

Asymmetry of different brain structures in homing pigeons with and without navigational experience

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SUMMARY

Homing pigeons (*Columba livia* f.d.) are well-known for their homing abilities, and their brains seem to be functionally adapted to homing as exemplified, e.g. by their larger hippocampi and olfactory bulbs. Their hippocampus size is influenced by navigational experience, and, as in other birds, functional specialisation of the left and right hemispheres ('lateralisation') occurs in homing pigeons. To show in what way lateralisation is reflected in brain structure volume, and whether some lateralisation or asymmetry in homing pigeons is caused by experience, we compared brains of homing pigeons with and without navigational experience referring to this. Fourteen homing pigeons were raised under identical constraints. After fledging, seven of them were allowed to fly around the loft and participated successfully in races. The other seven stayed permanently in the loft and thus did not share the navigational experiences of the first group. After reaching sexual maturity, all individuals were killed and morphometric analyses were carried out to measure the volumes of five basic brain parts and eight telencephalic brain parts. Measurements of telencephalic brain parts and optic tectum were done separately for the left and right hemispheres. The comparison of left/right quotients of both groups reveal that pigeons with navigational experience show a smaller left mesopallium in comparison with the right mesopallium and pigeons without navigational experience a larger left mesopallium in comparison with the right one. Additionally, there are significant differences between left and right brain subdivisions within the two pigeon groups, namely a larger left hyperpallium apicale in both pigeon groups and a larger right nidopallium, left hippocampus and right optic tectum in pigeons with navigational experience. Pigeons without navigational experience did not show more significant differences between their left and right brain subdivisions. The results of our study confirm that the brain of homing pigeons is an example for mosaic evolution and indicates that lateralisation is correlated with individual life history (experience) and not exclusively based on heritable traits.

Key words: homing pigeon, lateralisation, asymmetry, brain, navigation, mosaic evolution.

INTRODUCTION

Functional specialisation of the left and right hemispheres of the brain ('lateralisation') was first found in humans (e.g. Broca, 1865; Geschwind and Galaburda, 1985) but has now been documented in a variety of species including birds (Nottebohm, 1970; Rogers, 1996; Vallortigara et al., 1996; Güntürkün, 1997).

Since the first evidence of functional lateralisation in birds, studies have documented right–left differences in avian visual processing (e.g. Rogers, 1996; Vallortigara et al., 1996; Güntürkün, 1997), auditory processing (e.g. Howard et al., 1980; Rogers and Anson, 1979), song production (Williams et al., 1992; Floody and Arnold, 1997; Poirier et al., 2009) and aspects of spatial learning and memory (e.g. Rashid and Andrews, 1989; Clayton and Krebs, 1994a; Ulrich et al., 1999; Gagliardo et al., 2001; Kahn and Bingman, 2004). A number of laboratory studies in birds have suggested that the right hemisphere may play a preferential role in global representation of space (by constructing a detailed organisational and topographical map) and learning and memory for global, distally located spatial information whereas the left hemisphere shows a preference for learning and remembering features of goal locations, encoding object-specific cues (by discriminating and categorising stimuli) and the representation of proximal cues (landmarks) used to locate a goal in space (Rashid and Andrew, 1989; Ulrich et al., 1999; Vallortigara et al., 1999; Clayton and Krebs, 1994a; Tommasi and

Vallortigara, 2001; Prior et al., 2002). However, there are species-dependent differences (e.g. between chicks and pigeons), which have to be considered (Rogers and Deng, 1999; Tommasi and Vallortigara, 2001).

Such studies mostly describe functional cerebral lateralisation. Morphological asymmetries were described in different layers of the optic tectum (cell sizes) (Güntürkün, 1997) and in left and right hippocampi of homing pigeons (cell types, 'location cells' and 'path cells') (Hough and Bingman, 2004; Siegel et al., 2006).

Homing pigeons are well known for their homing abilities thought to be based on a genetic predisposition, multimodal learning, spatial cognition and motivation (Lipp, 1983; Wallraff, 2001; Cnotka et al., 2008; Mehlhorn and Rehkämper, 2009). Several orientation cues and mechanisms – olfactory cues, visual landmarks, sun compass, magnetic compass – are known to be involved in homing behaviour, and parameters such as motivation and experience are also known to be important for fast and successful homing (Papi et al., 1974; Visalberghi and Alleva, 1975; Schmidt-König, 1990; Bingman, 1993; Lipp, 1996; Walcott, 2005). The brain of homing pigeons is an example of mosaic evolution, which means that subsystems of the brain might follow different trends of (size) alteration independently from others (Mayr, 1963; Barton and Harvey, 2000; Rehkämper et al., 1988; Rehkämper et al., 2008). It seems to be functionally adapted to homing with several differences

from other domestic pigeon breeds or their wild ancestors, the rock doves (*Columba livia*) (Haase et al., 1977; Rehkämper et al., 2008). These differences become manifest, for example, in larger hippocampi or olfactory bulbs, which are both involved in homing (Bingman et al., 2003; Bingman et al., 2005; Wallraff, 2005; Rehkämper et al., 2008). To date it has been shown that a relatively large hippocampal volume in food-storing birds is associated with food-storing experience (Clayton and Krebs, 1994b; Clayton, 1996), in migratory birds with migratory experience (Healy et al., 1996) and in homing pigeons with navigational experience (Cnotka et al., 2008).

To summarise, it is well known that three parameters characterise the brain of homing pigeons: (1) it is well adapted to homing, (2) it is (at least functionally) lateralised, and (3) it is plastic due to experience.

This leads to the question in what way lateralisation is reflected in homing pigeon brain structure volume and whether some lateralisation or asymmetry in homing pigeons is caused by experience. Thus, we compared brains of homing pigeons with and without navigational experience referring to this.

MATERIALS AND METHODS

Experimental design

Fourteen homing pigeons (*Columba livia*, Gmelin 1789) originating from the same breeding stock were raised in the same loft under identical constraints. The size of the loft (108 cm × 140 cm × 200 cm) gave all of the pigeons the possibility to fly. After fledging, seven of them (two males, five females) were allowed to leave the loft to fly around, gain navigational experience and participate successfully in pigeon races. This meant that they participated in at least three (one pigeon) but in as many as six (three pigeons) or seven (three pigeons) races with distances of 50–284 km. Thus, the whole flight performance of every pigeon varied between 479 km and 1210 km.

The other seven pigeons (two males, five females) stayed permanently in the loft and did not share the navigational experiences of the first group. However, the size of the loft enabled these pigeons to fly. Thus, the design of our study ensures that the two pigeon groups only differed with respect to free flying and homing experience.

Brain preparation

After reaching sexual maturity, all 14 individuals were killed with an overdose of anesthesia and subsequently perfused with saline solution and a fixative (Bodian's solution) (Romeis, 1989) *via* the left ventricle. All brains were removed and immediately weighed. After being embedded in paraffin, all brains were completely serially sectioned (20 μm) in a coronal plane. Every fifth section was mounted and stained for perikarya using a silver technique (Gallyas, 1971) that allows a clear and reproducible delineation of the different brain areas.

Measurements

For morphometry the contours of the brain and brain subdivisions were drawn with a digital pen using a camera lucida. To arrive at the fresh volume, the resulting values were multiplied by the section thickness and the distance between the sections. Because the brain shrinks considerably during histological processing, there are differences between the measured volume in serial sections and the fresh brain volume. The extent of shrinkage is different in each brain. To obtain comparable values, each (structural) volume was multiplied by the conversion factor for shrinkage (*C*), where $C = \text{volume fresh brain} / \text{sum of serial section volumes}$ (Stephan et al., 1981).

Eight telencephalic brain subdivisions were considered: hyperpallium apicale, hyperpallium densocellulare, mesopallium, nidopallium (including entopallium and arcopallium), striatopallidal complex (including globus pallidus, lateral striatum, medial striatum and tuberculum olfactorium), hippocampus, septum and bulbus olfactorius. Fig. 1 illustrates some of these areas. All these measurements were done separately for the left and right hemispheres. Additionally six basic brain subdivisions (cerebellum, diencephalon, optic tectum, optic tract, tegmentum and whole telencephalon) were measured to calculate the net brain volume as the sum of all single brain subdivisions. In contrast to whole brain volume, the net brain volume does not include the volume of leptomeninges, ventricles, choroid plexus and remains of cranial nerves. Because of described morphological asymmetries in the optic tectum and its role in processing visual information (Güntürkün, 1997), measurements of optic tectum were done separately for the two hemispheres as well. All measurements were done blind, which meant that the investigator did not know which brain belonged to which individual pigeon.

Data analysis

Volumetric variables were assumed to be log-normally distributed and were described by geometric means ± standard deviation factors. This corresponds to the exponentiated means ± standard deviations of the log values. Relative differences between the left *versus* right telencephalic brain parts were calculated as quotients in each pigeon and were described by geometric means in both groups (experienced and non-experienced pigeons). Both groups were compared statistically by the *t*-test considering the logarithmised relative differences per pigeon.

As a secondary analysis paired *t*-tests were used to compare (log-) volumes on the left and right hand sides separated for both groups. 95% confidence intervals corresponding to the geometric means of the left and right telencephalic brain parts were presented graphically in both groups.

The level of significance was 5%. All tests were performed two-sided. For statistical calculations the software package SAS version 9.2 TS2M0 (SAS Institute, Cary, NC, USA) was used.

The original research reported herein was performed under the guidelines of the German law to prevent cruelty to animals.

RESULTS

Mean net brain volume and brain subdivision volumes (of the left and right hemispheres if available) in homing pigeons with and without navigational experience are given in Table 1. The seven pigeons with navigational experience had a (geometric) mean net brain volume of $2187.50 \pm 1.04 \text{ mm}^3$ and a telencephalon volume of $1070.24 \pm 1.05 \text{ mm}^3$. The seven pigeons without navigational experience had a mean net brain volume of $2244.06 \pm 1.04 \text{ mm}^3$ and a telencephalon volume of $1097.26 \pm 1.05 \text{ mm}^3$.

The comparison of the left/right quotients of both groups (Table 2) show one significant difference, i.e. pigeons with navigational experience show a smaller left mesopallium in comparison with the right mesopallium (0.953), pigeons without navigational experience show a larger left mesopallium in comparison with the right one (1.015). This difference is significant (Fig. 2A, $t=2.241$, $P=0.045$).

There are significant differences between left and right brain subdivisions in the two groups of experienced and unexperienced pigeons in the following brain structures: both, pigeons with and pigeons without navigational experience, show a larger left hyperpallium apicale in relation to the telencephalon (Fig. 2B, experienced pigeons: $t=4.090$, $P=0.006$; unexperienced pigeons:

Table 1. Volumes of (left/right) brain subdivisions (mm³)

Brain subdivisions	Volumes			
	Experienced pigeons (N=7)		Unexperienced pigeons (N=7)	
	Left	Right	Left	Right
Telencephalon	534.10±1.05	536.14±1.06	551.01±1.05	546.25±1.06
Hyperpallium apicale	73.64±1.09	65.75±1.08	76.70±1.09	71.02±1.09
Hyperpallium densocellulare	19.07±1.12	19.88±1.11	18.78±1.19	18.94±1.15
Mesopallium	88.02±1.11	92.40±1.10	94.61±1.09	93.24±1.10
Nidopallium	240.03±1.04	245.20±1.04	250.93±1.06	254.00±1.06
Striatopallidal complex	77.24±1.08	77.60±1.10	76.59±1.06	76.12±1.06
Hippocampus	21.59±1.12	21.16±1.13	19.09±1.16	18.77±1.16
Septum	7.50±1.04	7.52±1.05	7.61±1.06	7.53±1.06
Bulbus olfactorius	4.08±1.08	4.23±1.11	4.05±1.12	4.03±1.14
Tectum opticum	108.45±1.07	110.44±1.08	109.14±1.04	111.04±1.04
Net brain volume	2187.18±1.04		2244.06±1.04	

Values are geometric means ± standard deviation factor.

$t=4.933$, $P=0.003$). Additionally, pigeons with navigational experience show a larger right nidopallium ($t=2.663$, $P=0.037$), a larger left hippocampus (Fig. 2C, $t=2.500$, $P=0.047$) and a larger right optic tectum (Fig. 2D, $t=2.606$, $P=0.048$). Pigeons without navigational experience did not show more significant differences.

DISCUSSION

The present study reveals that several structures in homing pigeons show a volumetric lateralisation. Thereby, homing pigeons with navigational experience show a more lateralised brain than pigeons without navigational experience.

Before discussing the brain data in detail we would like to address the question whether these asymmetries reflect an enlargement of one side or a decrease of the other side. This is difficult to decide. We know that ontogenesis of the brain in mammals (and probably in birds too) is characterised by an initial overshooting generation of neuroblasts. Their survival depends on neurotrophic factors and on having established a 'meaningful' connection or not (Edelmann, 1993). In the latter case, the neuroblasts will degenerate and cause a volumetric decrease. A second aspect of neuronal ontogenesis is that the number of neurons in the adult brain might increase and/or develop new synaptical contacts, which could be mirrored by a volumetric enlargement. This has been shown particularly in birds (Nottebohm, 1970). Homing pigeons start flying at the age of 28

days. At this time they communicate with their parents and move around in the loft, which indicated a nicely developed brain. Thus, we think that at this time the remaining number of undifferentiated early neuroblasts is small. Based on these considerations, the asymmetries described here (and in previous papers) are thought to reflect an adaptive enlargement. However, in respect to function, it does not matter if the brain part under consideration is larger because of an increase of itself or a decrease of its counterpart.

The comparison of the left/right quotients of both groups revealed that pigeons with navigational experience show a smaller left mesopallium in comparison with the right one and pigeons without navigational experience a larger left mesopallium in comparison with the right one. This is (statistically) the most astonishing result because it incorporates the randomised groups. It means that the adaptive decrease of the mesopallium has taken place but it is in contrast to the hypothesis that the right hemisphere generally should mediate more emotional and instinctive reactions, while the left hemisphere deals with elaborated experience-based behaviours (MacNeilage et al., 2009; Valencia-Alfonso et al., 2009). Furthermore, particularly the mesopallium is associated with cognitive behaviour (Lefebvre et al., 2004) and thus an enlargement of the left mesopallium in pigeons without navigational experience is really unexpected given that navigation in birds is cognitive, particularly there is not necessarily any absolute volume difference

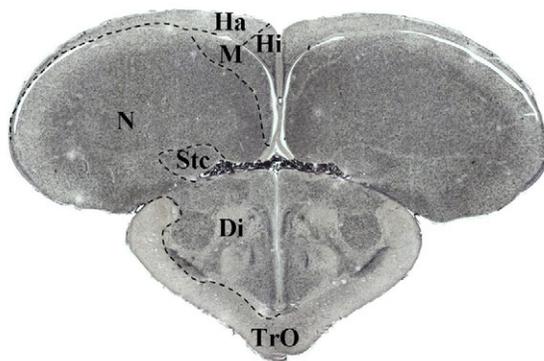


Fig. 1. Coronal section through the brain of a homing pigeon to illustrate selected subdivisions (Di=diencephalon, Ha=hyperpallium apicale, Hi=hippocampus, M=mesopallium, N=nidopallium, Stc=striatopallidal complex, TrO=tractus opticus).

Table 2. Quotients of left brain subdivision divided by right brain subdivision

Brain subdivisions	Quotients	
	Experienced pigeons (N=7)	Unexperienced pigeons (N=7)
Telencephalon	0.996±1.022	1.009±1.010
Hyperpallium apicale	1.120±1.076	1.080±1.042
Hyperpallium densocellulare	0.960±1.134	0.992±1.111
Mesopallium	0.953±1.070	1.015±1.032
Nidopallium	0.979±1.021	0.988±1.025
Striatopallidal complex	0.995±1.043	1.006±1.020
Hippocampus	1.037±1.040	1.017±1.055
Septum	0.997±1.063	1.011±1.036
Bulbus olfactorius	0.964±1.064	1.006±1.049
Tectum opticum	0.982±1.017	0.983±1.019

Values are geometric means ± standard deviation factor (bold: $t=2.241$, $P=0.045$).

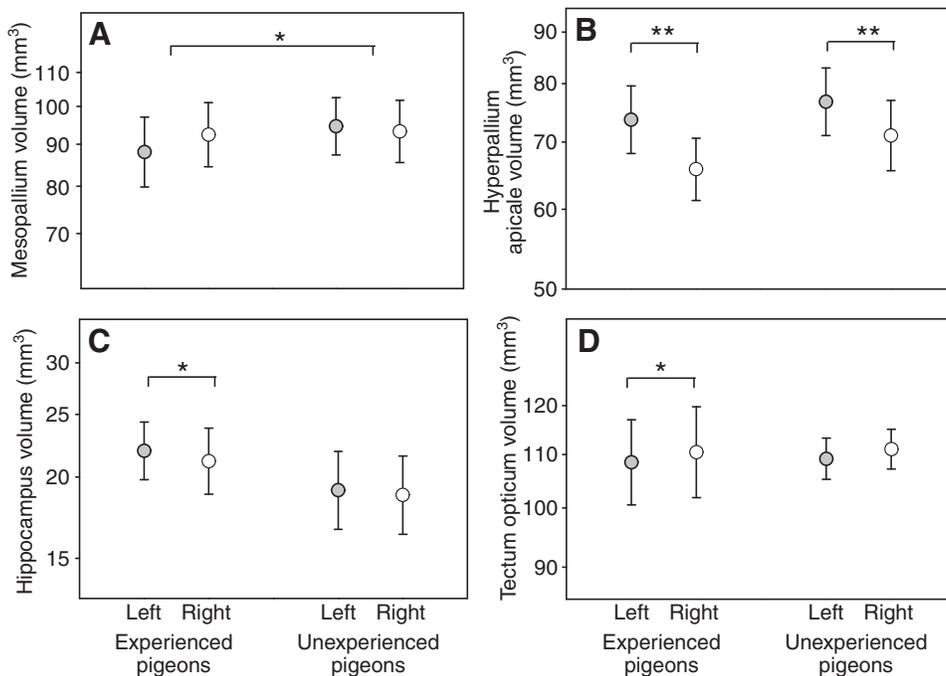


Fig. 2. Left and right brain structure volume of pigeons with and without navigational experience. Plots represent geometric means with 95% confidence interval. (A) Mesopallium, (B) hyperpallium apicale, (C) hippocampus, (D) optic tectum.

between the left mesopallium of the trained and untrained pigeons. However, more detailed analysis is needed for clarifying the role of the mesopallium in navigation.

A different explanation is proposed to understand the larger right nidopallium just in pigeons with navigational experience. Parts of the nidopallium are associative areas, involved in a lot of cognitive functions (Rehkämper and Zilles, 1991; Güntürkün, 2005) and presumed to be homologous to the mammalian isocortex (Lefebvre et al., 2004; Reiner et al., 2004).

Our nidopallium includes representation areas of sensory systems (Nieuwenhuys et al., 1998). As navigation is based on multimodal integration, we assume that the increase is due to an adaptive enlargement of such systems. This is supported by the fact that, e.g. the olfactory system is coined by an adaptive increase (Rehkämper et al., 2008). Up to date, a (functional) lateralisation or important role of the nidopallium in homing is unknown.

Two brain structures that are asymmetrical within the groups are as well multimodal but particularly involved with processing visual information: (1) the hyperpallium apicale, whereas the left one is larger in both pigeon groups in comparison with the right one, and (2) the optic tectum, whereas the right one is larger just in pigeons with navigational experience. Processing of visual stimuli by homing pigeons shows a strong lateralisation with superiority of the right eye and left hemisphere (Güntürkün, 1991; Ulrich et al., 1999; Prior et al., 2004). This hemispheric asymmetry might come about because the avian embryo lies in the egg with its left eye covered and its right eye exposed to light (Rogers, 1990). Such an asymmetry depends on light exposure and is minimised or changed by the absence of light during development (Rogers, 1982; Rogers, 1990; Andrew et al., 2009). In pigeons, the optic nerves almost completely decussate at the level of the chiasm, so the visual input to the right eye is processed more or less entirely by the left hemisphere (Nieuwenhuys et al., 1998). Similar to what occurs in mammals, processing visual information in pigeons occurs *via* two different main pathways: the thalamofugal and tectofugal pathway (Karten, 1979). But in contrast to mammals, the major part of visual information in birds uses the tectofugal way, which comprises the

optic tectum, the n. rotundus and the entopallium as its telencephalic target. The thalamofugal pathway projects *via* the dorsal thalamus into the Wulst, which consists of the hyperpallia apicale, densocellulare and intercalatum. In birds it is concerned, inter alia, with processing visual stimuli for orientation (Güntürkün, 1991; Shimizu and Bowers, 1999). The hyperpallium apicale as a whole is not generally larger in pigeons with navigational experience although it is involved in processing information for successful homing (Cnotka et al., 2008). It is not even generally larger in homing pigeons in comparison with other non-homing pigeons (Rehkämper et al., 2008). Our finding of a larger hyperpallium apicale on the left hemisphere in both pigeon groups indicates that the hyperpallium apicale is lateralised in homing pigeons in general and it demonstrates for the first time a (volumetrical) lateralisation in the thalamofugal system in pigeons. Thus, it could be another adaptation on homing but without being larger or being sensitive to experience.

Several authors describe morphological and functional asymmetries in the tectofugal visual system of pigeons (Güntürkün, 1997; Skiba et al., 2002; Nardi and Bingmann, 2007) but not for the thalamofugal visual system; however, the larger right optic tectum in pigeons with navigational experience is difficult to explain. Functional asymmetries in the tectofugal visual system of pigeons are described rather with superiority of the left hemisphere (Güntürkün, 1997; Skiba et al., 2002; Nardi and Bingman, 2007). However, Rogers (Rogers, 2009) argues that lateralisation patterns might depend on hemispheric asymmetries in sensory processing, which is in line with observations by Valencia-Alfonso et al. who featured the pigeon as a model system of the hemispheric lateralisation of visual abilities (Valencia-Alfonso et al., 2009). They described functional asymmetries in the whole visual system of the pigeon and speculated that these asymmetries depend on the interplay of descending and ascending visual information streams (between telencephalic and subtelencephalic structures).

As far as we know, to date, the only structure sensitive to navigational experience is the hippocampus (Cnotka et al., 2008), which shows inter alia functional lateralisation (Gagliardo et al., 2001; Gagliardo et al., 2002; Gagliardo et al., 2005). The left

hippocampus might play a more important role in the representation of a goal location in terms of environmental shape/geometry (Gagliardo et al., 2001; Gagliardo et al., 2002; Gagliardo et al., 2005), and Nardi and Bingman (Nardi and Bingman, 2007) proposed a relationship to the asymmetrical organisation of the tectofugal system whereas the left forebrain hemisphere, and therewith the left hippocampus, gets a higher degree of whole-field visual representation. Interestingly, this is in contrast to what has been described in chicks, which show a lateralisation in the thalamofugal system and a dominance of the right hemisphere for encoding geometric information (Rogers and Deng, 1999; Tommasi and Vallortigara, 2001; Tommasi and Vallortigara, 2004; Koshihira et al., 2003; Della Chiesa et al., 2006). The right hippocampus in homing pigeons appears to play an important role in local navigation near the loft, which is probably based on familiar landmarks (Gagliardo et al., 2001; Gagliardo et al., 2002; Gagliardo et al., 2005).

A morphological lateralisation of the hippocampus has been described by Hough and Bingman (Hough and Bingman, 2004; Hough and Bingman, 2008) and Siegel et al. (Siegel et al., 2006) (see Introduction), and in our study, the hippocampus shows a volumetric lateralisation on the left hemisphere in pigeons with navigational experience. Recently, we showed that the hippocampus in homing pigeons with navigational experience is enlarged (Cnotka et al., 2008), and now we have replicated the training effect on hippocampal volume by showing that there is also a lateralisation, which is caused by experience.

It is known that there are several, mostly environmental, factors such as light exposure, body posture, social rearing or testosterone exposure that could influence the degree of lateralisation during ontogenesis (Andrew et al., 2009; Pfannkuche et al., 2009; Schaafsma et al., 2009). Navigational experience seems to be a further influencing factor that could even induce a lateralisation seen as volumetric asymmetry.

It is speculated that lateralisation is ancient, closely associated with the bilateral symmetrical design of the brain (Vallortigara et al., 1999; MacNeilage et al., 2009). Among other advantages, the specialisation of the two sides of the brain has been supposed to increase neural efficiency by avoiding unnecessary duplication of neural circuitry and reducing interference between control systems (Rogers, 2000; Vallortigara and Rogers, 2005; Ghirlanda and Vallortigara, 2009; Tommasi, 2009). It has been shown that species that show gregarious behaviour are lateralised. Apparently, sociality and gregarious behaviour could have provided the constraints for a directional selection in favour of the asymmetries (Vallortigara et al., 1999; Rice, 2004). Solitary species are more likely to show lateralisation just in a few individuals of a population but not in general (Vallortigara et al., 1999; Halpern et al., 2005). The reasons for this are unclear but homing pigeons are gregarious.

The 'mosaic theory' suggests that the expansion of specific brain regions can occur independently of other regions (Barton and Harvey, 2000). Several examples of this are provided by Rehkämper et al. (Rehkämper et al., 2001), and include greater expansion of olfactory, spatial and somatosensory regions than of other brain regions. The results of the present study confirm that the brain of homing pigeons is an example for mosaic evolution under domestication (Rehkämper et al., 2008). If the brain composition of homing pigeons is represented by the 'developmental constraints theory' (Finlay and Darlington, 1995), we had to expect that changes in the size of one brain structure would be correlated with changes in all other brain structures. Recently, mosaic evolution has been demonstrated for the brain of wild mammals (Barton and Harvey, 2000), bats and whales (Clark et al., 2001) and wild avian species

(Iwaniuk et al., 2004; Iwaniuk and Hurd, 2005; Charvet and Striedter, 2009), and it seems to be that mosaic evolution characterises the diversification of avian and mammalian brain composition without excluding domesticated species. Apparently, it is not just the subsystems of the brain that might follow different trends of alteration independently from others but even the left or right parts of a subsystem. Our study indicates that experience could influence the degree of mosaic evolution. Apparently, under the conditions of free flying and covering longer distances, the neural efficiency of several brain structures could be increased by lateralisation, and the data given in the literature and our own findings indicate that lateralisation is correlated with individual life history (experience) of a pigeon. The role of a genetic determination remains unclear. The role of experience must be investigated further if its evolution is of interest because modern evolutionary theory is primarily based on heritable traits rather than on acquired characters (Vincent and Brown, 2005).

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