Navigational Experience Affects Hippocampus Size in Homing Pigeons

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\textbf{Key Words}
Homing pigeon \cdot Navigation \cdot Hippocampus \cdot Brain

\textbf{Abstract}
Homing (racing) pigeons (\textit{Columba livia} f.d.) are well-known for their homing abilities, which are thought to be based on a genetic predisposition, multimodal learning and spatial cognition. On average, the hippocampus, a forebrain structure that processes spatial information, is larger in homing pigeons compared to other non-homing pigeon breeds or their wild ancestor, the rock dove. Here we show that this characteristic hippocampus volume is dependent on flying and navigational experience. Twenty homing pigeons originating from the same breeding stock were raised in the same loft under identical constraints. After fledging, 10 of them were allowed to fly around the loft, gain navigational experience and participate successfully in races. The other 10 stayed permanently in the loft and thus did not share the navigational skill experienced by the first group. After reaching sexual maturity, individuals of both groups were sacrificed and morphometric analyses were carried out to measure the volumes of total brain, telencephalon, hippocampus and 12 other brain structures. Individuals with experience in flying and navigation had an 11.2\% larger hippocampus relative to the telencephalon compared to non-experienced individuals (\(p = 0.028\)). This effect is not seen in any of the other measured brain subdivisions. Given that plasticity in hippocampal volume has a genetic component, our results confirm that there is also an experience component, and that has certain implications for navigational ability. Evidently, experience is a precondition to full hippocampal development.

\textbf{Introduction}
Homing (racing) pigeons (\textit{Columba livia} f.d.) are a breed of the domestic pigeon and well-known for their homing abilities, which allow them to return to their lofts from unknown release sites more than one hundred kilometers distant. Due to strong selection, the homing abilities of these pigeons are superior even to that of rock doves, the wild ancestor of homing pigeons [Alleva et al., 1975; Visalberghi et al., 1978], and are presumably based on a genetic predisposition, multimodal learning and spatial cognition [Lipp 1983; Wallraff 2001]. Although much is known about navigational skills and spatial cognition in birds, there are still open questions. Several orientation mechanisms – olfactory cues, visual landmarks, sun compass, earth’s magnetic field – are known to be involved in homing behavior as well as parameters such as motivation and experience are also known to play roles...
Material and Methods

Experimental Design

Twenty homing pigeons originating from the same breeding stock were raised in the same loft under identical conditions. At the time of fledging, the pigeons were randomly assigned to two experimental groups as follows: 10 (5 male, 5 female) of them were allowed to fly around the loft, gain navigational experience and participate successfully in races. This means that they participated in at least three (1 pigeon), but in as many as six (6 pigeons) or seven (3 pigeons) races with distances of 50–284 km. Thus, the whole flight performance of every pigeon varied between 479 and 1210 km.

The other 10 pigeons (5 male, 5 female) stayed permanently in the loft and thus did not share the navigational experiences of the first group. The size of the loft (108 × 140 × 200 cm) enabled these pigeons to fly, so that physical exercise was nearly equal between the two groups. Thus, this design of our study ensures that the two pigeon groups differed only with respect to free flying and homing/navigational experience.

Brain Preparation

After reaching sexual maturity, the brains of all 20 homing pigeons were investigated. After their body weights were determined, all individuals were sacrificed by an overdose of anesthesia and subsequently perfused with saline solution and a fixative (Bodian’s solution) via the left ventricle. Brains were removed, weighed and embedded in paraffin. The brain weight was taken immediately (<60 min) after perfusion and the dissection weight was identical to the fresh brain weight [Stephan et al., 1981]. All brains were completely serially sectioned (20 μm) in a coronal plane. Every 5th section was mounted and stained for perikarya using a silver technique [Gallyas, 1971].

Morphometry

For morphometry the contours of the brain and brain subdivisions were drawn with a digital pen using a camera lucida. Then the resulting values were multiplied by the section thickness, the distance between the sections, and the conversion factor for shrinkage to obtain the fresh volume for each brain or brain subdivision [Stephan et al., 1981].

Six fundamental brain subdivisions (cerebellum, diencephalon, optic tectum, optic tract, tegmentum and telencephalon) were measured, followed by measurements of 8 telencephalic subdivisions: hyperpallium apicale, hyperpallium densocellularare, mesopallium, nidopallium (including entopallium and arcopallium), striatopallidal complex (including globus pallidus, lateral striatum, medial striatum and tuberculum olfactorium), hippocampus, septum and bulbus olfactorius. Figure 1 illustrates some of these areas. A definition of the borders of these areas is given by Rehkämper et al. [1991]. Based on these data the net brain volume was calculated as the sum of the single brain subdivisions. In contrast to brain volume, the net brain volume does not include the volume of leptomeninges, ventricles, choroid plexus and the remains of cranial brain nerves. All measurements were conducted blind, meaning that the investigator did not know which brain belonged to which individual pigeon or experimental group.
Volumetric Analyses

Volumetric data were analyzed by using a general linear model [Darlington, 1990]. The volumes of fundamental brain parts were compared in relation to net brain volume and the volumes of telencephalic subdivisions were related to the volume of the whole telencephalon. Thus, volume of brain subdivision was used as a dependent variable, treatment (experienced/non-experienced) as a categorical independent variable, and net brain volume or telencephalon volume as a (independent) covariate or confounding variable. The general linear model tests for effects of each of the independent variable, while keeping the other independent variables constant [Darlington and Smulders, 2001].

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

Results

Average body weights, net brain volume and brain subdivision volumes in homing pigeons with and without navigational experience are given in table 1. The 10 pigeons with navigational experience had a mean body weight of 469.52 ± 39.60 g (mean ± SD), a mean net brain volume of 2,241.04 ± 139.84 mm³, a telencephalon volume of 1,105.19 ± 87.60 mm³ and a hippocampus volume of 43.43 ± 5.82 mm³. The 10 pigeons without navigational experience had a mean body weight of 509.26 ± 42.62 g, a mean net brain volume of 2,282.39 ± 127.66 mm³, a telencephalon volume of 1,126.64 ± 72.04 mm³ and a hippocampus volume of 38.56 ± 4.47 mm³.

Individuals with experience of flying and navigation had an 11.2% larger hippocampus relative to the telencephalon compared to non-experienced individuals. The general linear model confirms a significant effect of navigational experience on relative hippocampus volume (F = 5.53, p = 0.028; fig. 2). This effect is not seen in any of the other measured brain subdivisions.
Discussion

It is known that experience is an important factor determining the homing performance of homing pigeons. Free flying around the loft and training flights from distant locations were found to improve the homing success and frequently the initial orientation of test birds [Matthews, 1953; Lipp, 1983; Wallraff, 2001]. On their first flights, young birds become familiar with a variety of orientation cues and learn to make use of them (learning a ‘navigational map’) to help them return home faster and more reliably [Wiltschko, 1983].

The most important result of the present study is that the size of the relative hippocampus volume of homing pigeons depends on experience. It is indisputable that the hippocampus plays an important role in learning, spatial memory and spatial cognition not just in mammals [Stephan et al., 1991; Sherry et al., 1992; Rehkämper et al., 2001; Jacobs, 2003] but also in birds [Bingman, 1993; Atoji et al., 2002; Jacobs, 2003; Bingman et al., 2003, 2005]. Natural selection, sexual selection and artificial selection have resulted in an increase in the size of the hippocampus in a remarkably diverse group of animals that rely on spatial abilities to solve ecologically important problems, and there is a common relationship between relative hippocampus size and spatial ability [Sherry et al., 1992]. Standing out among mammals are elephant shrews with extraordinarily large hippocampi that are correlated with superior spatial cognition for remembering many sheltering places in large home ranges [Sauer, 1973; Rehkämper, 1981; Stephan et al., 1991; Rehkämper et al., 2001]. Strong selection by humans for homing ability led to a relatively larger hippocampus in homing pigeons, but what is new in our results is finding that an enlargement of the hippocampus can occur as a result of experience.

In our study we have not determined what is responsible for this increase in volume, but it would be interesting to see why the hippocampus might be larger. Existing cells could increase their cell body size or build up larger dendritic arbors, new neurons or glia could be added, or there could be increased vascularization. Interestingly, seasonal variation in hippocampus size has also been observed in birds [songbirds: Nottebohm, 1981; food-storing birds: Smulders et al., 1995].

Previous studies have shown that the hippocampus is plastic in response to specific kinds of sensory input, experience (learning) or hormonal influences [Cramer, 1988; Clayton and Krebs, 1994; Jacobs and Spencer, 1994]. In mammalian species an influence of experience on hippocampal volume has been demonstrated in rats [Cramer, 1988], but most studies with birds investigate food-storing birds and thus the effects of food-storing experience [Clayton and Krebs, 1994; Clayton, 1995, 1996]. An

Table 1. Volumes of brain subdivisions (mm3) and body weight (g)1 with results from analysis (General Linear Model, GLM)

<table>
<thead>
<tr>
<th>Subdivisions</th>
<th>Volumes experienced pigeons (n = 10)</th>
<th>Volumes non-experienced pigeons (n = 10)</th>
<th>GLM results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Net brain volume</td>
<td>2,241.04±139.84</td>
<td>2,282.39±127.66</td>
<td></td>
</tr>
<tr>
<td>Telencephalon</td>
<td>1,105.19±87.60</td>
<td>1,126.64±72.04</td>
<td></td>
</tr>
<tr>
<td>Diencephalon</td>
<td>148.85±4.42</td>
<td>153.16±7.31</td>
<td></td>
</tr>
<tr>
<td>Tractus opticus</td>
<td>64.34±6.52</td>
<td>64.09±9.08</td>
<td></td>
</tr>
<tr>
<td>Tectum</td>
<td>219.22±14.76</td>
<td>224.42±12.55</td>
<td></td>
</tr>
<tr>
<td>Tegmentum</td>
<td>338.38±18.37</td>
<td>336.95±22.14</td>
<td></td>
</tr>
<tr>
<td>Cerebellum</td>
<td>365.21±29.25</td>
<td>387.25±32.55</td>
<td></td>
</tr>
<tr>
<td>Hyperpallium apicale</td>
<td>141.32±11.40</td>
<td>147.77±12.92</td>
<td></td>
</tr>
<tr>
<td>Hyperpallium densocellularare</td>
<td>38.38±3.74</td>
<td>38.45±5.06</td>
<td></td>
</tr>
<tr>
<td>Mesopallium</td>
<td>195.53±23.84</td>
<td>199.83±19.86</td>
<td></td>
</tr>
<tr>
<td>Nidopallium</td>
<td>503.62±45.11</td>
<td>518.51±35.04</td>
<td></td>
</tr>
<tr>
<td>Striatopallidal complex</td>
<td>158.88±12.90</td>
<td>159.66±13.59</td>
<td></td>
</tr>
<tr>
<td>Hippocampus*</td>
<td>43.43±5.82</td>
<td>38.56±4.47</td>
<td></td>
</tr>
<tr>
<td>Septum</td>
<td>15.34±0.68</td>
<td>15.54±0.92</td>
<td></td>
</tr>
<tr>
<td>Bulbus olfactorius</td>
<td>8.64±0.87</td>
<td>8.37±0.89</td>
<td></td>
</tr>
<tr>
<td>Body weight, g</td>
<td>469.52±39.60</td>
<td>509.26±42.62</td>
<td></td>
</tr>
</tbody>
</table>

1 Values are means ± SD.
*p = 0.028.
effect of migratory experience on hippocampal growth is seen in warblers [Healy et al., 1996]. In this study we have confirmed the plasticity of avian hippocampus in homing pigeons, and have shown for the first time that the hippocampus is also affected by navigational experience.

This finding is in line with the finding that pigeons raised while confined in an aviary have difficulties in perceiving spatial relationships among the landmarks in the home area, resulting in a less accurate spatial map and impaired navigation ability [Bingman and Mench, 1990; Gagliardo et al., 2007]. The hippocampus has been proposed to play a critical role in the neuronal regulation of a navigational system used by homing pigeons to locate their lofts once they are in the familiar area near home [Bingman and Mench, 1990; Gagliardo et al., 1999], and the exact formation of this navigational system depends on a bird’s individual experience [Wiltschko, 1983]. Hippocampus-lesioned pigeons allowed to fly freely from the loft frequently get lost, probably because they are impaired at learning to navigate by familiar landmarks near the loft [Strasser et al., 1998]. Under laboratory conditions it can be seen that such pigeons are particularly unable to use geometric information in contrast to feature cues [Vargas et al., 2004]. But if young hippocampus-lesioned pigeons are allowed to fly freely during their first summer (during the time of navigational map learning) they can also learn a navigational map (or ‘mosaic’ map) indistinguishable from that of unlesioned pigeons, provided that they are allowed to receive atmospheric odors [Ioalé et al., 2000]. Thus it would be interesting to take a closer look at the volume of the olfactory bulb. Generally, the olfactory bulb of homing pigeons is enlarged in comparison to non-homing breeds or rock doves [Rehkämper et al., 1988, 2008]. But in our study both experimental pigeon groups received olfactory cues, i.e., atmospheric odors from around their loft, which resulted in our finding of no differences in olfactory bulb volume (see table 1). A detailed study between olfactory deprived pigeons and pigeons that are allowed to receive olfactory cues would be interesting for demonstrating the possible plasticity of the olfactory bulb.

It is a matter of fact that homing pigeons have extraordinary large hippocampi. Our data indicate that experience has an influence on that brain structure. Future analyses will address structural details and developmental mechanisms behind that increase. This is of general interest to most researchers in the comparative neuroanatomy field and homing pigeons as domesticated animals are a more than suitable model.

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References


