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Maternal Behaviour in Septal Rat Females

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Summary

Dorsal lesions of the septum influenced the maternal behaviour of Wistar and Long-Evans females, as well as of their hybrids, in a different way. The phenomenon of infanticide appeared in Wistar females only, whereas mothering was not impaired in others. However, the mouse-killing activity was not enhanced in Wistar females displaying infanticide. On the contrary, they exhibited xenoparental behaviour. If these females had grown up in a species-typical environment, characterized by enriched social stimulation during their critical developmental period, no impairment of maternal behaviour following dorsal septal lesions occurred. The ablation of the whole septum caused a break-down of maternal behaviour with the appearance of infanticide in all females regardless of their stock origin and their individual life history. The specific role of the septum in the control of maternal behaviour is discussed.

Key words

Maternal behaviour – Septal lesion – Infanticide – Stock differences – Life history

Introduction

Some experimental data have drawn attention to the possible role of the septum in the performance of maternal behaviour. When septal lesions had been produced in females, the pattern of this kind of behaviour was changed. Several impairments appeared, e.g. altered nestbuilding (if present), retrieving of pups, taking up a nursing posture, etc. All these abnormalities were described by Carlson and Thomas (1968) and Slotnick and Nigrosh (1975) in mice, by Terlecki and Sainsbury (1975) in rats, and by Janzen and Bunnell (1976) in hamsters. Korányi *et al.* (1988) have also found a disruption in the artificially induced maternal behaviour of virgin female and male rats. Fleischer and Slotnick (1978) observed infanticide in rats, as a transitory postoperative phenomenon. On the contrary, Cruz and Beyer (1972) reported infanticide to be typical for septal rabbit females. There are two major reasons for a critical consideration of theories which attempt to assess the biological importance of changes in mothering. Firstly, the number of papers analysing this problem is really insufficient (see the review by Gray and McNaughton 1983). Secondly, some results seem to be unreliable since numerous experiments were carried out immediately or very soon after septal injury when the symptoms of the rage syndrome, typical for septal lesioned animals, had not yet expired (for review see Albert *et al.* 1982).

Thus, the present study was intended to analyse such changes of spontaneous maternal behaviour which were not caused by the immediate effects of the surgical intervention, but were typical and longlasting or even permanent, and which fatally influenced the life of the offspring.

Methods

Experimental groups

The following groups of rat females were used: females from the Wistar (W) stock, the Long-Evans (LE) stock, and their female hybrids of the first (F_1) and second (F_2) filial generations. Both hybrid groups partly consisted of animals having a W mother and a LE father, partly of animals with reciprocal parents. The females were further divided into two subgroups according to their previous history.

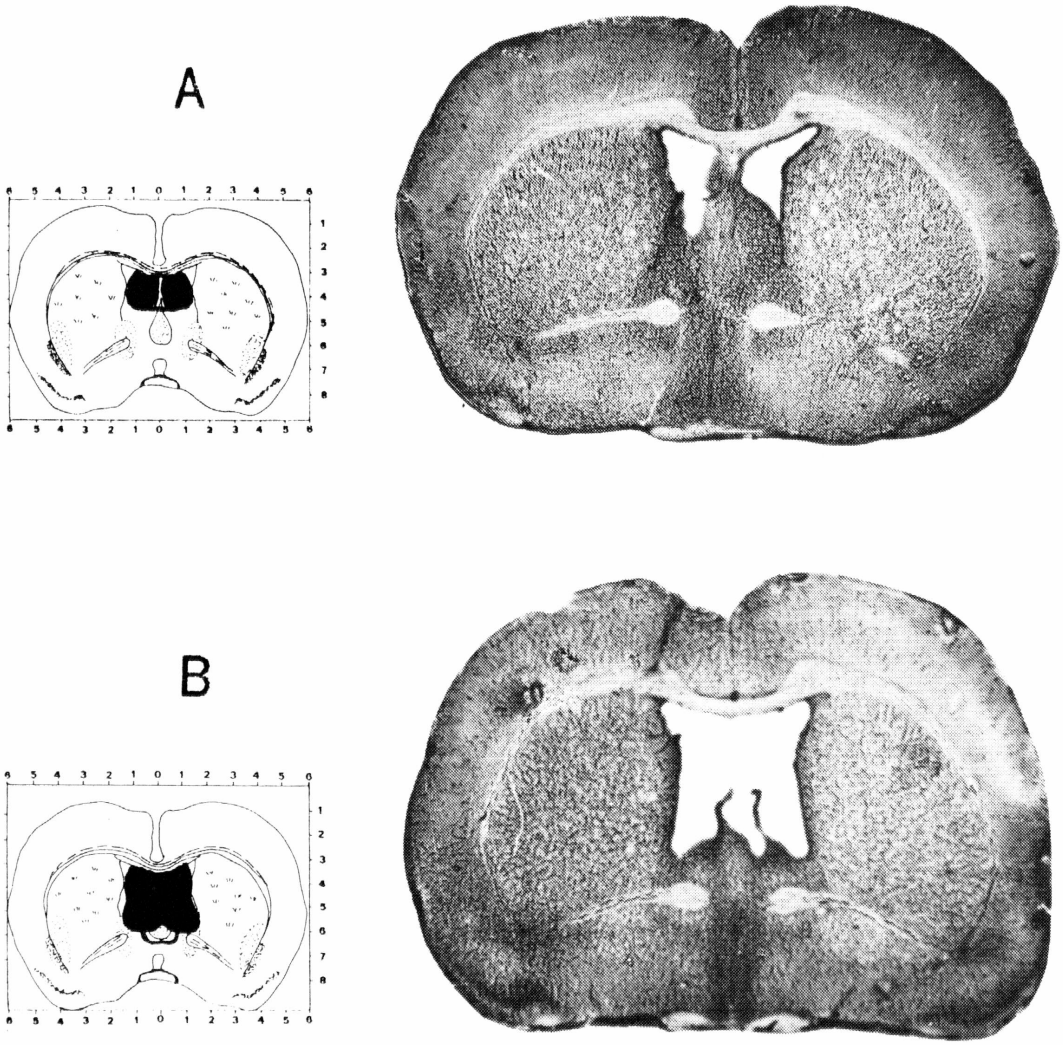

Fig. 1
Histological verification of the localization of septal lesions. Photomicrographs of representative frontal sections at the level of the septal region (stained with haematoxylin; the anteroposterior distance rostrally from the bregma was 1.0 mm). **A:** right, section from an animal with bilateral lesions of the dorsal portion of septum. **B:** right, section from another animal with total septal ablation. Note that adjacent brain structures of the corpus callosum, nuclei caudati, and commissura anterior were not damaged. Left, on tracings from the atlas plates, black area schematically indicates the expected (and actually achieved) extent of dorsal and total septal lesions, respectively.

The first subgroup was bred under so-called conventional laboratory breeding conditions, i.e. in usual isolated cages; rats of the second subgroup had lived from day 15 to day 45 in a so-called community, i.e. in a species-specific and diversified complex society. Conventional conditions consisted in keeping animals in small breeding cages, occupied by the rat mother and her offsprings until their spontaneous weaning on the 30th day of life. The pups were then separated according to their sex and randomly distributed into monosexual lots where they lived again in small isolated cages of the same size during the whole experimental period. The community included 6 adult rats: 4 rat mothers transposed together with their pups (having just reached the age of 15 days), and further 2 adult males. This society occupied a large compartmentalized space which was formed by five conventional cages interconnected through tubing-tunnels.

All animals were kept under natural conditions of illumination (spring, summer). A standard pelletted diet and tap water *ad libitum* were always at their disposal.

The numbers of females in the individual groups are given in tables and comprise animals after actual parturitions. The females were covered by males 30 days after surgery.

Surgical intervention

Standard septal lesions were made bilaterally and were localized in the dorsolateral regions of the septum. The stereotaxic coordinates (according to the rat brain atlas by Fifková and Maršala (1960), where bregma represents the zero reference point) were as follows: anterior = 1.0 mm; lateral = + and − 0.5 mm; vertical = 4.4 mm.

In some groups, the septum was entirely damaged for control purposes. In those animals, the lesion was bilaterally duplicated with the same electrode introduction at two vertical depths (= 4.4 and 5.9 mm) and at identical anterior and lateral coordinates as in the case of partial dorsal lesions.Thus, the lesion size comprised then both dorsal and ventral portions of the septal area. The stereotaxically introduced stainless steel electrode had a diameter of 0.2 mm and was insulated with INSL-X varnish (E-33 insulating tool dip; INSL-X Products Corp.,Yonkers, N.Y.) along its whole length except for 0.5 mm of the tip. Each electrolytic lesion was performed by the cathode (DC 0.5 mA, duration 40 s). The females were operated under sodium pentobarbital anaesthesia (40 mg/kg, i.p.; Nembutal, ABBOTT, St-Rémy-sur-Avre, France) at the age of 70–90 days. Before final evaluation of the experiments, the animals were sacrificed and the localization, size and shape of their lesions were histologically verified (Fig.1). Statistical evaluation was only performed in those animals where the lesion was correctly localized.

Experimental series

1) The first series was designed to analyse the role of the life history in the effects of septal lesions. For this reason, different parameters of maternal behaviour (such as nestbuilding, retrieving, licking the pups, assuming a nursing position and killing newborn offsprings, i.e. infanticide) in dorsally lesioned septal females from the W stock reared under conventional conditions were compared with similar paradigms observed in females that had spent their weaning and juvenile period in the community. Intact cage-bred animals served as controls. As previous experience with offspring breeding might have played a role, we took into consideration the behaviour of the same animals following the first, second and third parturition. The third parturition differed from the preceding ones from the point of view of odour traces: it was carried out in a new hitherto unsmelt environment, since we replaced the wood-shavings in the cage for this purpose by sheets of filter paper.

2) The second series was intended to answer the question on the existence of inter-stock differences in the postoperative patterns. Therefore, dorsally lesioned septal females from W and LE stocks and their hybrids of the first (F_1) and second (F_2) generations were studied. In a control experiment, the influence of inter-stock fostering was followed from birth to weaning. W females fostered LE young and *vice versa*. Female subjects reared from these young were then lesioned as adults (10 + 10 animals from each group). The maternal behaviour of primiparous females was kept under observation. Intact cage-bred W and LE females served as controls.

3) As infanticide is often reported to be related to mouse-killing (muricide) activity (for review see Albert and Chew 1980), the reaction to an adult dark mouse of either sex was investigated in intact W and LE, as well as in septal cage- and community-bred W females and in septal cage-bred LE ones. It is clear that females from the second series could be used here, moreover supplemented by community-bred W females after the first delivery from the first series. During this test, a mouse was always placed into the home cage of the rat female for no longer than 30 minutes. In cases of non-killers, further mice were added at time intervals of about one minute up to a number of 10–15 animals and the interreactions were observed.

4) The aim of the next series was to elucidate the importance of the size of septal lesions for impairment of mothering and for postoperative reaction of rats towards mice. More extensive septal lesions were obtained by new operations of intact females (not by supplementary enlarged destruction of

the remaining undamaged portions of the septum in dorsally lesioned animals). The fourth series was carried out in septal community-bred W females and in comparable septal cage- and community-bred LE ones. A comparison was made between the effects of lesions limited to the dorsal portions of the septal area with effects of injuries totally damaging this limbic structure.

Statistics

The numbers of all used and histologically verified animals are presented in five tables. The results were calculated by means of the χ square tests (with supplementary Yates correction); the obtained values (χ^2) and their significance level are also provided.

Results

In intact W females (25 animals altogether) as well as in LE ones (15 animals), a species-typical stable maternal behaviour was observed. They provided nestbuilding, nursed sucklings, elicited micturition and defecation by licking the pups, retrieved them, spent most of the time with their offsprings in the nest, etc. Neither mouse-killing activity (with the exception of one W female) nor xenoparental behaviour towards mice were seen. Therefore, as no abnormal elements of maternal behaviour and no aggressive features of activity occurred in these animals, we considered them to be suitable standard controls.

Table 1
Incidence of infanticide in cage- and community-bred Wistar rat mothers following dorsal septal lesions

Parturition range	Controls	n	Cage-bred dorsal septals	n	Community-bred dorsal septals	n	χ^2	p< df= 2
1st	0	10	9 *	11	0	21	32.3	.0001
2nd	0	10	10 *	11	1	18	29.8	.0001
3rd	0	10	6 *	10	0	17	19.3	.0001

The data indicate the number of females which displayed infanticide; n = total number of females in the group; χ^2 = values of verification tests of the probability differences between all 3 groups in each row of control and operated animals; p < = level of the statistical significance. Significantly increased incidence of infanticide among cage-bred septals, in comparison with controls, is marked by * (p< after three consecutive parturitions being 0.0008, 0.0002, and 0.0055, respectively).

Series No. 1: *Wistar females with dorsal septal lesions and a different life history*

Cage-bred septal W females regularly displayed infanticide after parturition, i.e. as primiparous ones in 82 %, as secundiparous in 91 % and as tertiparous in 60 % of the cases (the differences between the ranks of parturition were not statistically significant: $\chi^2=3.1$; df=2; p=0.216). These females usually killed all their pups immediately, or two days after parturition at the latest. They neither nursed the pups, nor displayed any other elements of mothering. On the other hand, mothers that did not kill the pups, exhibited a complete pattern of maternal behaviour. However, the septal W females that were reared in communities during the critical developmental period, presented the same pattern of mothering as intact females. One case of infanticide was observed in a single intact animal quite incidentally after its second parturition (Table 1).

Series No. 2: *Stock-dependent effect of the septal lesion*

In principle, dorsally lesioned cage-bred LE females displayed a normal pattern of maternal behaviour after parturition, similar to their intact controls. Infanticide occurred in a single female only. An equal pattern emerges from studies in both F_1 and F_2 septal hybrids. As indicated in Table 2, the behaviour of septal cage-bred W females, characterized by a high degree of infanticide, can therefore be regarded as exceptional. Fostering through dams of the opposite stock did not influence the incidence of infanticide. The genetic origin of the operated females was manifested throughout, i.e. all W rats displayed infanticide, whereas no case was observed in LE rats.

Table 2
Incidence of infanticide in females from different rat stocks without and with a dorsal septal lesion, and in their lesioned female hybrids

Group	n	Infanticide	χ^2
Controls Wistar	15	0	–
Cage-bred septals Wistar	32	25 *	22.0 $p<0.0001$
Controls Long-Evans	15	0	–
Cage-bred septals Long-Evans	18	1	0.86 n.s.
Septal F_1 hybrids	17	1	0.91 n.s.
Septal F_2 hybrids	16	0	–

Infanticide = femals displaying this behaviour; F_1, F_2 = first and second filial generations of female W/LE hybrids; χ^2 = values for septal lesioned Wistar, Long-Evans and hybrids compared to their intact controls (df = 1); * significant incidence of infanticide in septal Wistar females. The exceptional position of this group is indicated by the fact that the total $\chi^2 = 72.6$ for all six groups ($df = 5$; $p < 0.0001$) was no longer significant when septal Wistar group was omitted ($\chi^2 = 2.7$; $df = 4$).

Series No. 3: *Septal lesion and its effect on reactions of rats towards mice*

Following a dorsal septal lesion, mouse-killing was considerably enhanced in community-bred W females (in 48 % of the animals) and in cage-bred LE ones (in 50 %) (Table 3). Differences between these two operated groups and the intact controls were statistically significant ($\chi^2 = 11.8$; $df = 1$; $p = 0.0006$) in W and ($\chi^2 = 12.2$; $df = 1$: $p = 0.0005$) in LE. An entirely opposite behaviour was seen in operated cage-bred W females that killed their own pups (as seen in Table 1). They intensively carried all mice (successively placed by us into the cage) to one place, built a nest and took up a nursing position over them (Fig. 2). At first, under such circumstances, the mice vocalized, assumed a boxing posture, performed teeth-fighting and left the nest. The operated rat females repeatedly retrieved them and were able to "tame" up to 15 adult mice in this manner as that they finally remained in their place. No female who had displayed infanticide killed a mouse. The difference between this group and the others can therefore be considered a qualitative one. Those septal cage-bred W females that did not display infanticide also did not show any marked reaction to mice (Table 3).

Table 3
Reactions of intact and septal rat mothers upon mice

Group	n	Reactions					
		Killing			Retrieving		
		Cases	χ^2	p<	Cases	χ^2	p<
Controls Wistar & Long-Evans	30	1	–	–	0	–	–
Cage-bred dorsal septals Wistar	20	0	0.68	n.s.	20 *	45.9	0.0001
Community-bred dorsal septals Wistar	21	10 *	11.8	0.0006	0	–	–
Cage-bred dorsal septals Long-Evans	18	9 *	12.2	0.0005	0	–	–
Total χ^2		[df = 3]	27.6	0.0001		89.0	0.0001

n = total number of females in the group; Cases = number of females which exhibited killing or retrieving reactions; χ^2 = test values for septal groups in comparison with common controls (df = 1); * = statistically highly significant incidence of killing or retrieving, respectively. Total χ^2 = test values for all four groups proving a high probability of dependence of the two reactions under examination upon septal lesion, rat stock and life history.

Fig. 2
Illustration of a case of xenoparental behaviour: the septal cage-bred Wistar female that had killed her own pups, builds a nest for black adult mice and displays mothering.

Series No. 4: *Size of the septal lesion and its effect on mothering and on the reactions towards mice*

Destruction of the whole septum in community-bred W females and in cage- and community-bred LE ones, caused a break-down in the patterns of maternal behaviour with early total infanticide (Table 4). The different incidence of this phenomenon in only dorsally and in totally lesioned septal community-bred W females was statistically significant ($\chi^2 = 24.9$; df = 1; p = 0.0001). A similar difference between the effects of the dorsal and total septal lesions was observed in cage-bred LE females ($\chi^2 = 16.5$; df = 1; p = 0.0001). 60 % of totally lesioned septal LE rats displayed muricide, while mouse-killing occurred in 30 % of W females. In comparison with all other groups, it was exclusively in these totally lesioned septal W females that a positive reaction towards mice (namely retrieving) was seen which could be regarded as xenoparental behaviour (Table 5).

The newborn pups from the females that had repeatedly manifested infanticide were healthy and well developed which was proved in supplementary tests: all 20 pups randomly chosen in the nests and saved from being killed were fostered by an intact rat mother and survived.

The pattern of infanticide was not uniform. In half of the females, it acquired the form of pup cannibalism whereby the progeny was consumed. If, however, the pups were older than 2 days, they were killed without successive cannibalism; their dead bodies were then found unnursed, scattered over the cage and cold. If 2-day-old nursed pups from other rat mothers were placed before infanticidal females, they were also killed but not devoured. Equally, we have not observed that selected mouse-killing rats would behave in the predatory way, i.e. that they would eat the killed mouse. The natality of septal females (independently of whether the dorsal portion only or the whole septum had been lesioned) did not differ from the natality of intact controls and ranged from 80 to 100 %.

Table 4
Incidence of infanticide in rat mothers following dorsal septal and total septal lesions

Group	Dorsal lesion	n	Total lesion	n	χ^2	p<
Community-bred septals Wistar	0	21	11 *	12	24.9	0.0001
Cage-bred septals Long Evans	1	18	9 *	10	16.5	0.0001
Community-bred septals Long-Evans	0	11	10 *	10	17.2	0.0001
Total χ^2	1.814; (n.s.)		0.996; (n.s.)		[df = 2]	

The figures in lesion mode columns indicate the number of females which displayed infanticide. As missing infanticidal effects of dorsal septal lesions in community-bred Wistar females (Table 1) were fully comparable to those in dorsal septal cage-bred Long-Evans females (Table 2) (χ^2 = 0.006 ; df = 1 ; n.s.), it was also important to compare the effects of lesions covering the whole septal area, and to add a new corresponding group of community-bred septal Long-Evans females. According to the results obtained, all three groups were comparable (see total χ^2 values in the bottom line). * = statistically significant incidence of infanticide in females with a total lesion of septum in comparison with those having dorsal lesions only

Table 5
Reactions of rat mothers to mice following lesions of the dorsal part and the whole septum

Group	n	Reactions					
		Killing			Retrieving		
		Cases	χ^2	p<	Cases	χ^2	p<
Community-bred septals Wistar: dorsal lesion	21	10	–	–	0	–	–
Community-bred septals Wistar: total lesion	10	3	0.292	n.s.	3 *	3.97	.05
Cage-bred septals Long-Evans: dorsal lesion	18	9	–	–	0	–	–
Cage-bred septals Long-Evans: total lesion	10	6	0.013	n.s.	0	–	–
Total χ^2	[df = 3]		1.9	(n.s.)		15.5	0.0015

n = total number of females in the group; Cases = number of females which exhibited killing or retrieving reactions; χ^2 = test values for total lesions in comparison with dorsal lesions in the same rat stock; * = statistically significant incidence of retrieving. Total χ^2 = test values for all four groups indicating a high probability of dependence of retrieving only upon the size of septal lesion and the rat stock.

Discussion

If extensive septal lesions were produced, we have seen that both W and LE females performed infanticide instead of mothering. A relatively smaller extent of septal damage caused a differentiation between these two stocks. In septal W females, the previous way of life during youth was decisive. Only those rats that grew up in a deprivational (i.e. socially impoverished) environment became infanticidal. In general, rats with septal injuries undergo behavioural changes and their behaviour is referred to as the septal rage syndrome with hyperactivity and hyperemotionality. Many lesioned animals exhibit mouse-killing and intra-specific attack. Rage intensity undergoes alterations, becomes moderate and subsequently almost disappears. However, mouse-killing and intra-specifis attacks do outlast in some operated animals (Albert *et al.* 1982). Hence, the key problem of our study can be formulated as follows : did the observed negation of maternal behaviour represent an exclusive (i.e. specifically septal) impairment or was it only a part of the increased general aggressivity of septal animals ?

Miley and Baenninger (1972) found that septal rats either attacked other adult rats but not mice or, if they were mouse-killers, attacked juvenile young but not adults. Nonetheless, these findings were not reported by Miczek and Grossman (1972). However, Albert and Wong (1978) and Albert *et al.* (1982) confirmed the observations of Miley and Baenninger (1972) and suggested that identical brain structures were involved in the expression of inter- and intra-specific aggression in septal lesioned rats. They further supposed that in both cases it is a matter of aggressivity of the predatory type, because the killing occurred in hungry rats in a more intensive form and the killed animals were preferentially consumed to standard pelletted food. According to our own results, this may not be quite true. Whenever infanticidal rat mothers had eaten the youngs, it was always in the case of newborn pups and this eating may therefore have been connected with placentophagy. Older pups were only killed and not consumed. Infanticide was never coupled with muricide. Even xenoparental behaviour appeared towards mice that should be the object of aggression. Some discrepancies in the experimental results may be due to different research schedules and procedures used. Furthermore, variations in genotype derived from the adherence to different stocks of experimental animals could be of determinative importance. This suggestion was already put forward by Lathan and Thorne (1974) in relation to studies of mouse-killing behaviour in septal rats. The time interval between the lesion and the experiments is also important. If the tests were carried out in the period when the rage syndrome was still fully developed, the behaviour under investigation could have been either facilitated or inhibited. Hence, the validity of such results is very controversial. The most important point is to take into account whether the experimental results were obtained in rat mothers, i.e. in females under specific hormonal conditions, or in animals whose endocrine system was rather stabilized. We therefore suppose that infanticide in septal females was not related, as was shown in our present experiments, to an enhanced general motivation to aggression but resulted from a break-down of the mothering pattern. Following parturition, the lesioned rat mothers solved their relation to the litters in a negative way. The tests have also shown that the incidence of pup cannibalism was not a case of natural selection, but of an abnormal maternal behaviour, because the pups were fully viable. These results suggest that the septum possesses a specific irreplaceable function in the control of maternal behaviour.

The late effects of partial septal lesions were qualitatively different according to the genotype (i.e. with regard to stock attribution). Moreover, in W albino rat females, they depend on their previous life history. In the pertinent literature, this suggestion is supported by a number of reports from Donovick's laboratory (Donovick *et al.* 1973, 1979, Donovick and Burright 1984). These authors investigated the effects of septal lesions on the behavioural paradigms of exploration, fluid consumption and learning of a spatial alternation task. It is stated in their conclusions that "...the consequences of septal lesions on behaviour are a function of pre- and post-surgical history, genetic substrate, the environmental conditions present at the time of testing and anatomical locus of the lesion". But what is the exact relation between brain properties (that are even able to determine the effects of its damage) and the genotype, and furthermore between the environment where experimental animals had lived and their capability of adaptation to a brain lesion? Rajecki *et al.* (1978) and McVicker Hunt (1979) reviewed numerous data pointing out that brain development progresses differently in enriched (mainly by social stimulation) and impoverished environments. In our previous paper, the total content of ribosomal RNA in individual brain cells which is important for their functional capacity, was found to be dependent upon whether W rats had lived in a species-specific community or in a conventional laboratory breeding system using small isolated cages. In community-bred animals, the RNA content in the cells of the brain cortex and the limbic system was increased (Nováková 1984). Stock differences were also found: cage-bred W rats had a lower total RNA content in the cortical and limbic system cells, and a higher one in hypothalamic ventromedial cells in comparison with cage-bred LE rats. No difference between cage- and community-bred LE stock was found (Nováková *et al.* 1985). The

development of social behaviour in the compared stocks progressed in a qualitatively different manner. W females were able to create a society, where all young could survive and grow up (there and then) only if they had lived in a species-specific society during the critical period. But the LE females could do this without such an early experience with life in communities and they were able to create a typical and harmonic society even if the community was constituted of adult animals (Nováková and Šterc 1988). Therefore, LE rats have an inborn capacity for optimal brain development even under deprivational conditions. In order to reach such a level, it is necessary for W rats to spend their critical developmental period in a rich, stimulating environment (Nováková and Babický 1977). The optimally developed brain is then able to compensate better the consequences of smaller cerebral injuries in a functional way; this is obviously not the case of suboptimally developed brains. On the contrary, a postnatal influence of the dam was not observed.

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