 8–10 experiments. As a result, the reaction was developed in 82% of the individuals. Interhemispheric asymmetry for control of the reaction under discussion was not observed in males, since emotional resonance was revealed after both left and right hemisphere inactivation (Figure 39). Comparison with intact rats showed that weakening of interhemispheric asymmetry took place, due to a change in the function of the right hemisphere: During isolated action of this hemisphere the reaction was the same as during the function of the left. In other words, gonadectomy in males resulted in the increased activity of the right hemisphere (cf. Figure 15A, for unoperated rats). As a result, the reflex of emotional resonance was revealed not only during the function of the left hemisphere, as in the case of the intact rats, but also when only the right hemisphere was active. In females, gonadectomy exerted the opposite influence upon the lateralization of control for emotional resonance: The magnitude of interhemispheric asymmetry increased to almost threefold. Comparison with controls also revealed a change in the function of the right hemisphere, since, during its isolated action, disruption of the reflex was much greater than in intact individuals. Thus ovariectomy resulted in weakened activity of the right hemisphere as compared to the norm.

Study of the behaviour of gonadectomized rats in the open field showed that the number of the squares crossed during the first minutes of testing was practically the same as the corresponding magnitudes in intact animals (Figure 39, II). However, later motor activity in males was greater when the right hemisphere was functioning (but not when the left was functioning). Significant dominance of the right hemisphere was observed during the first period of testing and was characteristic of both motor and exploratory activity. In females, on the contrary, motor activity during this period was mainly determined by the function of the left hemisphere. The same hemisphere dominated in control of exploratory reactions in the first half of the experiments. Hence gonadectomy of adult rats caused inversion of hemispheric dominance for control of behaviour in the open field, in animals of both sexes, compared with intact animals. After orchidectomy the right hemisphere was dominant in males, whereas in females after ovariectomy it was the left. Expression of

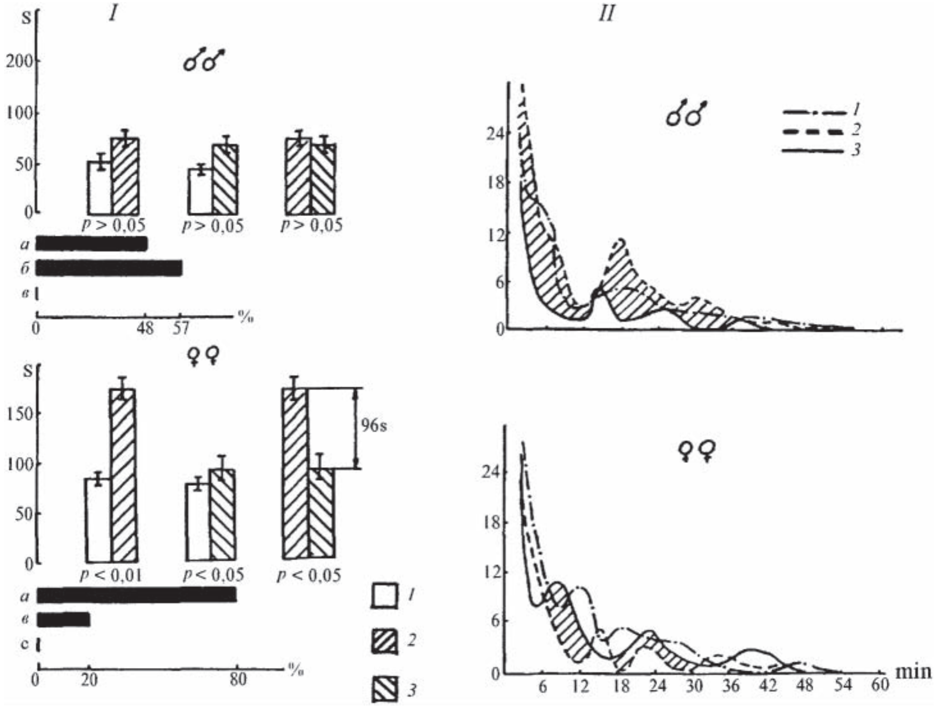

Figure 39: The influence of hemisphere inactivation on the reaction of "emotional resonance" **(I)** and motor activity in the open field **(II)** in rats gonadectomized at a mature age. **I:** ordinate: the period of staying in the preferred chamber, **1**–the norm, **2**–after left, **3**–right hemisphere inactivation, **a**–percentage of individuals with left hemisphere dominance; **b**–with right hemisphere dominance; **c**–percentage of ambilateral individuals. **II: abscissa:** time, min, **ordinate:** the number of squares crossed; **1**–the norm, **2**–after left, **3**–after right hemisphere inactivation.

interhemispheric asymmetry in gonadectomized rats was somewhat greater than in intact ones. The change of the dominant hemisphere in males may have been determined by increased activity of the right hemisphere, whereas in females activity of the right hemisphere was reduced: In the latter case, according to the mechanism of reciprocal interhemispheric relations, inhibitory influences upon the left hemisphere diminished, which in females resulted in right hemisphere dominance being replaced by left hemisphere one.

Thus removal of sex glands in adult rats affected mainly the right hemisphere in control of both the reaction of emotional resonance and behaviour in the open field, and caused reduction of the degree of interhemispheric asymmetry in the former case and reversal of the direction of asymmetry in the latter.

A question arises as to which factor in the above experiments was the critical one in regulating the degree of expression of interhemispheric relations: Sexual steroids as such, or their specificity in males and females, which seems to be determined by the genotype? We attempted to answer this question by injecting mature gonadectomized animals with hormones specific for animals of the opposite sex: The males received estradioldiproprionate, the females testosterone-proprionate, in doses indicated above.

Hormones were introduced two minutes before the test experiments. Functional interhemispheric asymmetry was studied in reactions of emotional resonance and behaviour in the open field.

Establishing an emotional avoidance reaction preceded in the same way as in intact rats, without major differences in the rate of establishment (Figure 40). With both hemispheres remaining active, the time the animals stayed in the preferred chamber did not exceed 50 s, either in males or in females, which proves the stability of expression of the reflex. During right hemisphere inactivation, the behaviour of the animals changed very little, whereas inactivation of the left caused a distinct disruption of the reflex. Hence it was the left hemisphere that dominated in carrying out the reaction of emotional resonance in animals of either sex. It is characteristic that the degree of interhemispheric difference was greater in males than in females. Comparison of the results obtained with those from intact individuals, and also with those from rats which had been gonadectomized when adult and had not received hormones, showed that estradiol injection administered to the males resulted in an increase of interhemispheric differences to a magnitude comparable to that in intact animals. In other words, estradiol administration to the males restores interhemispheric asymmetry which had been eliminated as the result of castra

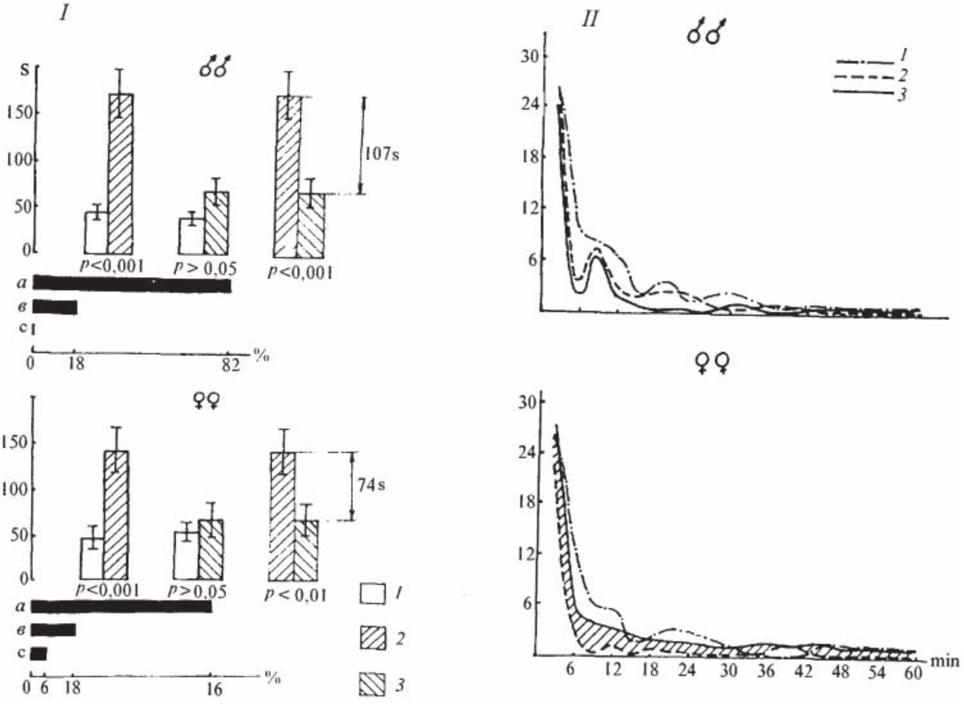

Figure 40: The influence of hemisphere inactivation upon the reaction of "emotional resonance" **(I)** and motor activity in the open field **(II)** in rats gonadectomized at a mature age with subsequent administration of estradiol-diproprionate to the males and testosterone-proprionate to the females. **I:** ordinate: the period of staying in the preferred chamber, **1**–the norm, **2**–after left, **3**–right hemisphere inactivation, **a**–percentage of individuals with left hemisphere dominance; **b**–with right hemisphere dominance; **c**–percentage of ambilateral individuals. **II: abscissa:** time, min, **ordinate:** the number of squares crossed; **1**–the norm, **2**–after left, **3**–after right hemisphere inactivation.

tion. It should be noted that intensification of asymmetry was determined by a change in the function of the right hemisphere, since it was with this hemisphere remaining active that the reflex was revealed to be considerably worse than in castrated rats (Figure 40, I). On the contrary, administration of testosterone to males did not result in major changes in interhemispheric asymmetry, as compared to those after adult gonadectomy, since in both groups of rats a distinct dominance of the left hemisphere was observed, the magnitude of interhemispheric asymmetry being greater than that in intact animals.

Thus estradiol administration to gonadectomized males was effective as regards interhemispheric asymmetry of the function under investigation, and to some extent similar to the influence of androgens in the intact organism, whereas testosterone administration to the ovariectomized females did not change the pattern of interhemispheric differences characteristic of these animals.

Testing gonadectomized rats after the introduction of steroid hormones in the open field did not reveal any significant differences in the number of recorded reactions between males and females (Figure 40, II). In males, interhemispheric asymmetry for motor and exploratory reactions was eliminated during the whole period of observation. In females, from the very first minutes of exposure up to the end of the experiment, distinct left hemisphere dominance was observed. The same can be said about the study of exploratory reactions in the first half of the experiment. In comparing these data with results obtained from intact and castrated rats, it was found that administering estradiol to males, as for the reaction of emotional resonance, changed the pattern of interhemispheric asymmetry observed in castrated individuals, but did not restore it fully. Injecting females with testosterone did not affect the direction of interhemispheric differences which had been recorded in ovariectomized rats: In both groups, the left hemisphere was dominant.

It was indicated above that gonadectomy and hormonotherapy were conventional techniques for investigating the influence of sex steroids. However, it should be born in mind that the influence of gonadectomy is due not exclusively to the absence of sexual steroids released by sex glands, but involves a chain of metabolic changes, every link of which may affect brain asymmetry. We wished to eliminate these drawbacks of the methodology. Therefore we performed an additional experimental series, where we studied interhemispheric differences in control of rats' behaviour in the open field, after administration to intact (un-gonadectomized) animals, of hormones specific for animals of the opposite sex. In males, after estradiol administration, a distinct interhemispheric asymmetry for motor activity was observed, of the same direction as that in intact rats. Left hemisphere dominance was recorded almost from the very beginning of the exposure, and practically to the end of the experiment. The left hemisphere also prevailed in control of exploratory reactions. It should be noted that the magnitude of interhemispheric differences in control of emotion was considerably greater than in intact rats. In females, after testosterone administration, interhemispheric asymmetry was not strongly expressed. A short-term dominance of the left hemisphere was observed only at the end of the exposure. Interhemispheric differences in exploratory reactions were also not significant. Thus, in this experimental series, a greater efficacy of estradiol upon males than that of testosterone upon females was confirmed, such as was also observed in gonadectomized rats.

Summing up this part of the study it may be concluded that removal of sex glands in mature rats exerted a different influence upon interhemispheric relations in animals of the two sexes, which was determined mainly by changed function of the right hemisphere.

Orchidectomy resulted in the increased activity of the right hemisphere, whereas ovariectomy reduced it. Testosterone and estradiol seem to exert a similar influence upon interhemispheric asymmetry in males. Under their combined action, the inhibitory pressure upon the right hemisphere may become stronger, which is indicated by the intensification of left hemisphere dominance in uncastrated rats after estradiol administration. The role of estradiol in regulation of interhemispheric asymmetry in rats is more specific, which is indicated by the fact that administering testosterone to the rats, castrated when adult, does not affect the magnitude of asymmetry, whereas in uncastrated individuals, it results in elimination of interhemispheric differences.

Data from the published literature also support the idea that removal of sex glands and administration of sex steroids in mammals of mature age cause different changes. Ovariectomy of females increases the binding of corticosterone derivatives in the rat hypothalamus, thereby removing sex differences, while orchidectomy of males is ineffective (Turner and Weaver, 1985). Removal of sex glands in females, as distinct from males, weakens their circling behaviour caused by electric stimulation of the hypothalamus (Robinson *et al.,* 1980). The same operation, performed on females, reduces the stimulating effect of amphetamine upon the striatal tissue; further action of estradiol and progesterone restored the effect of amphetamine, which points to the activating influence of estrogens upon dopamine metabolism (Becker and Ramirez, 1980). However, the reactivity of the parietal cortex in females, in response to light stimulation increases after ovariectomy (Polshin *et al.,* 1986). Removal of testes in males reduces the frequency of instrumental reaction to a level characteristic of females (Heinsbrock *et al.,* 1987). Gonadectomy in males (both neonatal and in adult animals) intensifies activity in the open field (Slob *et al.,* 1986), whereas in females it does not affect its expression (Bengelloun *et al.,* 1976; Slob *et al.,* 1986). However castration and androgenization of females do not affect sex differences under stress: Synthesis and secretion of corticosterone in females were greater than in males (Anischenko *et al.,* 1989). It should be noted that the above facts do not reveal the influence of sex hormones upon lateralization of functions. The activating action of androgens upon growth of neurones has been found in song birds of several species. The distinguishing characteristic of these species is that only males sing, and their hyperstriatum ventrale, *pars caudale* (HVc) controlling vocalization contains more neurones than that of females. For example, in the zebra finch this sexual dimorphism appears at a certain period of development, when the number of neurones is retained in males, but is reduced in females (Nordeen and Nordeen, 1988). The HVc controlling vocalization swells every spring in males, under the action of testosterone, and then shrinks. Left-sided functional asymmetry for control of vocalization was shown, yet no morphological asymmetry of nuclei was revealed (Nottebohm, 1977). Administration of testosterone to adult females gives rise to vocalization characteristic of males, the song complexity correlating with the size of the nuclei: The HVc was larger in the androgenized females than in the controls, but smaller than in the males (Pohl-Apel, 1985; Nordeen and Nordeen, 1988). Thus the data from the literature, as well as the results of our own experiments, indicate the influence of the current level of sex steroids upon functional sex differences, and also upon the reactivity of brain structures.

Later on we made an attempt to test this observation by recording electric reactions in the cortex of the left and right hemisphere, in intact and gonadectomized rats, after administration of sex steroids. The experiments were performed on adult rats of both sexes, using the technique of evoked potentials (EP). A subgroup of animals was gonadectomized two weeks before the experiments. EPs were recorded from symmetrical points in Field 18 (Krieg, 1946). Binocular stimulation was carried out by means of equalized light flashes. The following procedure was adhered to: After background EP recording, the hormone was administered (1 ml of the oil solution given intra-abdominally). Males and females were injected with testosterone-proprionate and estradioldiproprionate in doses given above. EPs were recorded 15 min after injection and later, at intervals of 30 min, for four hours. The experiment established that, in response to light stimulation in symmetrical points of Field 18, positive-negative EPs could be recorded. As a result, functional interhemispheric asymmetry was observed: The left hemisphere prevailed in the magnitude of the positive EP component.

Changes in the amplitude of response in males and females after estradiol and testosterone administration were similar (Figure 41). In males, after administration of hormones, the amplitude of both EP components increased. This effect was observed clearly two hours after the injection, and in both hemispheres a significant increase in the amplitude of the positive component took place. It should be noted that the graphs of the averaged EP magnitudes did not always reflect the individual peculiarities of EP dynamics, i.e. the periodic inversions of interhemispheric asymmetry. As a rule, after the first recording of EPs, their amplitudes in symmetrical points of the left and the right hemisphere were different. During subsequent recording, the asymmetry could retain its direction, or could be inverted. The phenomenon of the fluctuation of the dominant activity in rats has been described earlier, after prolonged binocular stimulation with light flashes of considerable intensity (Bianki and Filippova, 1973): Under conditions of functional overloading of the visual system, inversions of interhemispheric asymmetry of EPs in the visual cortex were observed every 36 min on average. In the present study, the change in the sign of asymmetry in intact animals was observed each 90 min, on average, which seems to be associated with weaker stimulation, and the presence of intervals between stimulation periods.

In females, after administration of sex steroids no significant change in asymmetry of EPs was observed. For the majority of females, as well as for males, periodic inversions of EP asymmetry, and prevalence of response amplitude in the left hemisphere, were common. Administration of hormones to gonadectomized rats caused an increased amplitude of the positive and negative EP components, in both hemispheres. The greatest effect was observed three hours after injection, and then the EP amplitude decreased.

Further analysis showed that only in uncastrated males did the amplitude of the positive component of the EP in the right hemisphere increase significantly more than in the left. In other words, in these animals the right hemisphere responded to hormonal action more strongly. In animals of the other groups, changes in EP amplitudes were relatively similar for right and left hemisphere. In gonadectomized male and female rats, as well as in intact animals, inversion of interhemispheric EP asymmetry was observed.

Thus administration of sex steroids activated the right hemisphere of males selectively, which agrees with results obtained from the above behavioral experiments. However, by means of EP recording, it was impossible to reveal the inhibitory the action of sex hormones upon the right hemisphere of the males which had been observed in the study of the conditioned emotional reaction, and in behaviour in the open field. This may be accounted for by the fact that, in the latter case, complex behavioral actions were investigated, which

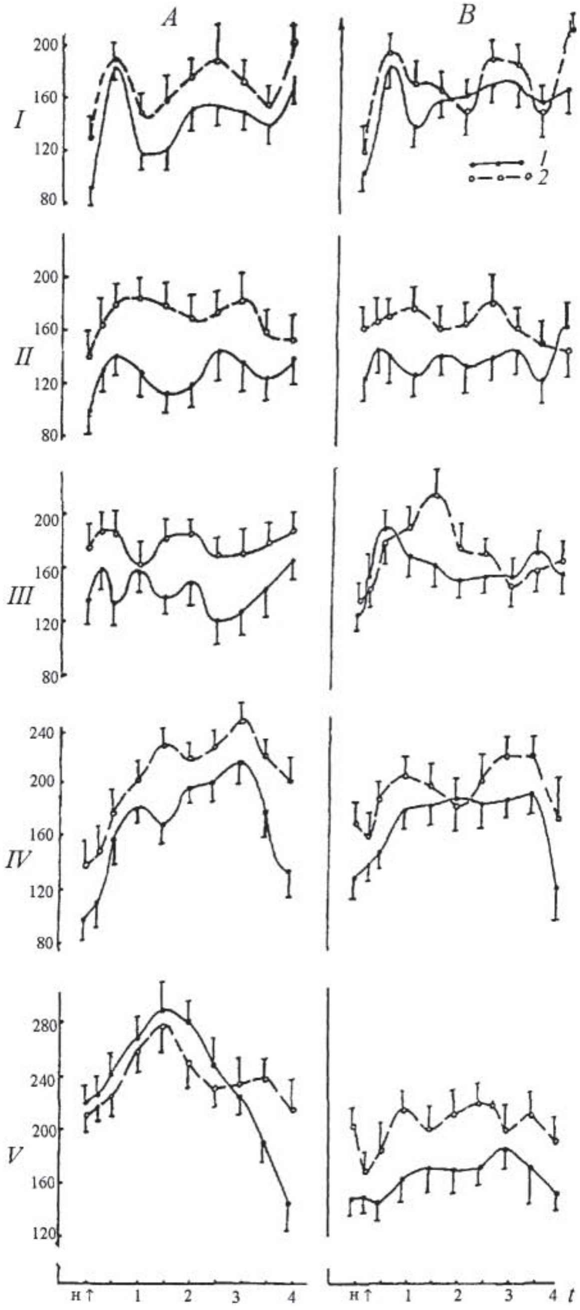

Figure 41: The influence of sex steroid hormones on EP dynamics in the rat visual cortex. **A**–positive, **B**–negative phase. **I**–intact males, **II**–intact females, **III**-control animals, **IV**–gonadectomized males, **V**–gonadoctomized females. **1**–EP amplitude in the right, **2**–in the left hemisphere. **Ordinate:** EP amplitude, mV, **abscissa:** the period of observation, hours; **H**=norm: before hormone administration, the **arrow:** the moment of injection.

were based on the integrative activity of the whole brain. It should also be noted that gonadectomy seems to have changed the interhemispheric relations found in intact rats. This resulted in reduction in the frequency of inversion of the asymmetry of interhemispheric EP, and in the magnitude of interhemispheric differences.

4.4. THE INFLUENCE OF CYCLIC CHANGES IN THE LEVEL OF SEX HORMONES UPON INTERHEMISPHERIC ASYMMETRY

The estrous cycle in female rats is known to consist of the following phases: proestrus, estrous, metaestrus, and diestrus. Let us consider changes in interhemispheric asymmetry in the course of the estrous cycle (Filippova, 1996).

At first, animals were tested using the open field method, during each of the four stages of the cycle. As a rule, hemispheric inactivation was carried out in the same individual during each stage of the cycle. During each stage, an approximately equal number of rats (about 20) was examined during left or right hemisphere inactivation, and also during their active state. The characteristics of behaviour were recorded using the "Etograph-neuron" setup, which makes it possible to record up to 20 reactions. In addition, motor and exploratory forms of behaviour, displacement activities (washing and sniffing) and emotional activities (freezing and defecating) were recorded. Each animal was tested for 10 min. The following reactions were recorded:

1) GMA-1–general motor activity during the first minute of the experiment.
2) GMA-5–general motor activity during (the first) 5 min.
3) GMA-10–general motor activity during 10 min.
4) MAC-5–motor activity in the centre of the field during 5 min.
5) MAC-10–motor activity in the centre of the field during 10 min.
6) MAP-5–motor activity in the periphery of the field during 5 min.
7) MAP-10–motor activity in the periphery of the field during 10 min.
8) GRHL-5–the general number of hind leg rearings during the first 5 min.
9) GRHL-10–the general number of hind leg rearings during 10 min.
10) RHLC-5–the number of hind leg rearings in the centre of the field during 5 min.
11) RHLP-10–the number of hind leg rearings in the periphery during 10 min.
12) PIO-5–the number of times the animal peeped into openings during the first 5 min.
13) PIO-10–the number of peepings into openings during 10 min.
14) FRE-5–the number of time the animal froze during the first 5 min of the experiment.
15) ERE-10–the number of time the animal froze during 10 min.
16) SNIF-5–the number of sniffings during the first 5 min of the experiment.
17) SNIF-10–the number of sniffings during 10 min.
18) WASH-10–the number of episodes of washing during the first 10 min of the experiment.

The behavioral reactions were assessed with respect to two parameters: the frequency of the ocurrence of the reaction (reactions 1–18), and their duration (reactions 14–18).

When comparing the data obtained from intact females during different stages of their estrous cycle, the number of reactions reflecting the level of exploratory and motor activity (RHLC-5, GRHL-10, PIO-10, M AC-10) appeared to be significantly greater in estrus,

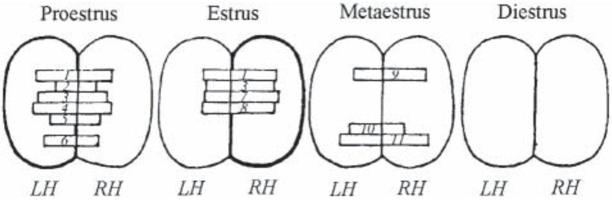

Figure 42: Interhemispheric asymmetry of the behavioral reactions of female rats in the open field during different phases of the estral cycle. The length of the segments against the background of each hemisphere shows the expression of reactions while the left (LH) or the right (RH) hemisphere is active. 1–GRHL-10, 2–GRHL-5, 3–RHLP-10, 4–MAP-10, 5–MAP-5, 6–SNIF-10, 7–PIO-10, 8–PIO-5, 9–GMA-1,10–FRE-5, 11–WASH-10.

while displacement activity (WASH-10, SNIF-10) during this period was expressed less strongly (Figure 42[11]). On the contrary, in diestrus displacement activity increased, and at the same time locomotor reactions and exploratory activity decreased. The only exception was GMA-1 which was expressed to a lesser degree in the metaestrus phase of the cycle.

Now let us consider the influence of hemispheric inactivation upon the rats' behaviour during different phases of the estral cycle. In proestrus, changes in the frequency of occurrence and duration of reactions PIO-10, GRHL-10, GRHL-5, RHLP-10, RHLC-5 were observed during left and right hemisphere inactivation, although the most strongly expressed decrease in activity was recorded during left hemisphere inactivation. During estrus the magnitudes of the parameters of reactions PIO-10, GRHL-10, GRHL-5, RHLP-10, MAC-10 also decreased during inactivation of either hemisphere, but during this period the deficit of behaviour was greater when the right and not the left hemisphere was inactivated. The only exception was GMA-1 which increased maximally during left hemisphere inactivation. Displacement activity (WASH-10, FRE-10, FRE-5, SHIF-5, SNIF-10 reactions) intensified during inactivation of either hemisphere. A greater expression of left hemisphere dominance in proestrus, compared to right hemisphere dominance during estrus was observed. In the metaestrus phase of the cycle, the influence of hemispheric inactivation was similar to that during proestrus. The reactions GRHL-10, GRHL-5, RHLP-10, WASH-10 were revealed more during the active state of the left hemisphere. At the same time, unlike estrus and proestrus, in metaestrus, both left and right hemisphere inactivation caused intensification (rather than decline) of motor reactions, i.e. of MAC-10, MAC-5, GMA-1 reactions. Moreover, this intensification was stronger during right hemisphere inactivation. In diestrus, significant differences between the characteristics of the animal behaviour during hemisphere inactivation and in intact animals were revealed for the smallest number of recorded reactions. For GRHL-10, GRHL-5 and RHLP-10, (using both indices) greater reduction was observed during right hemisphere inactivation. Motor activity during metaestrus also increased during inactivation of either hemisphere, but especially after right hemisphere inactivation.

Thus at the stage of proestrus and estrus, when motor and exploratory reactions were at their peak of expression, both left and right hemisphere inactivation caused a decrease in active forms of behaviour. In metaestrus and diestrus, during right and left hemisphere inactivation, motor activity in the centre of the field increased, and also GMA-1. The passive forms of behaviour increased during inactivation of either hemisphere.

The presence of interhemispheric asymmetry was revealed by comparing the parameters of identical reactions during right and left hemisphere inactivation (Figure 44). Interhemispheric differences in control of some reactions were expressed significantly during all phases of the estrous cycle except for diestrus. Thus, in proestrus, the left hemisphere dominated for motor and exploratory behaviour. This was the case in GRHL-10, GRHL-5, RHLP-10, SNIF-10, MAP-10, and MAP-5. In estrus, interhemispheric differences were established only for exploratory reactions GRHL-10, RHLP-10, PIO-10, and PIO-5, the leading hemisphere being the right one this time. In the metaestrus phase of the cycle, the right hemisphere dominated for control of passive forms of behaviour FRE-5, WASH-10, whereas the left one prevailed in the control of GMA-1 (Figure 42). Consequently, interhemispheric asymmetry with the left hemisphere being dominant was expressed at the stage of proestrus; in estrus inversion of interhemispheric differences was observed; in metaestrus right hemisphere dominance decreased; in diestrus interhemispheric differences were eliminated. The above direction of asymmetry seemed to be critical for the right hemisphere dominance for control of general motor activity, seen in intact rats when the phase of the estrous cycle was not identified. Since the duration of estrus is longer than that of proestrus, it may be supposed that, in any random sample of animals, there was a greater number of individuals in estrus than in proestrus.

Since interhemispheric asymmetry was expressed most of all during proestrus and estrus, it was during these stages that we investigated the role of the left and right hemisphere in the model of emotional resonance. It was found that, in transition from proestrus to estrus, the average number of the rats' transitions from chamber to chamber increased, and the time the animals stayed in the preferred chamber was shortened, in other words the emotional reaction was more pronounced (Figure 43). The corresponding indices in proestrus constituted 3.6 transitions and 72.2 s, whereas in estrus there were 5.1 transitions which lasted 46.1 s. When the hemispheres were inactivated, a change in the above indices was observed in both cases. Thus, in proestrus, after left hemisphere inactivation, the average number of transitions increased to 4.2, the average period of staying in the dark chamber was reduced to 44.3 s, i.e. facilitation of emotional resonance occurred. During right hemisphere inactivation, changes in the rats' behaviour were less pronounced, the average number of transitions being 2.7, the period of staying in the preferred chamber being 65.7 s. In contrast, in estrus, left hemisphere inactivation resulted in reducing the average number of transitions as compared to the intact animals, to 3.7, and prolonging the stay in the dark chamber from 48.1 to 69.4 s on average, i.e. the emotion was inhibited. These changes were even more pronounced after right hemisphere inactivation: The average period of stay in the dark chamber was 74.7 s., the number of transitions was 3.8. Thus, after inactivation of the cerebral hemispheres in proestrus the reaction in question was facilitated, in estrus it was inhibited, the role of the hemispheres being different. It is concluded that in intact animals, in proestrus the left hemisphere was dominant for emotional reaction, whereas in estrus the right one dominated for the activating influence.

When comparing the above data, obtained by studying the estrous cycle, to those available in the literature it should be noted that the prevalence of active forms of behaviour during proestrus and estrus agrees with the dynamics of the motor activity of rats in the running wheel, described earlier (Polshin and Mhktiarov, 1984). Estrogens, whose secretion increases in proestrus, seem to exert a stimulating influence upon the animals' motor

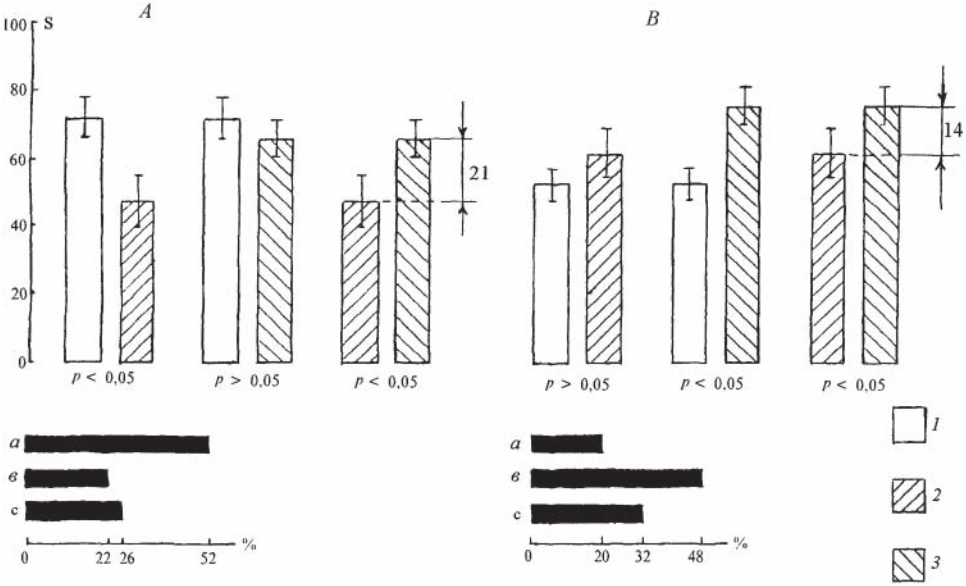

Figure 43: The influence of hemisphere inactivation on the reaction of "emotional resonance" in female rats during proestrus **(A)** and estrus **(B)**. **ordinate:** the period of staying in the preferred chamber; **abscissa** time, min, **1**–the norm, **2**–after left, **3**–right hemisphere inactivation, **a**–percentage of individuals with left hemisphere dominance **b**–with right hemisphere dominance **c**–percentage of ambilateral individuals.

activity. An activating influence of estradiol upon brain structures was observed in a number of studies. Thus, estradiol injection intensified the activity of neurones in the amygdala (Schiess *et al.,* 1988). In the opinion of some authors, estrogens can modulate the activity of hippocampal and hypothalamic neurones (Jones *et al.,* 1990; Schumacher *et al.,* 1989). The stimulating action of phenamine upon dopamine secretion in the nigrostriatal system increased during proestrus and estrus (Becker *et al.,* 1982; Becker and Beer, 1986). It is during this period that the content of dopamine and its derivatives in the striatum increases (Crowley *et al.,* 1978). Increased estrogen content in proestrus may have caused higher emotionality in rats in our experiments, which was critical for the inhibitory character of cortical influences; in the transition to estrus, the force of emotions diminished and the inhibitory character of the neocortex was replaced by an activating one. The relative prevalence of activating influences in the hormone-saturated phases of the cycle precludes inversion of the conditioned reactions, which was noted during rats' relearning in the maze (Arushunian *et al.,* 1988). The results of our study testify to the fact that the predominant role of the left hemisphere is associated with estrogen concentration. The dominance of the right hemisphere in estrus is difficult to explain by the action of just one factor. According to the conceptions developed in our laboratory, the dominanta principle underlies interhemispheric asymmetry (Bianki, 1985, 1989). On the basis of this principle, we can suggest that left hemisphere dominance during proestrus exerts an inhibitory action upon the right hemisphere. In the transition to estrus, reinforcement of the left hemisphere dominanta diminishes, due to a change in hormonal influences. As a result, the inhibitory action upon the right hemisphere weakens, and inversion of asymmetry sets in. Inversion of interhemispheric asymmetry in the transition from proestrus to estrus may also be associated with the force of emotions. Earlier it was shown that the left hemisphere controls relatively weak emotions, whereas stronger emotions are controlled by the right hemisphere (Bianki *et al.,* 1985; Murik, 1985). Such a direction of asymmetry was observed in our experiments when the rats' reactivity weakened, in the transition from proestrus to estrus.

4.5. THE INFLUENCE OF PREGNANCY UPON INTERHEMISPHERIC ASYMMETRY

Pregnancy is known to be accompanied by sharp changes in females' hormonal status. During this period, endocrine regulation is carried out mainly by the hormones of the pituitary gland, the ovaries and the placenta. Among them, the steroid hormones, estrogens and progesterone have a special place. Their concentration, and also content of chorionic gonadotrophin are increased several-fold during different stages of pregnancy in mammals (Karsh *et al.,* 1987). As a result, according to the mechanism of negative feedback, secretion of gonadotrophic pituitary hormones decreases: This includes follicle-stimulating hormone (FSH) and luteinizing hormone (LH). During pregnancy, there is an increase in prolactin and oxytocin, and secretory activity of the adrenal glands is elevated. As mentioned above, the action of estrogen exerts a modulating influence upon brain structures. In particular, this is indicated by changes in the convulsive threshold in women after exogenous hormone administration (Schumacher *et al.,* 1989), by increased neuronal activity under the action of estradiol (Schiess *et al.,* 1988), and also by the stimulating action of estrogens upon dopamine secretion in the striatum (Crowley *et al.,* 1978; Becker *et al.,* 1982; Becker and Beer, 1986). It was shown that, during pregnancy, resistance to stress in rats was intensified (Chernositov *et al.,* 1994a). Functional brain asymmetry in rats, tested by the direction of motor reactions, correlates with the asymmetry of the size of the paired organs in the reproductive system–the uterine horns, and the ovaries. Unilateral extirpation of one uterine horn and an ovary caused changes in motor asymmetries, which intensified in the remaining horn as pregnancy developed (Chernositov *et al.,* 1994b).

Investigation of the influence of pregnancy in women upon interhemispheric asymmetry was carried out by A.B.Poroshenko and his associates (1985a,b). In these studies, it was shown that the lateral disposition and function of the placenta during unigerminal pregnancy forms the gestational influence on functional asymmetry of the brain. This is indicated by the reduction of visual EPs in the hemisphere contralateral to the side of the placental disposition. Hazards during pregnancy are accompanied by inversion of asymmetry of interhemispheric EPs. The probability of early toxicosis is increased when the laterality of the placental disposition does not coincide with the direction of the motor asymmetries in the mother's body (Poroshenko, 1985; Poroshenko *et al.,* 1985a,b). Thus changed levels of hormones during pregnancy affect the behaviour in both humans and animals, and also the characteristics of electrophysiological indices of function of the cerebral hemispheres.

The above data gave rise to a suggestion that some factor associated with a change in hormonal status can also influence interhemispheric relations and their electrophysiological manifestation–such as transcallosal responses (TCR). Our study was performed on drugged pregnant cats, using the method of multiple topographical recording of homotopical TCRs (Bianki *et al.,* 1992). The age of the embryo did not exceed four weeks. Non-pregnant cats served as controls. The sequence of TCR recording from different cortical zones was as follows: First from the visual and parietal zones, then from the auditory cortex of the right hemisphere, from the somatosensory and sensorimotor zones of the right hemisphere, and finally from symmetrical somatosensory and sensorimotor areas of the left hemisphere.

In the above experiments TCR characteristics were found to be considerably different between pregnant and non-pregnant cats. Pregnancy results in the intrahemispheric reorganization of the stream of transcallosal excitation, which results in shifting the focus of maximum activity in pregnant cats in the latero-caudal direction. The following changes in amplitude-temporal TCR parameters in the cortical areas under investigation were recorded in pregnant cats: The latency was diminished in the somatosensory area of both hemispheres, and also in the sensorimotor area of the left hemisphere, whereas in the visual, auditory and parietal cortical zone it increased, the greatest changes being observed in the auditory cortex of the left hemisphere. The TCR amplitude mainly declined in the somatosensory and auditory cortex of the right hemisphere, and increased in the visual and parietal cortex (also in the right hemisphere). In the sensorimotor area, the TCR amplitude increased in the left hemisphere of pregnant cats and declined in the right. In other words, in pregnant cats a change in the amplitude-temporal parameters of TCRs occurred in different cortical sites, which can be treated as an index of the changes in functional importance of some cortical areas in the course of pregnancy, observed earlier by some authors (Kulikov *et al.,* 1982; Karpov, 1990).

A considerable redistribution of transcallosal functional connections during pregnancy is reflected in the organization of interhemispheric asymmetry. Let us consider first the changes in interhemispheric differences in pregnant cats using the index of the average TCR amplitude in different cortical areas. Thus, in the sensorimotor area, a decline of TCR asymmetry, from right hemisphere dominance in non-pregnant cats, to an individual form of asymmetry in pregnant ones was observed. In the visual cortex, asymmetry increased, with a distinct right hemisphere dominance in pregnant cats. In auditory cortical fields, unlike the rest of the areas under investigation, left hemisphere TCR asymmetry increased. In the sensorimotor area of the cortex inversion of dominance from left- to right-hemispheric was observed as the magnitude of interhemispheric differences grew. In the parietal zone of the cortex, interhemispheric TCR asymmetry in pregnant cats diminished.

Using the index of positive-negative TCRs, in the somatosensory cortex, asymmetry with right hemisphere dominance appeared to be present only in the group of non-pregnant cats (Table 19). Among pregnant animals, individuals with right hemisphere dominance with respect to TCR amplitude in the visual cortex prevailed, whereas among non-pregnant animals, the left hemisphere was dominant. The number of animals with unidirectional left hemisphere asymmetry of TCRs in the parietal cortex decreased. Interhemispheric differences of negative-positive TCRs in the group under investigation were less strongly expressed on the whole than those of positive-negative responses (Table 20). As a rule, interhemispheric asymmetry was individual. Thus in pregnant animals, negative-positive TCRs in all the cortical areas under study were characterized by diminished asymmetry, while asymmetry of positive-negative TCR could decline,

Table 19. The number of animals with asymmetrical amplitudes of components of positive-negative TCRs for pregnant and nonpregnant cats

The cortical area under investigation	*Groups of animals*	*The number of animals*	*The positive component*			*The negative component*		
			with functional interhemispheric asymmetry	*with the dominant*		*with functional interhemispheric asymmetry*	*with the dominant*	
				right hemisphere	*left hemisphere*		*right hemisphere*	*left hemisphere*
Somatosensory	Pregnant	13	9	4	5	9	4	5
	Nonpregnant	13	10**	8*	2	10**	5	5
	All the females	26	19**	12	7	19**	9	10
Visual	Pregnant	13	11*	7	4	12**	9*	3
	Nonpregnant	13	12**	3	9	12**	3	9*
	All the females	26	23**	10	13*	24**	12	12
Auditory	Pregnant	12	10**	2	8	10**	2	8*
	Nonpregnant	13	9	3	6	10*	4	6
	All the females	25	19**	5	14*	20**	6	14*
Sensorimotor	Pregnant	12	11**	2	9*	12**	5	7
	Nonpregnant	13	10*	8*	2	9	8*	1
	All the females	25	21*	10	11	21**	13	8
Parietal	Pregnant	13	13**	6	7	11**	5	6
	Nonpregnant	13	11**	1	10**	11**	5	6
	All the females	26	24**	7	17*	22**	10	12

Note. Significance of asymmetry is not less than 0.95 (*), 0.99(**).

Table 20. The number of animals with asymmetrical amplitudes of components of negative-positive TCRs for pregnant and nonpregnant cats

The cortical area under investigation	*Groups of animals*	*The number of animals*	*The positive component*			*The negative component*		
			with functional interhemispheric asymmetry	*with the dominant*		*with functional interhemispheric asymmetry*	*with the dominant*	
				right hemisphere	*left hemisphere*		*right hemisphere*	*left hemisphere*
Somatosensory	Pregnant	11	8	5	3	8	5	3
	Nonpregnant	11	9*	7	2	9*	7	2
	All the females	22	17**	12*	5	17**	12	5
Visual	Pregnant	13	11*	5	6	11**	5	6
	Nonpregnant	13	8	3	5	8	3	5
	All the females	26	19**	8	11	19**	8	11
Auditory	Pregnant	12	10**	5	5	10**	5	5
	Nonpregnant	13	10**	6	4	11*	6	5
	All the females	25	20**	11	9	21**	11	10
Sensorimotor	Pregnant	12	8	4	4	8	4	4
	Nonpregnant	10	8*	3	5	9	4	5
	All the females	22	16*	7	9	17**	8	9
Parietal	Pregnant	13	8	2	6	7	3	4
	Nonpregnant	13	11**	5	6	11**	5	6
	All the females	26	19**	7	12	18*	8	10

Note. Significance of asymmetry is not less than 0.95 (*), 0.99(**).

change in direction even to the point of inversion (Bianki, 1985), or else it could be intensified. On the whole, the above data are indications of restructuring of the pattern of TCR asymmetry in different cytoarchitectonic areas in pregnant cats.

It was shown that, in pregnant cats, interhemispheric restructuring of the transcallosal stream of excitation, and also changes in interhemispheric asymmetry, occurred with different participation of the left and the right hemisphere. The latency of response in the somatosensory cortex was mainly reduced in the right hemisphere. TCR amplitude in pregnant females in the sensorimotor cortex diminished as a result of its reduction in the right hemisphere. In the visual area, TCR amplitude increased in the right hemisphere, i.e. this hemisphere became dominant in pregnant animals. In the auditory cortex of pregnant females, weakening of the TCR amplitude in the right hemisphere resulted in left hemisphere dominance. In the sensorimotor cortex an increased amplitude of responses in the left hemisphere, and its decrease in the right, was observed. At the same time pregnancy caused intensification of the interhemispheric asymmetry for which the left hemisphere was responsible. Transformation of TCR amplitude characteristics is mainly associated with the right hemisphere. As a rule this was observed in the primary projection areas of cortex in pregnant cats. At the same time, in the left hemisphere, changes are found mostly in the temporal characteristics of the transcallosal stream. They are mainly observed in the sensorimotor cortex.

Thus in cats, during pregnancy, a certain restructuring occurs, of both the mosaic of interhemispheric influences and the characteristics of interhemispheric asymmetry. At the same time, changes in the functional state of cortical primary projection areas in the right hemisphere, and the sensorimotor cortex of the left one is observed, with weakening of functional interhemispheric asymmetry; on the whole, the brain comes to have lower contrast.

4.6. CONCLUSION

First of all, let us compare some data described in the present chapter with those available in the literature. It was shown that sex hormones exert an influence upon the cerebral cortex, and probably upon some subcortical formations, changing interhemispheric asymmetry. It is known from the literature that sex steroids act upon the size and ultrastructure of the corpus callosum, the thickness of the cortex and neuronal plasticity (Diamond *et al.,* 1982; Juraska *et al.,* 1989; Fitch *et al.,* 1990). There is an opinion that the prenatal action of sex steroids, and also their influence during the critical period of brain differentiation, is crucial for the formation of sex differences in adult individuals (Ross *et al.,* 1981; Geschwind, 1983; Rosen *et al.,* 1983; Holman and Hutchinson, 1991). The main role belongs to androgens, since female sex hormones are secreted by gonads under normal conditions only during the period of sexual maturity. The action of testosterone, a hormone released by the testes, upon the brain is realized after it is transformed into estradiol. Cells sensitive to estradiol were found in the brain cortex of male and female rats, at least during the first week after birth (McLusky and McEven, 1978; McLusky *et al.,* 1979; Sheridan, 1979). In the mammalian cortex, sex differences were observed in the number of progesterone receptors: In females they were more numerous than in males (Maggi and Lucchi, 1987). Interhemispheric asymmetry in steroid binding sites was shown in rhesus monkeys (Sholl and Kim, 1990) and in rats (Demotes-Mainard *et al.,* 1990). In both cases, asymmetry was characterized by sexual dimorphism. The number of receptors in the frontal cortex of adult male rhesus monkeys was greater in the right hemisphere, while their number in the parietal cortex was greater in the left. In females, no significant interhemispheric differences were revealed. In early ontogeny, the number of estrogen receptors in female rats was greater in the right hemisphere, whereas in males this was the case in the left hemisphere. A similar direction of asymmetry is characteristic of males and females as regards dopamine receptors in the striatum. As a rule, orchidectomy performed on males (Guillamon *et al.,* 1986; Matsumoto and Arai, 1986; Holman and Hutchinson, 1991) or androgenization of females (Rosen *et al.,* 1983; Guillamon *et al.,* 1986; Fitch *et al.,* 1990; Roof and Havens, 1992) during the prenatal period, changed sex differences.

In the present chapter it was shown that extirpation of sex glands immediately after birth eliminated functional interhemispheric asymmetry which had been observed in intact rats in control of the behaviour in the open field and during emotional reaction. Subsequent administration of sex steroids to adult animals did not restore interhemispheric asymmetry. Thus, the function of sex glands during the neonatal period seems to be crucial for further establishment of interhemispheric differences in males and females. Androgen secretion during the prenatal period exerts an inhibitory influence mainly upon the cortex of the left hemisphere in males, and possibly upon the left part of the nigrostriatal system and hypothalamus in females.

While investigating functional interhemispheric asymmetry in adult animals, using the techniques of gonadectomy and sex steroids administration, it was found that in males this was determined mainly by the inhibitory action of sex hormones upon performance of the functions under investigation, whereas in females the effect was one of activation. In both cases sex steroids act more upon the right hemisphere. This is indicated by EP recording after hormone administration. There are some data in the literature pointing to a greater role of the right hemisphere, and also the right side of the peripheral nervous system in regulation of functions associated with sexual behaviour. The right side of the hypothalamus in female rats is more sensitive to estradiol (Roy and Lynn, 1987) and may exert an inhibitory action upon male sexual behaviour (Nordeen and Yahr, 1982). The right part of the hypothalamus contains more LH-releasing factor (Gerendai *et al.,* 1978). Right hemisphere functional asymmetry of the vagus nerve in regulation of secretion of luteinizing hormone releasing factor was noted: An elevated level of this releasing factor in the hypothalamus was observed after the extirpation of the right ovary in female rats, and after the deafferentation in the right testis in males (Gerendai *et al.,* 1978; Gerendai and Motta, 1990). In female mice, there are more cells responsive to the LHRH in the right half of the brain than in the left (Inase and Machida, 1992). While refraining from direct comparisons between functional asymmetry in humans and non-human animals, it should be noted that the right hemisphere is thought to be more sensitive to the chemical and pharmacological actions (Frumkin and Grim, 1981). Disruption of sexual function in men is associated mainly with deficit of the right hemisphere (Costlett and Heilman, 1986; Sanders and Ross-Field, 1986).

The results of investigating the influence of natural changes in sex hormone content during the estrous cycle supported earlier findings on the action of sex steroids, observed in experiments. In females, during the proestrus period, estrogen and gonadotrophin content increases, and the left hemisphere dominates for control of the reactions under investigation, whereas in estrus hormone concentration is decreased, inversion of asymmetry ensues, and the right hemisphere dominates. A similar regularity of the changes of interhemispheric asymmetry was observed during the menstrual cycle in women. Increased concentration of estrogens during the postmenstrual period is conducive to the activation of functions associated with the left hemisphere, e.g. fine motor skills and verbal perception (Hampson and Kimura, 1988; Barnes, 1989). During the pre-menstrual and menstrual cycle phase, when estrogen and gonadotropin content diminish, performance in visuomotor tasks improved (Diamond *et al.,* 1972; Giannini *et al.,* 1988; Altemues *et al.,* 1989). In our view, fluctuation of hemispheric dominance during the estrous cycle in rats clearly demonstrates the modulating influence of sex hormones upon interhemispheric asymmetry in adult animals, which agrees with the opinion of some investigators (Turner and Weawer, 1985; Heinsbroeck *et al.,* 1987; Starkstein *et al.,* 1989).

When studying the influence of natural changes in the level of sex steroids during pregnancy, first the modulating role of pregnancy hormones in regulating the contrasting function of the two cerebral hemispheres was established, and, second, the advantage of the right hemisphere in the process of functional restructuring during pregnancy was revealed.

Summing up the results of the above experiments, it can be concluded that sex steroid hormones exert both an organizing and a modulating influence upon interhemispheric asymmetry. The organizing influence is observed during the perinatal period: Gonadectomy in newborn animals prevented the formation of functional hemisphere specialization for control of emotional reactions and behaviour in the open field of adult individuals. Administration of sex hormones to such rats at an age of three months appeared ineffective. During the prenatal period, androgens seem to exert an inhibitory influence upon the left hemisphere. This can be shown by the dominance of the right hemisphere, in animals of both sexes, when males prevail over females in the litter, and by left hemisphere dominance in males and elimination of interhemispheric asymmetry in females, when they prevail in the litter. A similar action upon the left side of the hypothalamus of the females may be exerted by androgens, since prevalence of males in the litter delays sexual maturation in female individuals.

Gonadectomy, and also administration of sex steroids at a sexually mature age, cause changes in interhemispheric relations, which indicate the modulating influence of sex hormones upon interhemispheric asymmetry. Sex hormones act mainly on the right hemisphere, exerting an inhibitory influence on males, and an activating one on females. In males, this is indicated by intensification of right hemisphere functional activity after gonadectomy, and its decline after administration of sex hormones. In females, ovariectomy caused inhibition of right hemisphere function, whereas administration of sex steroids resulted in its intensification. However, during the hormone-saturated phase of proestrus, the left hemisphere dominated for emotional reaction and motor activity, whereas in estrus it was the right hemisphere. The basic level of sex steroids and gonadotrophins (in the body of mature intact females) may be conducive to the activation of the right hemisphere, whereas a temporary increase in the sex hormone content in the course of the estrous cycle results in the dominance of the left hemisphere.

Thus it can be concluded that androgens exert a predominantly inhibitory action upon the highest regions of the central nervous system. During the perinatal period, this influence is received mainly by the left hemisphere, whereas during the postnatal period the recipient is the right one. The above hormonal actions cause right hemisphere dominance in males during an early period of ontogeny, and left hemisphere dominance during the later period. Hence androgens in mature males may modulate interhemispheric asymmetry, i.e. They intensify left hemisphere dominance, and decrease right-sided dominance. Estrogens exert a predominantly activating influence during the postnatal period. This influence is exerted mainly upon the right hemisphere, but it may be stronger or weaker depending on the phase of the estrous cycle. During a certain period of the estrous cycle the activating influence may be exerted upon the left hemisphere. The modulating action of sex hormones upon the male brain possesses a relatively stable unidirectional character, whereas in females it is dynamic, and transitory, which seems to reduce functional interhemispheric asymmetry when assessing the sample as a whole.

One might think that the asymmetric action of sex hormones is conditioned by the interhemispheric asymmetry in the receptors of sex hormones and gonadotrophins. The role of pregnancy hormones in the regulation of contrasting brain function, and the predominant role of the right hemisphere in the process of functional restructuring during pregnancy should be also noted.

Let us make a brief summary. The following was shown. Sex steroid hormones may exert both organizing and modulating action. Male sexual hormones (androgens) mainly exert an inhibitory action upon the higher regions of the CNS and the subcortical structures. During the prenatal period of development, the action of male sex hormones is stronger upon the left hemisphere. During the postnatal period, it is stronger upon the right hemisphere, which may be influenced by the preceding development of the left hemisphere. Female sex hormones (estrogens) mainly exert an activating influence on both the left and right hemispheres during the postnatal period. They are capable of changing the interhemispheric contrast of brain function. The influence of sex hormones may be more effective upon the cerebral hemispheres of the males, and upon the subcortical formations of the females.

5. A Neurobiological Model of Sexual Dimorphisminthe Brain (by Way of Conclusion)

First let us do some summing up. It should be recollected that, in working with animals (rats, cats), two types of models were used: behavioral and electrophysiological. The following main results were obtained (Table 21).

Table 21. Functional peculiarities of the brain in animals of both sexes

Males	*Females*
1a. A higher level of analytical-synthetic activity.	1b. A lower level of analytical-synthetic activity.
2a. A tendency for a greater variance of the level of analytical-synthetic activity.	2b. A tendency for a lower variance of the level of analytical-synthetic activity.
3a. The strategy of specialized response.	3b. The strategy of generalized response.
4a. A stronger species-specific functional interhemispheric asymmetry (interhemispheric contrast).	4b. A weaker species-specific functional inter hemispheric asymmetry (interhemispheric contrast).
5a. A greater variance of species-specific functional interhemispheric asymmetry.	5b. A lower variance of species-specific functional interhemispheric asymmetry.
6a. An inhibitory action of androgens upon the right hemisphere.	6b. An excitatory action of estrogens upon both hemispheres, but more on the right one.
7a. —	7b. An asymmetrizing influence of female sex hormones during the estrous cycle upon the cerebral cortex.
8a. Left hemisphere dominance for control of general motor activity.	8b. Right hemisphere dominance for control of general motor activity.
9a. Left hemisphere dominance for carrying out interhemispheric connections in the association cortex and the auditory area.	9b. Right hemisphere dominance for carrying out interhemispheric connections in the association cortex and the auditory area.
10a. Functional interhemispheric asymmetry is more expressed in the visual cortex.	10b. Functional interhemispheric asymmetry is more expressed in the auditory cortex.
11a. A more dynamic functional interhemispheric asymmetry.	11b. A less dynamic functional interhemispheric asymmetry.
12a. The character of functional interhemispheric dynamism: left-right-left hemisphere.	12b. The character of functional interhemispheric dynamism: right-left-right hemisphere.
13a. A tendency for left hemisphere dominance.	13b. A tendency for right hemisphere dominance.
14a. Intrahemispheric contrast is more expressed.	14b. Intrahemispheric contrast is weaker.

It was shown that, in animals, sex differences could be observed at the level of carrying out analytic-synthetic activity. Similar data can be also found in studies performed on man: In that case a relatively higher level of discrimination is, as a rule, achieved by males compared to females (1a, 1b). In males, in a number of cases, a definite tendency was also observed for greater variance, compared to female in the level of analysis (or discrimination) when solving different tasks (2a, 2b). These data point to the fact that under certain conditions, males are characterized by a somewhat greater adaptive ability than females (their analysis of environmental signals is relatively more subtle and has a wider range). During the solution of some other tasks it was possible, on the basis of the relation between level of performance and its variance, to form the idea of individuals of different sexes using different strategies in processing the same information. The strategy of specialized reaction (indicated by a comparatively high level of discrimination within a relatively narrow range of stimuli) was distinguished from the strategy of generalized reacting (shown by a comparatively low level of discrimination, but within a larger range of stimuli) (3a, 3b). The first of these was especially characteristic of males, the second, of females. Consequently, both in man and animals, some sex differentiation in behavioural strategies is observed. It is natural to suppose that these specific strategies may be essentially different in different species, but the very fact of their sex specificity is rather remarkable.

In experiments on animals, it was possible to establish that species-specific functional interhemispheric asymmetry (hemispheric specialization) is, as a rule, expressed more strongly in males than in females (4a, 4b). This regularity is manifested during the assessment of the degree of asymmetry, both for behavioural and electrophysiological indices. A similar regularity is also indicated by the majority of investigations on humans. The fact that variance of species-specific functional asymmetry is greater in males than in females is also of interest (5a, 5b). Consequently, the male brain is more asymmetric, whereas the female brain is more bilateral. Therefore, the female brain may be more reliable, and tuned up to the perception of a wider spectrum of stimuli, while the male brain is relatively more highly specialized. Asymmetry of specificity in males may correspond more to group activity, in females, to individual behaviour, characteristic of taking care of progeny.

It is important to note that functional interhemispheric asymmetry in males and females differs not only in its magnitude, but is also characterized by some differences in physiological mechanisms underlying it (6a, 6b). In males, in most cases, left-sided (but sometimes right-sided) interhemispheric asymmetry is observed. In its formation and modulation, both neural and hormonal factors are involved. In sexually mature males, the male sex hormones (androgens) exert an inhibitory action upon the right hemisphere, this being conducive to the intensification of left hemisphere asymmetry and weakening of right hemisphere asymmetry. In females, in most cases the right hemisphere dominates, but sometimes it may be the left. In this case, sex hormones (estrogens) also play the role of modulating factors, but in a different way. They act to excite both hemispheres, especially the right one, thereby intensifying right-sided and weakening left-sided asymmetry.

It should be noted that, alongside this, hormonal factors also have an action, depending on the phase of the estrous cycle in females (7b). During late proestrus, left-sided asymmetry can be observed, whereas during estrus it is right-sided. Therefore, in a pooled sample, owing to the presence of animals in different phases of the sexual cycle, species-specific interhemispheric asymmetry or symmetry can be observed, resulting from the algebraic summation of right- and left-sided individual asymmetry.

The problem of sex specificity in the changeability of functional interhemispheric asymmetry is also of interest. Males turned out to possess a more changeable species-specific functional interhemispheric asymmetry, whereas in females it was individual asymmetry that was more changeable. This is testified to by the greater variance of species-specific interhemispheric asymmetry in males, compared to females. Alongside this, in females, changeability of individual asymmetry is more strongly expressed, which is determined by fluctuations in hormone content during the estrous cycle. Within this context, prevalence of individual functional interhemispheric asymmetry in females, compared to males, can also be accounted for. In addition, in females, a wider range of variation of asymmetry than in males was observed.

There are some indications that functional interhemispheric asymmetry in individuals of different sexes may be not only quantitative, but also qualitative. For instance, in control for general motor activity, the left hemisphere may prevail in males, the right one, in females (8a, 8b). Cases of regional interhemispheric asymmetry may also be observed. Thus, in females, right-sided dominance of interhemispheric connections between the association cortex and the auditory area was observed in females, whereas in males they were left-sided (9a, 9b). In cats functional interhemispheric asymmetry of the auditory cortex was more strongly developed in females, while in the visual area it was greater in males (10a, 10b). This may reflect different proportions of afferent supply in the course of reproductive behaviour.

The dynamics of functional interhemispheric asymmetry is one of its most important properties. In the overwhelming majority of cases it is expressed more strongly in male individuals compared to females (11a, 11b). Thus, for instance, in forming conditioned reflexes, males passed through the phases of dynamic hemisphere dominance more rapidly than females. The same can be said about the dynamics of postnatal ontogenesis etc. The above differences in the dynamics of functional interhemispheric asymmetry in animals of different sexes is manifest in the sequence of hemisphere dominance. Thus, in the course of postnatal ontogenesis in males, during transcallosal signal processing, the sequence of hemisphere dominance "LH-RH-LH" is found for some indices, mainly connected with exploratory activity, while in females, the sequence "RH-LH-RH" was associated mainly with the avoidance reaction (12a, 12b).

Of considerable interest is the problem of the direction of summated interhemispheric asymmetry in individuals of different sexes. As shown in experiments, both in males and in females, both right- and left-sided asymmetry may be formed. Nevertheless, in males the asymmetry is usually left-sided, while in females it tends to be right-sided (13a, 13b). This can be compared with the following facts. First, during the perinatal period in males, hormonal inhibiting influences are directed to the right hemisphere, in females, excitative influences spread to both hemispheres but mainly affect the right hemisphere. It is natural that initial conditions for left hemisphere dominance are thereby created in males, those of right hemisphere dominance, in females. Second, in those cases when repeated dynamics of interhemispheric asymmetry can be observed (12a, 12b), the balance of asymmetry in males has a tendency to be left-sided, in females, right-sided.

Such are the main results obtained from studying the sex specificity of functional interhemispheric asymmetry, which may be also regarded as interhemispheric contrast. In studying interhemispheric contrast corresponding single hemispheres in animals of both sexes were compared. An important indicator was the gradient of contrast, which characterized the focality (focussing), or degree of structure of the transcallosal focus of activity. In male individuals, the brain appeared usually to be functioning with higher contrast than in female individuals (14a, 14b). In this case the left hemisphere dominated in males, the right one, in females. Under certain conditions, the male left hemisphere was not only functionally more differentiated, but the role of the cortex was more strongly expressed with regard to its activity, it received transcallosal excitation earlier, and its inhibitory processes were more strongly expressed.

The above facts suggest that it is of utmost importance to differentiate animal samples according to their sex in psychological, medical, and other studies. Otherwise the investigator runs a risk of obtaining artefactual results, without revealing any of the fundamental regularities.

The experimental material accumulated by now, and the corresponding theoretical concepts, make it possible to advance a neurobiological (neurohormonal) model of sexual dimorphism in the brain. The neurobiological approach means, in this case, that one considers the accumulated influence of neuronal and hormonal factors from the point of view of biologists. The neurobiological conception of sex is based on the "dominanta" model of interhemispheric relations (Bianki, 1989, 1993; Bianki, 1988, 1991), which stems from A.A.Ukhtomsky's conception (1966) and is, moreover, supported by factual data indicating the influence of sex steroid hormones upon functional brain asymmetry. Let us dwell on these premises in greater detail.

In constructing the dominanta model of interhemispheric relations we proceeded from the fact that the cerebral hemispheres function according to the principle of asymmetry, whereas in the dynamics of functional interhemispheric asymmetry the principles of the dominanta and complementarity are realized, the latter maintaining reliable functioning of the system. The paired functioning of the brain, according to the dominanta principle, is considered as a self-regulating system with inhibitory feedback. The action of the summation-reciprocal dominanta mechanism is carried out in the following way: In one of the hemispheres, under the influence of different excitation streams, a focus of increased excitability is formed, which possesses the main properties of the dominanta, i.e. it is capable of summating the inflowing excitation, and exerting a reciprocal influence upon the opposite hemisphere. The main unit of interhemispheric relations seems to be a pair of homologous modules, with excitatory-inhibitory connections between them. The constellation of modules is, as a rule, a zone of excitation surrounded by a zone of inhibition. The model consists of rigid links, represented by a relatively "diffuse" right hemisphere with dominance of the primary projection cortical areas, and the relatively "focal" left hemisphere, with dominance of the primary projection areas, and flexible links functioning by means of the dominanta mechanism of interhemispheric relations. All the streams of excitation participating in the formation of dominanta may serve as a switch of the dominating activity. In the case of normal brain activity, vertical and horizontal streams of excitation are in constant interaction. The organizer of this interaction is the dominanta. It is important, that, in the opinion of J.C.Eccles (1989), circuits of reciprocal reverberation may be the foundation not only of interhemispheric but also of intrahemispheric relations, and thalamocortical interactions.

Here it is expedient to emphasize several points. First, the dominanta passes through several stages in its development. At the initial stage, incoming excitation is mainly summated in the dominant focus (Figure 44, I), and only then does conjugate inhibition ensue

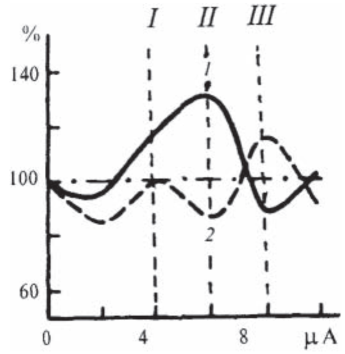

Figure 44: The dynamics of dominanta development and conjugate inhibition, **abscissa:** polarization of one of the symmetrical sites with an anode of direct current, µA, **ordinate:** EP amplitude in the polarized **(1)** and nonpolarized **(2)** cortical site, **I**–the early phase of the dominanta. **II**–the late phase of the dominanta. **III**–dominanta inversion.

(Figure 44, II). Second, the dominanta can be inhibited and disinhibited. In particular, endogenous inhibition is to be distinguished, which is referred to as "reinforcement" of the dominanta (extraboundary inhibition), accompanied by positive induction and inversion of hemispheric dominance, and exogenous inhibition–on the side of the dominant focus (Figure 44, III). Third, the dominanta is a constellation of nervous centres, formed as a system, in the course of the current activity of the organism, with variable values for the functions of individual links. This constellation takes shape and is supported by the process of inhibition.

In his time, A.A.Ukhtomsky (1966) noted the possible role of hormonal factors in the initial appearance of some dominant states. According to his concepts, the dominanta, alongside impulses passing between centres, may also be initiated and supported by humoral factors. He wrote: "…In the nervous centres a sufficiently inert group of centres is prepared by the elective action of hormones, and having once appeared in the organism, it will determine the animals' behaviour, until impulses arriving from the sensitive periphery find the most easily excitable apparatus." (1966, p. 28). It should be recollected that, in the anterior hypothalamus and the preoptic area, there are receptors for sex hormones. It is their excitation, together with sensory signals, that may determine the formation of the dominanta in the corresponding nervous centres. From the above it follows that it is necessary to consider the organizing and modulating role of sex steroid hormones in a modern model of sexual dimorphism in cerebral organization.

The neurobiological model of sexual dimorphism in the brain can be described in the following way (Figure 45). In individuals of both sexes, functional interhemispheric asymmetry is based on the physiological dominanta, which can be regarded as a self-regulated system with an inhibitory feedback. This system consists of interrelated primary and secondary dominant foci, formed and supported by nervous and hormonal influences. The primary dominant focus, being a dynamic constellation of nervous centres, is formed in the dominant hemisphere, and possesses all the main properties of the dominanta. In the nondominant hemisphere a secondary, sketchy dominant focus is formed.

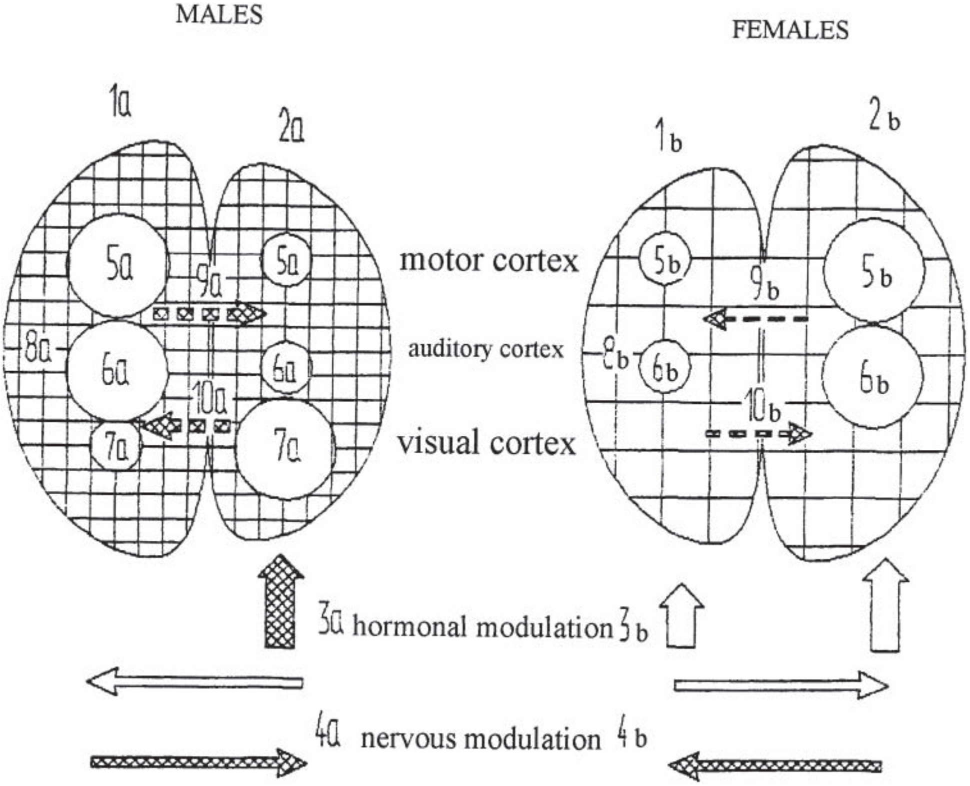

Figure 45: The scheme of the sexual dimorphism in the brain, **1a, 1b**–the left hemisphere, **2a, 2b**–the right hemisphere, **3a, 3b**–hormonal influences: the *shaded arrows* indicate inhibitory influences, the *white ones* indicate excitatory influences, the thickness of the arrows reflects the degree of the corresponding influences; **4a, 4b**–nervous influences: the *shaded arrows* indicate inhibiting influences, the *white ones* indicate excitatory influences, the thickness of the arrows reflects the degree of the corresponding influences; **5a, 5b**–the motor cortex: the magnitude of the circles reflects the degree of hemisphere dominance; **6a, 6b**–the auditory cortex; **7a, 7b**–the visual cortex; **8a, 8b**–the degree of cortical differentiation (marked by the density of the net); **9a, 10a** and **9b, 10b**–the direction of inversion of hemisphere dominance.

The main admission made here is that functional interhemispheric asymmetry in females is based on an earlier stage of development of the dominanta; that of males is based a later one. Both stages possess their biological advantages. In this case dependence on the "age" of the dominanta with regard to the ability of the dominanta for conjugate inhibition of other centres, and its own endogenous inhibition, is taken into account.

In individuals of different sexes, functional interhemispheric asymmetry differs first of all in its predominant lateralization. In males, the left hemisphere is usually dominant (1a), in females, though to a much lesser degree, it is the right one (2b). In accordance with this, the primary dominanta in males is mainly localized in the left (dominant) hemisphere, while in females it is usually positioned in the right one. In the contralateral hemisphere, in representatives of different sexes, the secondary dominant focus is formed. The above lateralization may be determined primarily by the influence of sex steroid hormones. In males, this is the inhibitory action of androgens upon the right hemisphere (3a), in females, the excitatory influence of estrogens upon the right hemisphere (3b). It should be specially emphasized that in both cases the right hemisphere acts as the determinant of lateralization (2a, 2b).

In representatives of the female sex, species-specific functional interhemispheric asymmetry (interhemispheric contrast) differs in magnitude. In males, it is usually more strongly expressed than in females (1a-2a, 1b-2b). Underlying this phenomenon are both nervous and hormonal modulating factors promoting asymmetry. In males, the summation-reciprocal mechanism of interhemispheric relations (4a) is more strongly expressed, which may be the consequence of a more developed dominanta, compared to females. Males also possess a more effective modulating mechanism, which is the inhibitory action of androgens upon the right hemisphere (3a). In females, the magnitude of asymmetry is determined by a relatively less well-developed summation-reciprocal modulating mechanism (4b), and also by a seemingly less effective hormonal mechanism, which is the activating action of estrogen on both hemispheres but mainly upon the right (3b).

In males and females, functional interhemispheric asymmetry (interhemispheric contrast), is distinguished by its regional manifestations, which may reflect differences in the mosaicism of the dominant constellation. Thus, for instance, in males, the left hemisphere dominates for control of general motor activity (5a), in females, the right (5b). In males, left hemisphere dominance is observed for carrying out interhemispheric connections between the association cortex and the auditory area (6a), in females, it is that of the right hemisphere (6b). In males, interhemispheric asymmetry appears to be more strongly expressed in the visual cortex (7a), whereas in females this is the case in the auditory area (6b). The existence of the sex specificity of the mosaicism of the dominant constellation is indicated by differences in intrahemispheric contrast which appeared to be more strongly expressed in male, compared to female individuals (8a, 8b). All this may be associated with the characteristics of the development of reciprocal inhibition in the dominantas of different ages. A more developed dominanta in males, compared to females, must exert a stronger inhibitory action upon nervous centres of both its own and the opposite hemisphere, which results in an increased contrast in the dominant constellation.

In individuals of different sexes, functional interhemispheric asymmetry differs in its dynamicity. As a rule, it appears to be more agile in males (9a, 10a) than in females (9b, 10b). Sex differences are also reflected in the peculiarities of dynamics. In males, the reaction starts with left hemisphere dominance, then right hemisphere dominance ensues, then it is left hemisphere dominance again (9a, 10a). By contrast, in females, the right hemisphere is the first to dominate, then it is the left, and then the right one (9b, 10b). Underlying the dynamics of interhemispheric asymmetry may be the onset of extra-boundary inhibition in the dominant hemisphere (endogenous end of the dominanta), with the subsequent activation of the nondominant hemisphere, according to the mechanism of positive induction. It is natural to suppose that endogenous inhibition is more easily developed at the later phase of development of the dominanta in males, compared to the early stage of its development in females.

Thus, according to the neurobiological (neurohormonal) conception of sexual dimorphism, in the brain of individuals of both sexes, the physiological dominanta is formed in the corresponding zones and not in the cortex of the hemisphere as a whole, under the influence of nervous and hormonal factors. In this case, in males it is characterized by a greater degree of development or progressive elaboration than in females. In males, the dominanta is more frequently lateralized in the left hemisphere, in females, in the right. In accordance with the degree of development of dominanta in males, a greater expression and dynamicity of functional interhemispheric asymmetry was observed in females, as well as a greater contrast of the dominant constellation. On the whole, the functioning of the cerebral hemispheres in male individuals is more specialized, more focal, more differentiated, amd shows higher contrast (mainly owing to the left hemisphere), while in representatives of the female sex, cortical action is less specialized, more diffuse, less differentiated and shows lower contrast (mainly due to the right hemisphere). It is these properties that determine, to a large extent, the adaptive abilities of the male and female brain. Individuals of the male sex reveal, as a rule, advantages in analysing the local characteristics of the environment and adaptation rate, those of the female sex, have advantages in generalized reactions. Hence different strategies arise are used by the male and the female brain during information processing. A greater diffusion of the female brain function also maintains its comparative reliability as compared to males.

Thus, the specificity of cerebral organization in humans of different sexes is based on extensive evidence, which indicate its great biological significance. The right hemisphere frequently acts as evolutionally more ancient, the left one, as a relatively new formation. The right hemisphere seems also to play the main role in the regulation of sexual behaviour. Judging from the above, it does not follow at all that functional interhemispheric asymmetry in humans and higher animals possesses similar characteristics. On the contrary, proceeding from the concepts of the adaptive role of functional interhemispheric asymmetry, one can suggest that in different animal species and in humans, it may vary to a considerable degree, not only as concerns its direction but also the degree of its expression, determined both by genetic and environmental factors in the corresponding species, populations, and even lines.

It does not seem possible to speak of the role of asymmetry in terms of “value”. In our experiments species-specific asymmetry was more frequently found in males than in females. This appears to be associated with the fact that the species-specific form of asymmetry was studied, this prevailing in males. If individual asymmetry were studied it would be more strongly expressed in females. However, in general, discussing the “evaluative” role of asymmetry in different sexes does not appear to be reasonable: In populations, they are usually as complementary as are the left and the right hemispheres.

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