

BRAIN COMPOSITION AND ECOLOGICAL NICHES IN THE WILD OR UNDER MAN-MADE CONDITIONS (DOMESTICATION)

Constraints of the evolutionary plasticity of the brain

G. REHKÄMPER, H.D. FRAHM and M.D. MANN¹

*C. and O. Vogt Institute of Brain Research, University of Düsseldorf,
D-40225 Düsseldorf, Federal Republic of Germany*

1. Introduction

The brain generates behaviour and behavioural peculiarities allow species to make use of ecological niches which are not occupied by other species. This relationship can be used to demonstrate the plasticity of the brain. Whereas the identification of different parts of the brain in many cases is relatively easy to do, the definition of an ecological niche is sometimes a problem. This is true because an ecological niche is defined by many parameters working together in a complex manner. Sometimes, however, a single parameter might excel and be called dominant. These cases are attractive to the neurobiologist. Such dominant parameters of an ecological niche are, for example, lack of light or only one food source. Animals which make use of such ecological niches are seen to alter "normal" brain morphology. In the following discussion we will introduce some examples which demonstrate the evolutionary plasticity of the brain.

2. Trigeminal-Guided Foraging Behaviour

There are some mammals that obviously use their vibrissal apparatus to detect prey under water. These include the so-called semiaquatic insectivores *Neomys*, *Limnogale*, *Microptamogale*, *Potamogale* and the Desmaninae. These animals brains are relatively large, and it has been shown that the brain stem contributes to this large brain insofar as it has an unusually large size. In all cases this is due to an enlargement of the sensory nucleus of the trigeminal nerve within the brain stem ([67] for review). This reflects the innervation of the vibrissae by a branch of the fifth cranial nerve. On the cortical level, Rehkämper [46] studied the laminar and areal differentiation and found that in *Desmana* there is an internal granular lamina (lamina IV in term of Brodmann [8]), which is hardly discernible in many other insectivores. In *Desmana*, it even surpasses the differentiation in the laboratory rat in respect to relative thickness and packing density.

¹On sabbatical leave from University of Nebraska Medical Center, Omaha, Nebraska, USA

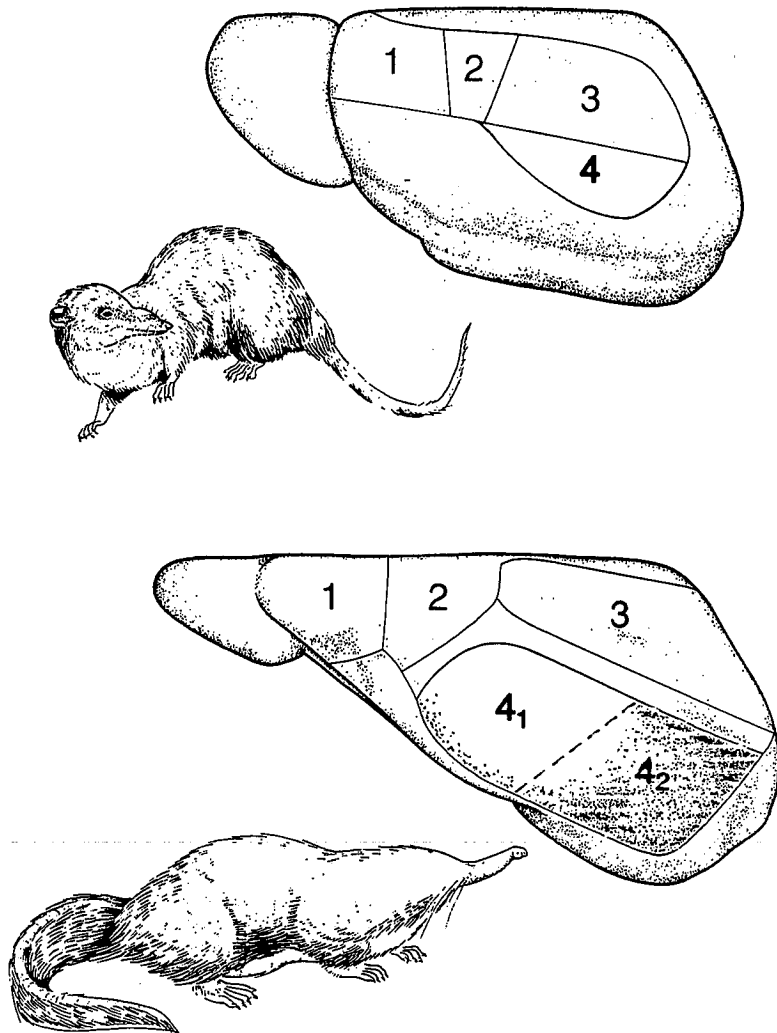


Figure 1. Isocortical organisation in the shrew *Crocidura* and in the Russian desman (*Desmana*). Both, disproportional enlargement of area 4 and differentiation into two subareas correlates with a more elaborated trigeminal system.

If these cytoarchitectonic criteria are used a remarkable areal differentiation is obvious in *Desmana* (Fig. 1). The lateral cortical area, Area 4 of Rehkämper [46], which forms an indivisible unit in many insectivores, as for example *Crocidura*, can be separated into two subareas, 4.1, 4.2. This indicates a functional differentiation which can be better understood if one realises that, in such small brains as are found in many insectivores, areal and functional differentiation is poor. Künzle and Rehkämper [34] used tracing techniques to

demonstrate that, in the small brained *Echinops*, sensory and motor areas might be unified and build an amalgam which has been described for small marsupial brains as well [35]. Clearly, the level of isocortical differentiation of *Desmana* surpasses this situation.

The topography of the two subareas allows a comparison with better understood cortices as for example found in the laboratory rat [76]. In the rat, subarea 4.1 is seen in the position of the somatosensory areas of the parietal region.

It really looks as if the peculiar mode of life in *Desmana*, which depends on trigeminal oriented detection of prey is concordant with a cortical differentiation which shows a very progressive development of the somatosensory representation areas. There is a lack of electrophysiological data to demonstrate the function of these subareas, and there is hardly a chance to investigate *Desmana* in terms of electrophysiology because the animal is not available for experimental research. However, an intensification of quantitative, comparative morphology might help to substantiate the hypothesis.

A trigeminal system is found not only in mammals but also in birds. The bill is innervated by a branch of the trigeminal nerve, and the brainstem bears the sensory nucleus of the trigeminal system. This nucleus projects directly to the telencephalic nucleus basalis via the quinto-frontal tract [72] and reaches the basal nucleus, which can be regarded as part of the neostriatum [47]. Kinkel [31] has measured the size of the sensory nucleus of the trigeminal nerve in the brain stem of galliform, passeriform and trochilid species. There is hardly any difference between these groups. This corresponds to the observation that in daily life none of these use the trigeminal system in an elaborated way. This is different in anseriform birds. Their bills bear many mechanoreceptors [3], and it is obvious that their search for food depends on tactile information. Ebinger [20] quantitatively investigated the sensory nucleus and the basal nucleus. These data demonstrate clearly that in anseriform birds the somatosensory system is very large. In the mallard, the sensory nucleus of the trigeminal nerve measures 19.2 cubic mm and the telencephalic basal nucleus 100.0 cubic millimetres. The body weight is 1,092.6 grams. Compared allometrically with the situation in galliform birds, the sensory nucleus is 20.7x larger in anseriform birds. These morphometric data support discussions in a paper by Pettigrew and Frost [44], who studied the brain of the dunlin (*Calidris alpina pacifica*). This animal also relies on the trigeminal system, and the authors propose that in the telencephalon of this animal the basal nucleus is like a "tactile fovea" which can be understood as an extreme specialisation of the trigeminal system.

Summarising these data it can be formulated that use of the trigeminal system for foraging is reflected in differentiated and large areas and nuclei in the brain stem as well as in the telencephalon.

3. Olfaction, Particularly in Birds

The olfactory system in birds is often neglected, though for example Bang and Cobb [1] have demonstrated an enormous variability of size and shape of the olfactory bulbs. Nevertheless, there exists the popular notion, that olfaction does not play a role in avian biology, except in the Kiwi whose extremely large olfactory bulbs could not be ignored. Today this view has changed and there are ethological as well as anatomical indications of a remarkable importance of olfactory orientation in birds. Of particular interest is olfactory processing in homing pigeons (see chapter by Papi, present volume) (this will be discussed later in § 6.).

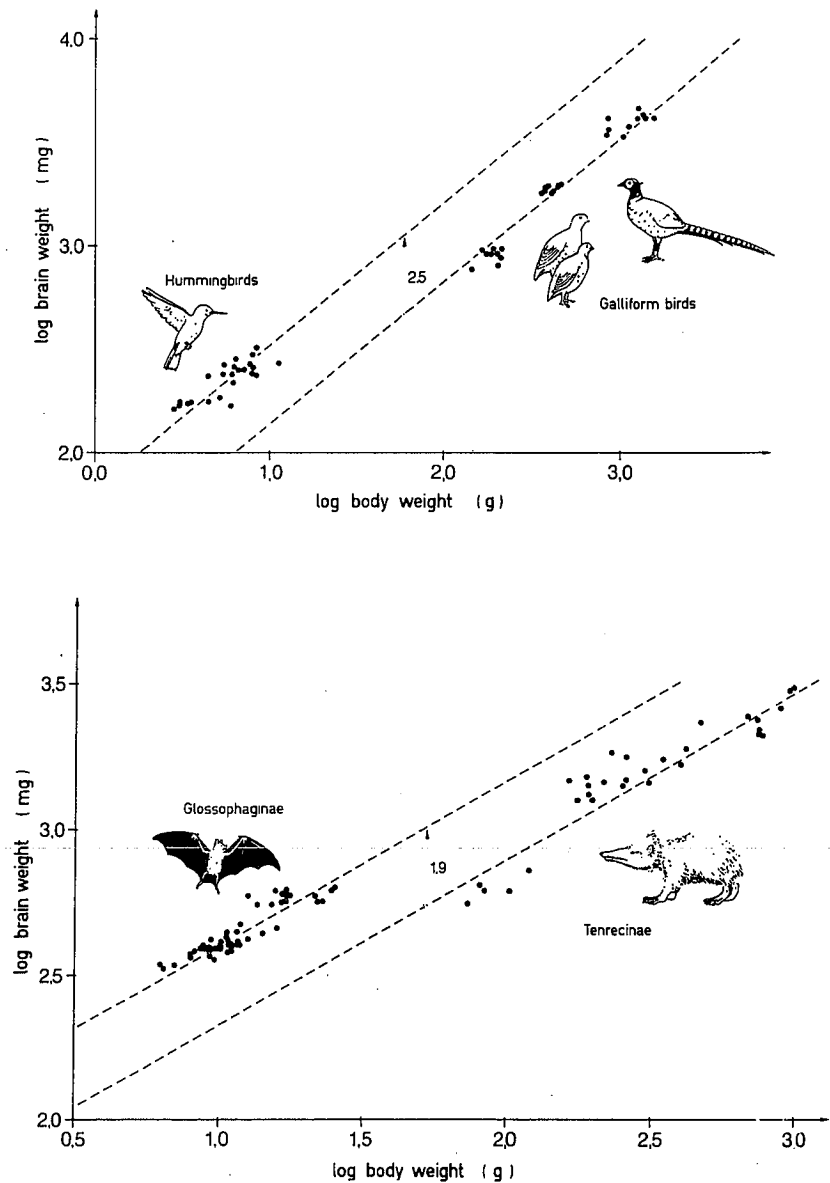


Figure 2. Encephalisation in hummingbirds (above) and nectar-feeding glossophagine bats (below).

Furthermore, there are recent investigations which focus on anseriform birds (*Anser*, *Anas*, *Cairina*). These have a curious specialisation of the mediorostral telencephalic wall which has not been mentioned by older authors, for example Huber and Crosby [28]. There is a large area which is cortically organised and thus quite unusual for an avian brain. It is trilaminated and looks like the mammalian prepiriform cortex, which is the most important

centre for processing of olfactory information. Ebinger *et al.* [21] have used tracer techniques and demonstrated that this area of anseriform birds in fact receives massive input from the olfactory bulb. They proposed that this area of the avian brain is equivalent to the mammalian prepiriform and retrobulbar regions. Furthermore, this paper mentioned other telencephalic target areas of bulbofugal fibres, such as parts of the medial neostriatum, medial ventral hyperstriatum, parolfactory lobe, paleostriatum, septum and the laterocaudal hemispheric surface with a so-called piriform cortex. The latter projection shares similarities with the mammalian periamygdalar cortex, and this similarity is stressed by Ebinger *et al.* [21] proposition to use the mammalian term "regio periamygdalaris" in birds as well. A recent paper of Bingman *et al.* [4] on the olfactory system of pigeons supports many of these findings.

Thus, olfaction in birds might be as important as in mammals. In the particular case of anseriform species it has to be stressed, that the prepiriform and retrobulbar cortices occupy a remarkable part of the mediorostral hemispheric surface. However, we have no idea which behaviour of anseriform birds depends on olfaction, and ethological studies are needed.

4. Nectar Feeding

The evolution of angiosperm plants, which developed blossoms, has been accompanied by the evolution of animals that make use of nectar, which is offered by these plants, to make sure that fertilisation will take place. Seen as a whole such nectarivory is a domain of invertebrates, particularly butterflies and bees. There are, however, two groups of American vertebrates which join with these insects: during daytime, hummingbirds, and at night, glossophagine bats.

Nectarivory depends on the capability of hovering flight which alone allows flowers at the very end of fine branches to be reached. This behaviour requires a well developed sensorimotor coordination. The requisite sensory capacities include taste, because only nectar of a defined glucose concentration is used [63], equilibrium and proprioception. The motor part deals with controlling sucking and flight. This background made it understandable that brain size in glossophagine bats and in hummingbirds is much larger than in reference groups (Fig. 2).

As reference groups, those mammals and birds are chosen which demonstrate the smallest brains in relation to body size within each of the two classes. They are thought to represent minimal conditions. For mammals these are Malagasy hedgehogs of the subfamily Tenrecinae [52, 67] and for the avian group these are galliform birds [6, 47]. An allometric axis running through the centre of the data of each group defines a line of reference for comparison with other groups, e.g. glossophagine bats or hummingbirds. This line enables a comparison even if the body weights are different. A factor (= index or residual in other papers) of enlargement is then calculated which expresses how much larger the brain (or a brain part) of the group of interest is in comparison to the reference group ([67, 69] for detailed review of this allometric method). Throughout this paper all brain part volumes are corrected for histological shrinkage.

Using this approach, hummingbird brains can be shown to be 2.5x as large as galliform ones [51], and in glossophagine bats the factor of enlargement is 1.9, if brain size is compared to brain size of Malagasy hedgehogs. However, total brain size and encephalisation indicate that there is something going on in the brain, but the brain as a whole is functionally heterogeneous and thus a more detailed analysis is needed to understand brain size in relation to a particular biology.

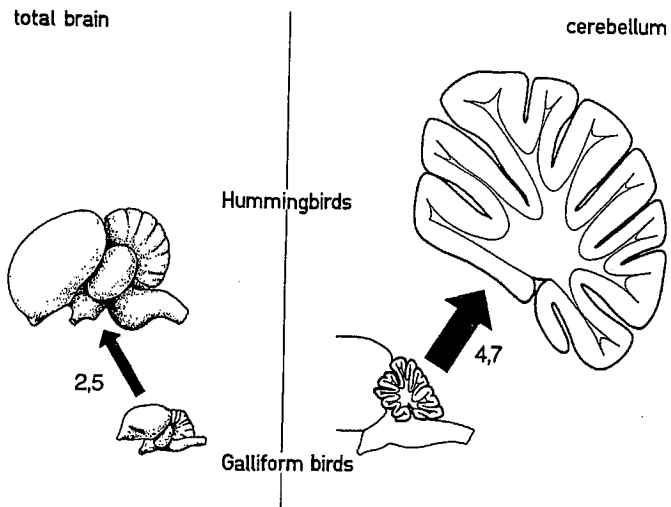


Figure 3. Disproportionate enlargement of the cerebellum in hummingbirds.

In hummingbirds, Kinkel [31] measured the size of functionally identifiable brain parts and nuclei (Table 1). In comparison to galliform birds remarkable enlargements are found. These concern the cerebellum and nuclei situated in the brain stem. The cerebellum is more than 4x larger in hummingbirds than in galliform birds, and its factor of enlargement even surpasses the factor of enlargement of the total brain (Fig. 3). Thus, the cerebellum is one of the most outstanding parts in the hummingbird brain. This is associated with similar enlargements of the red nucleus and the inferior olive. All these areas work together as part of the so-called extrapyramidal motor system. This is well investigated in mammals and might be organised similarly in birds. The red nucleus plays a crucial role. It is under control of the telencephalon via the cortico-rubral tract and at the same time influenced by the cerebellum via its cerebello-rubral pathways. The nucleus itself gives origin to a rubro-spinal tract, which reaches motor neurones of the spinal cord, and a rubro-olivary tract. The latter projects to the inferior olive which sends climbing fibres to the cerebellar cortex. Thus, a feedback mechanism is established. Kennedy [30] has proposed that the red nucleus plays a crucial role in the extrapyramidal system insofar as it switches learned motor programs into the extrapyramidal system where these programs control semiautomatic movements. It can be hypothesised that the hovering flight is such a semiautomatic movement and thus the large size of the respective brain areas would meet the biological demands.

It is a lucky situation for comparative neurobiology that glossophagine bats have adapted to a very similar niche as hummingbirds. Though the brains are different - avian versus mammalian brain - it has been argued that the force of functionally oriented selection leads to very similar morphological solutions [53]. Stiefken [70] has measured the size of nuclei of the extrapyramidal system and demonstrated that this is true (Table 2). The cerebellum as well as the inferior olivary nucleus are disproportionately enlarged in glossophagine bats compared with Malagasy insectivores (Fig. 4). Unfortunately the red nucleus is cytoarchitectonically poorly defined, and thus a volume determination seems to be hardly possible. Nevertheless, the parallelism in brain development is obvious.

TABLE 1. Slopes, y-intercepts (log b) and factors of enlargement of different brain structures in trochilid and passeriform birds as compared allometrically with galliform species. Data from [31]. The slopes are established as proposed by [47].

Area	Galliformes			Passeriformes		Trochilidae	
	slope	log b	factor	log b	factor	log b	factor
Ruber	0.79	-1.955	1	-1.548	2.5	-1.454	3.2
Oliv. inf.	0.70	-1.833	1	-1.363	3.0	-1.256	3.8
Ncll. cer.	0.74	-1.105	1	-0.741	2.3	-0.518	3.9
Intmed.	0.68	-2.699	1	-2.125	3.8	-1.896	6.4
Hypogloss.	0.53	-2.268	1	-1.921	2.2	-1.793	3.0
III/IV	0.69	-1.796	1	-1.406	2.5	-1.135	4.6
VI	0.64	-2.284	1	-1.870	2.6	-1.530	5.7

Specimens of the following species have been investigated: Galliformes: *Coturnix coturnix*, *Perdix perdix*, *Phasianus c. colchicus*; Passeriformes: *Passer domesticus*, *Garrulus glandarius*, *Pica pica*, *Corvus c. corone*; Trochilidae: *Phaethornis spec.*, *Colibri delphinae*, *Colibri thalassinus*. Hypogloss. hypoglossal nucleus, III/IV oculomotor/trochlear nuclear complex, Intmed. intermediate nucleus, Ncll. cer. cerebellar nuclei, Oliv. inf. inferior olivary nucleus, Ruber red nucleus, VI abducens nucleus.

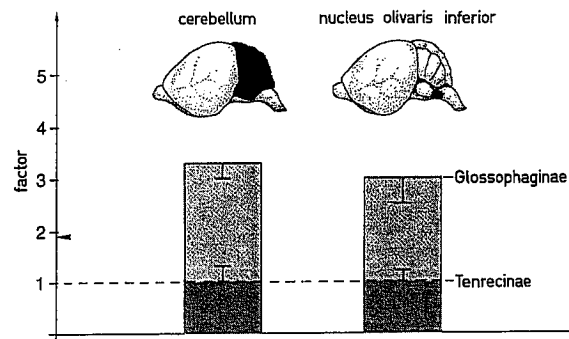


Figure 4. Enlargement of cerebellum and inferior olivary nucleus in glossophagine bats. Data from [70].

Stiefken [70] studied the cerebellum of glossophagine bats in more detail. It is composed of different parts which are associated with specific subfunctions. Stiefken [70] has identified several subunits in the cerebellum of glossophagine bats using transverse and sagittal series through the brains of many species. The enlargement of the paraflocculus-flocculus complex is remarkable. The flocculus plays a crucial role in controlling vestibulo-ocular, optokinetic and truncoocular reflexes [71]. Furthermore, it is integrated in the coordination of the neck musculature [29]. The paraflocculus receives afferent fibres from the pontine area [27] and there are hints of auditory influences [38]. Since the pontine area is a relay for motor pathways, originating in the cerebral cortex and leading to the cerebellum, and since echolocation is obviously used to orient, this development in glossophagine bats can be understood as part of the motor control of the hovering flight. Motor control is also carried out with the aid of the uvula, explaining its 4.4x enlargement in glossophagine bats compared to Malagasy insectivores [70]. This cerebellar area receives afferent fibres from the vestibular nuclei, the pontine nuclei, the inferior olive and the spinal cord. It sends efferent fibres to the cerebellar nuclei and the vestibular nuclei. The latter are integrated into the extrapyramidal system and thus the large uvula of glossophagine bats also has to be understood as an adaptation to the necessity of elaborate motor control which makes hovering flight possible.

TABLE 2. Slopes, y-intercepts (log b) and factors of enlargement of different brain structures in glossophagine and vespertilionid bats as compared allometrically with insectivores.

Area	Insectivora			Vespertilionidae		Glossophaginae	
	slope	log b	factor	log b	factor	log b	factor
Ruber	0.71	-2.964	1	-2.551	2.6	-2.109	7.2
Oliv. inf.	0.47	-1.211	1	-1.025	1.5	-0.732	3.0
Cerebell*	0.68	0.801	1	1.037	1.7	1.325	3.3
Lob. ant.	0.60	0.115	1	0.230	1.3	0.466	2.2
Pf/Flocc	0.86	-0.788	1	-0.185	4.0	-0.069	5.2
Uvula	0.56	-0.289	1	-0.078	1.6	0.350	4.4

Vespertilionid data are given to illustrate the situation in bats, which are, in contrast to glossophagine species, not specially adapted to nectarivory and hovering flight.

Data from Stephan et al. [68]; all other data are from Stiefken [70]. Specimen of the following species have been investigated: Insectivora: Tenrec ecaudatus, Scifer setosus, Hemientetes semispinosus, Echinops telfairi; Vespertilionidae: Myotis albescens, Myotis altarium, Pipistrellus crassulus, Eptesicus serotinus andersoni, Ia io; Glossophaginae: Glossophaga longirostris, Glossophaga soricina, Monophyllus plethodon, Leptonycteris curasoae, Leptonycteris nivalis, Lonchophylla thomasi, Lonycteris spurrelli, Anoura caudifer, Anoura geoffroyi, Choeronycteris godmani. The slopes are established as proposed by Rehkämper et al. [51]. Cerebell cerebellum, Lob. ant. anterior lobe of the cerebellum, Oliv. inf. inferior olivary nucleus, Pf/Flocc parafloccular/floccular complex, Ruber red nucleus.

Additionally the data of Kinkel [31] on hummingbirds point to another aspect which is different from glossophagine bats but biologically relevant. Hummingbirds are active diurnally, and their orientation is visually dominated. Measurements of the motor nuclei innervating the eye muscles reveal high factors of enlargement. Obviously eye movement plays an important role in the biology of hummingbirds. It might be argued that the necessity for stereoscopic vision and thus the foreword movement of the laterally situated eyes is reflected in the data.

Summarising, it can be said that the key to nectarivory is the capability of hovering flight, which depends on well-differentiated control nuclei of the extrapyramidal system. This is as true in glossophagine bats as in hummingbirds.

5. Subterranean Life

Many invertebrates and vertebrates, particularly mammals, have adapted to underground life. This environment is partly defined by darkness and the necessity of a tunnel system as infrastructure for foraging and social contacts. Subterranean mammals are to be found among insectivores and rodents as well as among marsupials.

Darkness severely reduces the effectiveness of the visual system, and in fact there are at least some subterranean species called blind. Among insectivores, the Chrysochlorids are said to lack completely an optic nerve [13]. Their lateral geniculate body is minute [2]. Cortical organisation is difficult to interpret. The organisation of cytoarchitectonic areas does not differ from what is seen in other insectivores [46], but a functionally oriented approach is needed to elucidate the function of the occipital cortex which serves vision in sighted animals. Among marsupials, *Notoryctes* shares a lot of similarities with Chrysochlorids. In fact, this species seems to make use of the congruent ecological niche in Australia. However, no data are available on the visual system in this rare species.

Many ethological and morphofunctional data exist for the fossorial rodent *Spalax ehrenbergi* [41]. Two aspects of its biology are of peculiar importance for the neurobiologist. The first point concerns the tunnel system in which *Spalax* lives. This is very large and is needed to get food, mainly roots and other plant parts. Careful study reveals that

TABLE 3. Fresh volumes and factors of enlargement of different brain parts of *Spalax* as compared to the laboratory rat. The factor of enlargement is based on data obtained from Madagassian hedgehogs (Stephan et al. [67], for explanation see text).

Volume (in mm ³)	<i>Rattus</i> (n=8)	<i>Spalax</i> (n=5)	factor (<i>Rattus</i> = 1)
Brain	1708.49	2014.48	2.0
Telencephalon	943.52	1139.66	2.1
Diencephalon	153.06	191.79	2.1
Tegmentum	286.58	296.09	1.7
Cerebellum	232.33	303.03	2.2
Tectum	48.23	28.02	0.9
Motor structures:			
motor-cortex*	66.04	114.36	3.1
striatum	90.48	136.21	2.6
ncl. motorius n. trigemini	0.81	1.62	3.4
Sensory structures:			
olfactory structures (1)	143.96	179.81	2.1
auditory structures (2)	35.78	16.79	0.7
Somatosensory structures:			
somatosensory cortex	127.94	125.31	1.7
ncll. VPM/VPL thalami**	10.46	8.56	1.4
Body weight	233.7	106.24	

* *Rattus* (n=10) [73, 76]

** *Rattus* (n=7); *Spalax* (n=7)

(1) olfactory bulb, paleocortex (see Stephan [66])

(2) cochlear nuclei and inferior colliculus

Spalax digs the tunnel system with its teeth, which powerfully loosen the soil. Afterwards the neck and head push the loosened soil away. As a result chewing muscles and those for the neck are extremely large. The anatomy of the head which is flattened like the shovel of a bulldozer reflects this peculiar mode of digging.

The second point concerns the sensory world of *Spalax*. The eyes of this species are vestigial and covered by skin [12]. This condition develops during an ontogenesis which starts quite normally [10]. That part of the visual system associated with the hypothalamically controlled endocrinal system is further elaborated in ontogeny [15, 16], whereas that one serving image analysis appears reduced. This condition is associated with a minute lateral geniculate body and the lack of a visual cortex [40, 50].

Despite this severe reduction of a sensory system, which is quite large in many mammalian species, brain size of *Spalax* as well as size of diencephalon and size of the parts of the telencephalon bearing the isocortex are not reduced, but clearly enlarged. In fact, the brain in *Spalax* is 2.74x larger than that of Malagasy insectivores. It might be useful to include the laboratory rat in this comparison. Biologically it is more a "generalist" than *Spalax*. At the same time it is well understood neurobiologically. Compared to the rat brain, the *Spalax* brain comes out to be nearly twice as large (factor 2.0, Table 3).

The question arises whether these changes in brain size can be explained in terms of the extreme adaptation to subterranean life. Because the brain as a whole is morphologically and functionally heterogeneous, we need to look for the size of functionally identified subareas of the brain. Volumetric data reveal that motor areas are heavily enlarged. This is true for the cerebellum (Table 3) and the inferior olivary nucleus. These two brain parts belong to the extrapyramidal system and are part of a circuit, cerebellum - red nucleus -

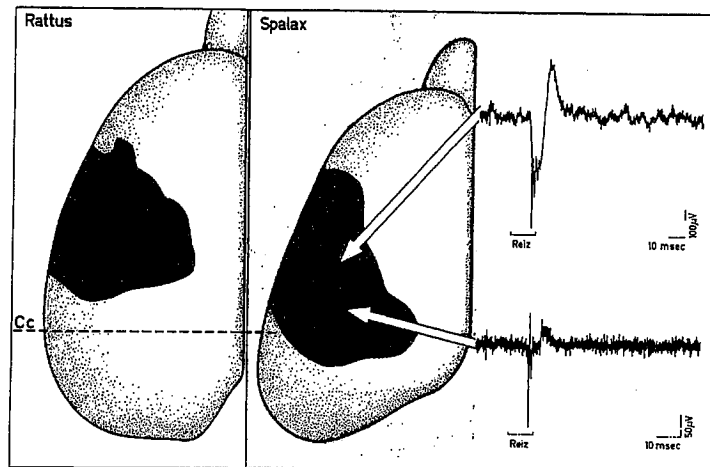


Figure 5. Topography of the somatosensory representation area in *Spalax* brain (dorsal view) as compared to the laboratory rat. Borderlines in *Spalax* are found using electrophysiological recording (right; from [40]). Reiz = stimulus applied to mechanoreceptors of the skin.

olivary nucleus - cerebellum, which is said to generate semiautomatic movements (see above). Furthermore, the motor nucleus of the trigeminal nerve, which innervates the chewing muscles exclusively, is disproportionately enlarged (Table 3).

So, quantitative brain anatomy directly reflects biological demands if digging is understood as a semiautomatic movement comparable to the hovering flight in bats and birds: cerebellum and inferior olive are needed to control use of neck muscles and those for chewing during digging activity and the large motor nucleus of the trigeminal corresponds to the large chewing muscles innervated by it.

Additional findings support that hypothesis. The striate body (caudate nucleus and putamen) is also found to be enlarged in *Spalax* compared to that in many insectivores, laboratory rats and prosimian primates (Table 3). This reflects the specialisation of motor coordination because the caudate/putamen can be regarded as the telencephalic control station of the extrapyramidal system. It is linked via the thalamus to the red nucleus and thus to the olivary-cerebellar complex.

It is well known that the cortical part of the motor system is characterised by a high density of α -adrenergic receptors ([77] for review). Using that as a marker the motor cortex can be identified and its volume measured. Allometrically it is more than 3x larger in *Spalax* than in the laboratory rat (Table 3, the reference axis used in this approach could not be taken from *Spalax* and rat data. It was obtained from isocortex as a whole versus body weight in Malagasy hedgehogs [67]).

The specialisations described probably contribute in large measure to the general enlargement of the *Spalax* brain. However, other functional areas are situated within the thalamus and the isocortex, for example sensory areas which might also be important for this peculiar biological adaptation. One may well ask if another sensory system has been elaborated in order to balance the loss of vision. The olfactory, auditory and somatosensory

systems have been studied in the context. The size of the olfactory structures (olfactory bulb and the adjoining cortices) are not outstanding in comparison to those in small-brained insectivores but larger than in the laboratory rat (Table 3).

It has been claimed that the auditory system has increased in size by taking over the nuclear masses of the "useless" visual system [9, 25]. However, measurements of the cochlear nuclei as well as the inferior colliculus reveal no outstanding development (Table 3).

Possibly the somatosensory system has developed in a progressive way. This hypothesis was tested using a multimethod approach. First, electrophysiological recordings were used to delineate the boundaries of the somatosensory isocortex (Fig. 5). These boundaries were marked with small injections of pontamine sky blue which can be seen in transverse sections. The experimental materials were transferred to paraffin series which are suitable for architectonic and volumetric analysis, including correction for shrinkage. Thus, the size of the functionally identified somatosensory cortex was determined [49]. On average the somatosensory cortex of *Spalax* measures 125 cubic mm and thus is 1.7x larger than in the laboratory rat if compared allometrically (Table 3). (Again the slope was taken from isocortex volume to body weight relation in Malagasy hedgehogs).

Furthermore electrophysiologically-controlled tracing studies demonstrated that the somatosensory nuclei of the thalamus (Nucleus Posterior, Nucleus Ventralis Postero-Medialis and PosteroLateralis VPM/VPL) reach the surface of the diencephalon in *Spalax*, whereas they are situated in the depth of the diencephalon in the laboratory rat and all other mammals [50]. This points to an enlargement of these nuclei in *Spalax*. Thus, using the results of the tracing experiments, we made measurements of VPM/VPL in a paraffin series, and then did allometric analysis. In fact, the hypothesis of an enlargement of the somatosensory nuclei is supported. The VPM/VPL complex in *Spalax* measures 8.6 cubic mm and is 1.4x larger than that in the laboratory rat (Table 3). (Again the slope was taken from the VPM/VPL complex to body weight relation in Malagasy hedgehogs).

There are two aspects of the biology of *Spalax* which correlate with a well-developed somatosensory system. First, the whole body seems to be very sensitive to mechanoreception. The width of the tunnel tube is hardly larger than the width of the animal, and thus *Spalax* is in permanent contact with its surroundings. Of peculiar interest are the vibrissae of the head and a stripe of stiff hairs which can be found on the upper lip. The latter are very sensitive and their mechanical stimulation leads to strong electrophysiological responses of the somatosensory cortical area [40]. It may well be that *Spalax* uses these stiff hairs for orientation within its tunnel system.

The second point concerns communication underground. Since *Spalax* is territorial and extremely aggressive against other conspecific individuals a communication system is needed to avoid conflicts. *Spalax* produces low frequency vibrations by beating the tunnel roof with powerful excursions of its head. Such vibrations are transmitted by the soil and can be sensed by conspecific individuals at a distance (seismic communication). Nevo *et al.* [42] have extirpated the cochlea and found that small vibratory stimuli nevertheless evoke brain potentials. They concluded that perception of such low frequency vibration is done through the somatosensory system. Though the location of reception is not yet identified, the strong development of the nuclei of the somatosensory pathway would support this interpretation.

Thus, we can summarise, that the ecological niche of *Spalax*, which is defined by a subterranean mode of life in a self-constructed tunnel system built with the aid of teeth and head, is specifically reflected in the brain. Large motor control areas and a complete loss of a part of the visual system (image analysis) are characteristic. The visual system has been replaced by an elaborated somatosensory system which has probably become the main sensory system for spatial orientation. At the same time, the somatosensory system may serve intraspecific communication.

6. Living in Man-Made Environments

Comparative investigations of domesticated animals and their wild ancestors have shown that domestication alters brain size and brain composition dramatically ([26] for review). Sensory systems, motor systems and the limbic system as well as associated regions are affected. Many domesticated species are subdivided into different breeds. From a zoological point of view such breeds are evolutionary units below the species level and can be compared to subspecies. Whereas it is very difficult to identify the selective criteria which have led to the development of subspecies in the wild or “naturalistic settings”, the selective criteria of breeds which live in a “semi-naturalistic setting” are well formulated and one can argue that each breed is adapted to a peculiar ecoethological niche defined by man. Most of the breeds have been established during a relatively short time, and in fact new breeds can be seen to appear regularly. This cooperates in the interest of scientific evolutionary biology, the main problem of which is long periods of evolutionary development that cannot be studied experimentally but must be reconstructed. In the evolution of breeds this is different, and thus domestication research can be understood as a sort of experimental approach to evolutionary plasticity. Since the experiment plays a crucial role in natural science the heuristic value of domestication research should not be underestimated.

Active breeding affects body size, body shape or physiological capabilities of the animal (e.g., milk production). However, it also affects behaviour. Some examples originating from practical and scientific experiences should underline this point. There is strong evidence that such differences are genetically fixed. In sheep, the Merino breed is not only characterised by an enormous wool production but also by a deep-rooted flocking instinct which has been selected for because it allows a single herder to watch over very large flocks [7]. Sheep of the Texel breed and similar ones are said to use head-butting much less than other breeds, when fighting for females [59]. Cattle of the Galloway breed rest more often and for longer periods than Friesian breeds [36]. Aggressive behaviour of the Eringer breed and Spanish fighting bulls is much stronger than in other cattle breeds [57]. Fighting cattle used to have larger interindividual distances than other breeds [60, 62]. Bulls in general might refuse to service cows of other breeds and might even attack them [58]. Dairy cows allow themselves to be serviced more times than other breeds [56], and they have lower flight distances than beef cattle [45]. Genetically hornless cattle are said to be less aggressive than horned breeds [59, 61]. Feddersen-Petersen [22] has investigated the ontogenesis of behaviour in different breeds of dogs and reported many differences. Labrador Retrievers have a delayed ontogenetic development of locomotor behaviour. Poodles exhibit certain parts of social behaviour only late during development. Hunting dogs, such as Golden Retrievers, use their olfactory orientation very early.

TABLE 4. Fresh volumes (in mm³), body size (in ml) and factors of enlargement of brain and brain parts in homing pigeons as compared to non-homing breeds such as Fantail and Strasser (see also Rehkämper et al. [48]).

Area	slope	Fantails (n=6)				Strassers (n=7)			Homing pigeons (n=8)		
		vol	sd	fact		vol	sd	fact	vol	sd	fact
Body vol.		321.9	27.4			553.9	67.0		438.3	43.4	
Brain vol.	0.376	1916.0	59.4	1		2371.6	83.0	1	2286.7	141.8	1.05
Tegment.	0.359	264.4	12.1	1		324.3	17.6	1	311.2	18.8	1.04
Cerebel.	0.416	314.5	13.8	1		400.2	12.8	1	359.4	38.5	1.00
Tectum	0.306	190.2	6.5	1		227.3	14.3	1	222.4	15.8	1.06
N. opticus	0.478	52.2	6.7	1		66.9	6.8	1	58.8	6.2	0.98
Dienceph.	0.235	111.6	9.8	1		126.6	8.2	1	128.9	4.1	1.08
Telenceph.	0.390	944.5	24.6	1		1165.8	63.0	1	1143.9	92.7	1.07
Hacc Hdor	0.475	179.7	11.7	1		236.4	18.0	1	215.1	20.4	1.02
Hyp. vent.	0.340	173.7	5.6	1		206.1	11.1	1	205.1	25.2	1.07
Neostriat.	0.371	414.0	12.4	1		506.4	34.4	1	501.6	38.6	1.08
Palaeostr.	0.397	130.3	7.8	1		158.1	19.9	1	159.5	14.7	1.10
Hippocam.	0.272	23.7	6.2	1		29.9	8.3	1	34.3	6	1.27
Septum	0.380	12.1	1.6	1		14.4	2.1	1	13.5	1	1.01
Prepirif.	0.568	3.0	0.4	1		4.2	1.9	1	3.7	1.4	1.01
Bulb. olf.	0.429	8.0	0.5	1		10.2	0.9	1	11.1	1.2	1.21

Bulb. olf. olfactory bulb, Body vol body volume, Brain vol brain volume (mm³), Cerebel. cerebellum, Dienceph. diencephalon, Fact factor of enlargement Hacc accessory hyperstriatum, Hdor dorsal hyperstriatum, Hippocam. hippocampus, Hyp. vent. ventral hyperstriatum, Paleostr. paleostriatum, Prepirif. prepiriform region, sd standard deviation, Tegment. tegmentum (brain stem), Telenceph. telencephalon.

Additionally there are some neuroanatomical studies which focus on this problem. Stephan [65] states that there are differences in the pattern of gyrification in different breeds of domestic sheep. Ebinger [19] reports on differences in brain composition between different breeds of dogs, Bronson [11] and Röhrs [55] do the same in cats. Reduction in brain size, which is typical for domesticated species, is said to be different in different breeds of domesticated laboratory rats [33]. Catecholamine content in pigeon brains of the Carneaux breed is lower than in other breeds [18].

Despite these examples from ethological and neuroanatomical observations, papers which concentrate on breed differences *expressis verbis* are rare. We studied different breeds of domesticated pigeons, hens and rabbits and tried to correlate morphometry of the brain with behavioural differences. Homing pigeons are selected for their homing ability. They return to their home loft from several hundred kilometres. Haase *et al.* [24] have shown that their brains are 5% larger than those of non-homing pigeon breeds such as fantails and strassers.

An analysis of brain composition revealed many differences between homing and non-homing pigeons [48]. We measured 14 brain parts. There was in no case a difference between the two non-homing breeds (Table 4); however, homing pigeons have larger factors for the size of the tectum (1.06), olfactory bulbs (1.21), hippocampus (1.27), neostriatum (1.08) and palaeostriatum (1.10) than the two other breeds. The remarkable size of the olfactory bulb provides new insights (Fig. 6). After a long and controversial discussion there is no doubt that olfaction plays an important role in navigation [43] (see also chapter by Papi, present volume).

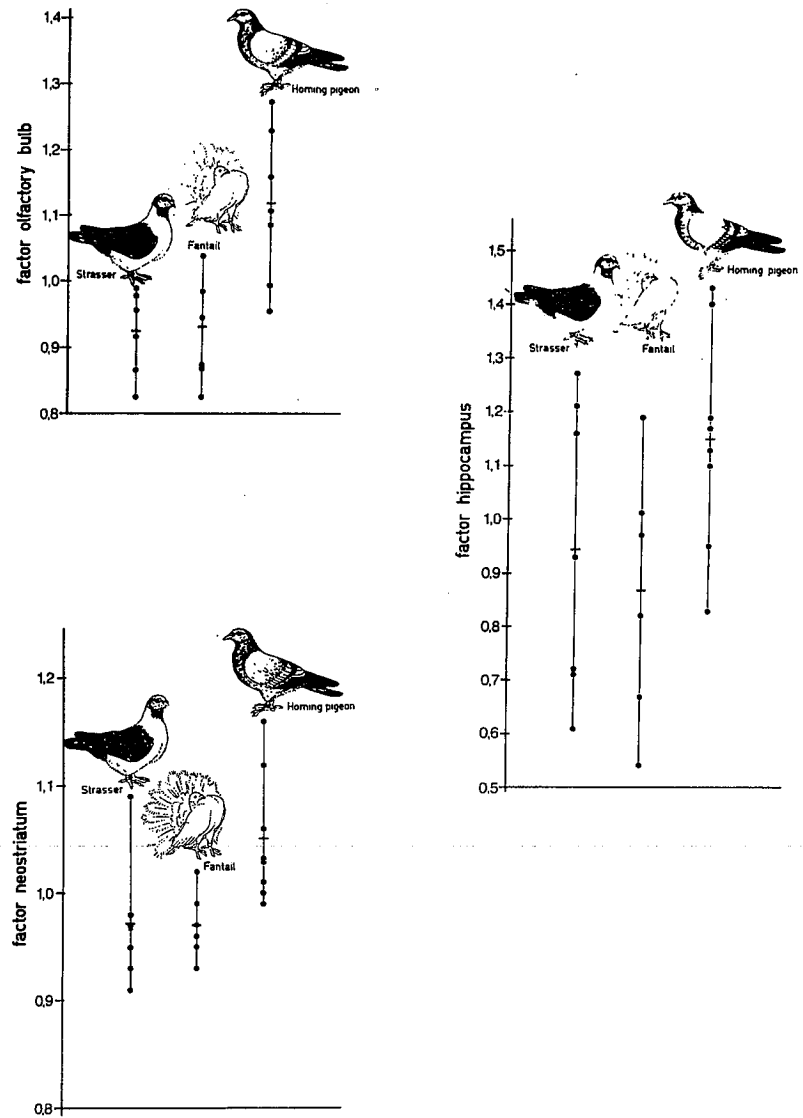


Figure 6. Enlargement of olfactory bulb, neostriatum and hippocampus in homing pigeons compared to the non-homing breeds Strasser and Fantail (see Rehkämper *et al.* [48]).

At the same time, it is quite obvious that homing ability depends on the integration of information of many sensory systems. Thus integrative parts of the brain should also be studied. We demonstrated [53] that the neostriatum, particularly its large caudally situated area Ne 16 [54], receives afferent fibres directly or indirectly from all main sensory areas and at the same time sends efferent fibres to superior motor control regions, for example the archistriatum (Fig. 7). Thus the caudal neostriatum has the “infrastructure” for multimodal

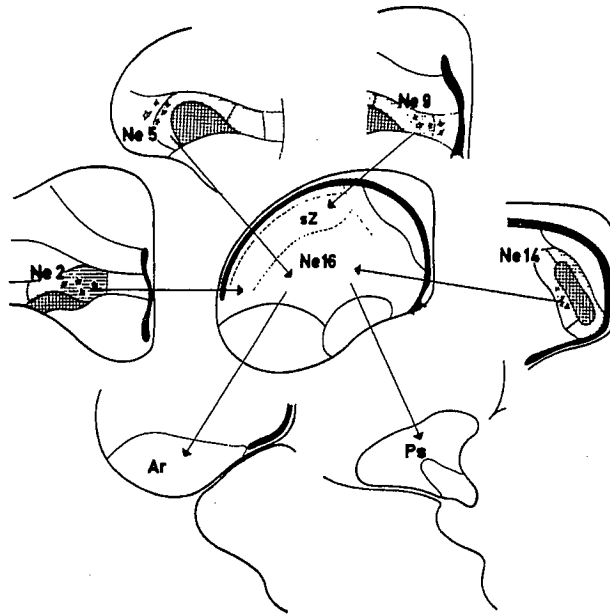


Figure 7. The caudal neostriatum of the pigeon with area Ne 16 and the sickle-shaped zone (sZ) and its connectivity. Ne 2 = secondary area to the somatosensory basal nucleus (cross-hatched); Ne 5, Ne 9 = secondary area to the visual ectostriatum (cross-hatched); Ne 14 = secondary area to the auditory field L (cross-hatched). Ar = Archistriatum; Ps = Paleostriatum. Afferent fibres from ventral hyperstriatum are not depicted (see [5]).

integration as postulated for navigation. This interpretation fits with the quantitative data which demonstrate that the neostriatum is disproportionately enlarged in the homing pigeon brain (Fig. 6).

Most outstanding is the large size of the hippocampus, which is significant though a large, interindividual, variability is seen (Fig. 6). Its role in learning and memory has been proved in mammals and birds [32], and there is evidence that this is also true in homing pigeons [5]. Bingman *et al.* [4], while describing the connections of the piriform cortex (= periamygdalar cortex as proposed by [21]) with the parahippocampal region proposed that the hippocampus is part of a neural system that regulates navigational map learning by integration of olfactory information. Their proposition would be consistent with the large size of the homing pigeon hippocampus.

More than a hundred breeds of the domestic chicken are known. Among the oldest ones are silky hens and Japanese Chabos. Silky hens have many curious characters such as silky feathers; heavily pigmented muscles, inner organs and bones; five instead of four toes and sometimes a hood on their skull. Their behaviour has not been studied systematically, but they are known to panic quickly. In addition, the learning ability of hooded chickens, to which they may be related, is not very good [64]. It should be mentioned that the macromorphology of the brain of hooded silky hens is dramatically altered in comparison to non-hooded ones, but there is no difference in brain size and composition.

TABLE 5. Body weight, brain weight and fresh volumes of different brain parts (mean \pm sd) in two breeds of the domestic chicken (silky hens, Chabos). Additionally, the proportion of the brain parts in relation to total brain are given.

	Silky hens (n=8)			Chabos (n=11)		
Body Weight g	950 \pm 224			578 \pm 122		
Brain Weight mg	2840 \pm 229			2578 \pm 229		
	mm3		% brain	mm3		% brain
Telencephalon	1343.1 \pm	167.4	50.5	1306.9 \pm	127.9	54.0 **
Hyp. acc.	204.1 \pm	26.1	7.7	212.3 \pm	20.8	8.8 **
Hyp. dors.	30.3 \pm	11.5	1.1	33.0 \pm	6.1	1.4 ns
Hyp. vent.	232.2 \pm	32.8	8.7	203.5 \pm	26.9	8.4 ns
Neostriatum	642.5 \pm	95.6	24.1	632.8 \pm	68.7	26.1 **
Paleostriatum	205.3 \pm	16.5	7.8	197.1 \pm	18.6	8.2 ns
Hippocampus	8.8 \pm	2.4	0.3	10.6 \pm	1.9	0.4 *
Septum	13.0 \pm	1.7	0.5	12.0 \pm	2.1	0.5 ns
Bulbus olfactorius	6.9 \pm	1.3	0.3	5.6 \pm	1.8	0.2 ns

ns, no significance; *, $p = .05$; **, $p = .01$, Student's t-test

Hyp. acc. accessory hyperstriatum, Hyp. dors. dorsal hyperstriatum, Hyp. vent. ventral hyperstriatum, Hyp. vent. ventral hyperstriatum, Paleostriat. paleostriatum, sd standard deviation, Telencephal. telencephalon

Chabos are unique as well. They originate from south east Asia and Japan and are said to have existed 300 years or more. They have extremely short legs, large combs and tails, and short bodies. As adults, they are very calm and tame. Chabos are not bred for economic purposes but are selected as pets that live in close relation to man. Their brain composition is different from that in silky hens (Table 5). Particularly, they have a proportionally larger neostriatum. This part serves complex functions which are part of cognitive processes including learning (see above) [37]. To get an indication of the learning abilities of adult Chabos we tested them in a conditioning box. They were to learn to replace the normal scraping behaviour, used to get food, with the unnatural pecking on a glass window to gain access to a food box. In fact, 7 of 10 Chabo hens quickly learned this skill. This is a strong indication of cognitive abilities, which must be investigated more intensively.

Rabbits are only recently domesticated. They originate from wild rabbits which survived the last ice age in Northern Africa and Spain [14, 26, 39, 75]. Nearly 1,000 years ago, man started to use these animals for meat and wool (Angora rabbits). To date, there are nearly 70 different breeds, and breeding of rabbits has become a hobby. Selection criteria concentrate on body shape, colour and weight. There is no breed that has been selected for ethological criteria. However, there are some breeds, the morphological characters of which are assumed to be of ethological relevance. In these breeds, which are called "Widder" in the German Language, the ears lost their upright posture and hang down. In some breeds these pendulous ears become apparent during the first months of the life, after being born with relatively normal ears. In the "Englische Widder", however, the new born rabbits already have pendulous ears. In this breed the outer ears will grow to the remarkable length of 30 cm or even more (Fig. 8). The ear muscles are no longer able to move these outer

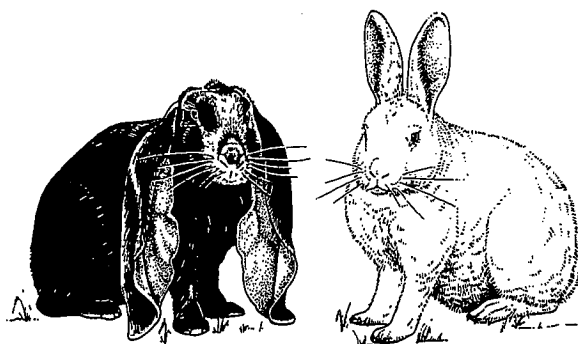


Figure 8. Two different breeds of domesticated rabbits: "Englische Widder" on the left and "Weisse Neuseeländer" on the right. Note the very different shape of the outer ears.

TABLE 6. Body weight, brain weight and fresh volumes of different brain parts of the auditory pathway in two breeds of the domestic rabbit (Weisse Neuseeländer, Englische Widder). Additionally, the proportions of the brain parts in relation to tegmentum (brain stem) are given.

	Weisse Neuseeländer (n=6)			Englische Widder (n=3)		
Body weight (g)	3463 ±	332		4063 ±	706	
Brain weight (mg)	11353 ±	579		12072 ±	510	
Structure	mm ³		% Tegn	mm ³		% Tegn
Tegmentum	1757.86 ±	105.77		1958.65 ±	47.56	
Ncll. cochl.	35.04 ±	3.71	1.99	30.65 ±	4.80	1.57 *
Coch. dors.	18.35 ±	2.05	1.04	15.75 ±	2.21	0.80 **
Coch. vent.	16.69 ±	2.01	0.95	14.90 ±	2.87	0.76 ns
Ncl. trapez.	2.12 ±	0.16	0.12	2.26 ±	0.34	0.12 ns
Oliiva sup.	5.22 ±	0.43	0.30	3.81 ±	0.72	0.20 **
O. sup. lat.	3.49 ±	0.30	0.20	2.53 ±	0.63	0.13 **
O. sup. med.	1.73 ±	0.24	0.10	1.27 ±	0.14	0.07 **

ns, *, ** indicate the statistical significance of the differences between the breeds (no significance, $p = .05$, $p = .01$, Student's *t*-test). Coch. dors. dorsal cochlear nucleus, Coch. vent. ventral cochlear nucleus, Ncl. trapez. Nucleus of the trapezoid body, Ncll. cochl. cochlear nuclei, Oliiva sup. superior olivary nuclei, O. sup. lat. lateral nucleus of the superior olivary nucleus, O. sup. med. medial nucleus of the superior olivary nucleus, sd standard deviation, W. weight.

ears as is a common behaviour in rabbits with normal ears. Darwin [17] mentioned this breed and demonstrated that there were changes in the bony part of the outer ear. It can be assumed that perception of acoustic stimuli in this breed is altered compared to rabbits with normal ears. This alteration might affect frequency perception by changing neurones which are to be found at every level of the auditory pathway including the cochlear nuclei. Furthermore, directional hearing might be limited because this facility is closely coupled with the structure of the outer ear. It depends on nuclei in the brain which receive afferent

fibres from both sides. The superior olivary complex is the first relay of the auditory pathway which fulfils this precondition and in fact its medial nucleus is specialised for directional hearing. We studied the volume of the auditory nuclei in "Englische Widder" and compared their size proportional to the brain stem volume with the data from "Weiße Neuseeländer", which have normal ears, of nearly the same body size (Table 6). Proportionally, the cochlear nuclei as well as both parts of the superior olivary nucleus are significantly smaller in "Englische Widder" than in "Weiße Neuseeländer".

It is an open question whether these differences are determined genetically or are achieved via individual functional adaptation during CNS development. Ontogenetic studies are needed to clarify this point. However, there are reports that sheep which have no outer ears are deaf and the lack of the outer ear is genetically determined [74], but Fischer and Atmadilaga [23] present alternate interpretations.

7. Conclusions

The intention of this report was to point out the strong correlation between plasticity of brain composition and specific behaviours which enable animals to make use of a certain ecological niche. Prey hunting under water is accompanied by an elaboration of the trigeminal system including cortical representation areas. Nectar feeding is possible because of a quantitatively differentiated extrapyramidal system that serves hovering flight. A subterranean life and digging using teeth, as seen in *Spalax*, is reflected in large motor control areas and a reduction of the visual system together with an increased size of the somatosensory system.

Quantitative neuroanatomy has helped to formulate new questions, such as why geese have extremely large olfactory cortices. Little is known concerning the ethological relevance of this observation.

Finally attention is drawn to the heuristic power of comparative neurobiological studies of different breeds in domestic animals. This approach allows the study of evolutionary brain plasticity under clearly arranged constraints and may fulfil the demands of an experimental approach. The homing ability of homing pigeons depends on olfactory information, multimodal cognitive processes and hippocampal learning, thus they have large olfactory bulbs, neostriati and hippocampi (see chapters by Papi, and Bingman *et al.*, present volume). Japanese Chabos which are very tame have remarkable cognitive capacities; in contrast to other breeds their neostriatum which serves cognitive processes contributes to a larger measure to the brain. Rabbits with pendulous ears, which limit stimulus perception, have been shown to have poorly developed auditory systems in comparison to breeds with normal ears. These last examples clearly indicate that the plasticity of brain structure and composition allows alterations in a short time. Thus, evolution of the brain is not necessarily a long-term phenomenon but happens quickly. Brain structure and behaviour are inextricably linked and the malleability of both is remarkable.

Acknowledgements

We wish to thank Claudia Stolze (histology, ethological experiments), Sally Mann (histology) and Christine Opfermann-Rüngeler (graphics) for their skillful support, as well as Prof. Dr. Karl Zilles for his help in autoradiographic studies of the *Spalax* brain.

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