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Lateralization of magnetic compass orientation in pigeons

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The aim of our study was to test for lateralization of magnetic compass orientation in pigeons. Having shown that pigeons are capable of learning magnetic compass directions in an operant task, we wanted to know whether the brain hemispheres contribute differently and how the lateralization pattern relates to findings in other avian species. Birds that had learnt to locate food in an operant chamber by means of magnetic directions were tested for lateralization of magnetic compass orientation by temporarily covering one eye. Successful orientation occurred under all conditions of viewing. Thus, pigeons can perceive and process magnetic compass directions with the right eye and left brain hemisphere as well as the left eye and right brain hemisphere. However, while the right brain hemisphere tended to confuse the learned direction with its opposite (axial response), the left brain hemisphere specifically preferred the correct direction. Our findings demonstrate bilateral processing of magnetic information, but also suggest qualitative differences in how the left and the right brain deal with magnetic cues.

Keywords: magnetic compass; lateralization; pigeons

1. INTRODUCTION

In the past two decades a number of hemispheric asymmetries have been shown in birds, mainly in the field of visually guided behaviours (Vallortigara *et al.* 1999; Rogers & Andrew 2002; Güntürkün 2003). Most of the studies used the method of monocular occlusion. In birds the visual input of one eye is mainly processed by the contralateral brain hemisphere. The fibres of the avian optic nerves cross over completely, and birds are lacking a structure comparable to the corpus callosum, which allows for immediate interhemispheric information transfer in higher mammals. As a consequence lateralization in birds can be studied by temporarily covering one eye.

In pigeons, lateralization has been shown for a number of spatial tasks (e.g. Prior & Güntürkün 2001; Prior *et al.* 2002; see Prior 2006 for a review), including homing in the field. In homing experiments superiority of the left brain hemisphere was demonstrated (Ulrich *et al.* 1999; Gagliardo *et al.* 2001; Prior *et al.* 2004; Gagliardo *et al.* 2005*a,b*). Although a stronger difference in vanishing directions under overcast (Ulrich *et al.* 1999) and a similar lateralization pattern at familiar and unfamiliar release sites (Prior *et al.*

2004) suggested the use of magnetic cues, owing to the complexity of the stimulus situation other explanations for lateralized performance were possible. Under conditions with strict control of cues lateralized magnetic compass orientation has been shown in two migratory species in funnel cages, the European robin, *Erithacus rubecula*, and the Australian silvereye, *Zosterops lateralis* (Wiltschko *et al.* 2002, 2003). Furthermore, lateralized magnetic compass orientation was found in domestic chicks during imprinting learning in a square-shaped arena (Rogers *et al.* 2008). In either species, birds showed significant magnetic compass orientation only when using both of their eyes or the right eye only.

Thus, although an involvement of magnetic orientation in lateralized homing performance of pigeons is likely, other factors could not be excluded in earlier experiments. However, recently we demonstrated magnetic compass learning in an operant task where only magnetic cues were available to the birds (Wilzeck *et al.* in press). Therefore, in the present study we combined the learning of magnetic compass directions in an operant task with the method of monocular occlusion in order to study the possible contribution of either brain hemisphere to magnetic orientation.

The main questions were (i) whether the magnetic compass in pigeons was lateralized, (ii) whether the pigeons would also show a lateralization in favour of

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One contribution of 13 to a Theme Supplement 'Magnetoreception'.

the right eye and left brain hemisphere, and (iii) whether they would show unimodal or axial choice behaviour.

2. MATERIAL AND METHODS

2.1. Subjects

The subjects were 10 adult homing pigeons (*Columba livia* f. *domestica*) from the loft at the Zoology Department of Frankfurt University with pre-experience in binocular magnetic compass learning. All animals were familiar to regular handling, and during their first year of life all of them had participated in flock training up to 40 km in the cardinal directions. Later on they had taken part in different homing experiments. Birds were housed as a group that also included their breeding partners in a large wooden pen with free entrance to an open air aviary. Eggs were removed to avoid breeding. They were kept at water ad libitum and at minimum 85 per cent of their free-feeding weight. They were fed with a grain mixture for pigeons during experimental sessions and received supplemental feedings after the experiments.

2.2. Apparatus

Experiments were carried out in a wooden hut, which was located in a garden-like outdoor facility adjacent to the Zoology Department of Frankfurt University. At this place the local natural geomagnetic field was undisturbed. The experimental apparatus was a square-shaped operant chamber (figure 1). The 45 × 45 cm aluminium box, 44 cm high, consisted of four identically constructed side walls each equipped with a pecking key at the height of the pigeon's head and a feeder placed on the ground. All mechanical devices in or close to the operant chamber were operated pneumatically in order to prevent disturbances of the magnetic field. The pecking keys were circular semi-transparent plastic discs (2.5 cm in diameter), which could be illuminated from the back. The operant box was lit by a halogen lamp with a wavelength spectrum close to natural daylight. It passed a diffuser of white Plexiglas that was integrated into the lid covering the box. The floor of the apparatus was covered with paper for easy cleaning. Input and output devices in the box were controlled by a remote computer, which also allowed online monitoring by the experimenter. The computer recorded a detailed trial-by-trial protocol of all operations, in particular the number of choices made, the position chosen and the exact sequence of choices (OLCUS, FBI Science).

2.3. Magnetic field conditions

The apparatus was situated in the centre of two pairs of Helmholtz coils (2.20 m and 2 m in diameter) with the axes aligned horizontally in N–S and E–W, respectively. This allowed for deflecting the magnetic North to 90° East, 180° South and 270° West. The intensity and the inclination of experimental fields were identical with that of the local geomagnetic field. The test fields were always established before an individual bird was

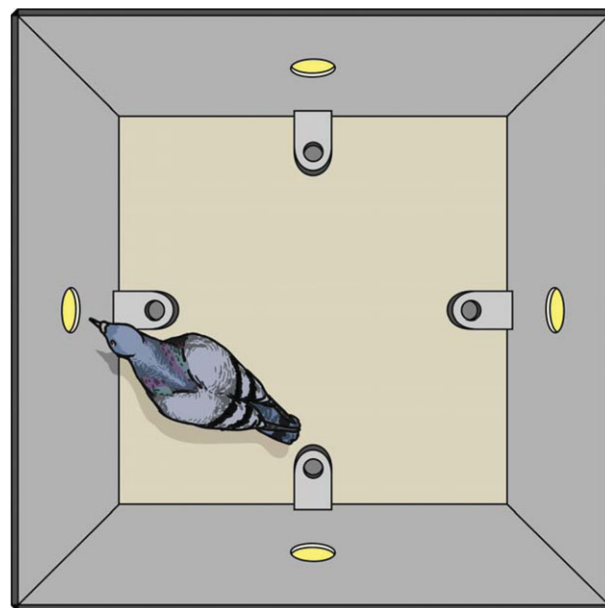


Figure 1. Operant box for the learning of magnetic compass directions, seen from above. Each wall was 45 cm long and equipped with a central pecking key and a pneumatically driven feeder (illustration by Robert Nippoldt).

placed into the box and then not shifted within experimental sessions. Each pigeon was assigned to one of the cardinal magnetic directions and learned during training to obtain a reward when choosing this direction. The magnetic direction changed between sessions with respect to the operant box and the hut in a balanced manner so that magnetic North was for the same number of times in geographic North, East, South and West. Hence, the magnetic compass direction was the only cue the pigeons could use to detect the position of the accessible feeder. The test fields were always established before an individual bird was placed into the box and then never shifted within experimental sessions.

2.4. Magnetic compass testing

All of the birds were comparably experienced with the particular apparatus and training procedure. Eight of them had taken part in an experiment on magnetic compass learning under normal binocular conditions (Wilzeck *et al.* in press), and two new birds were trained to a similar degree. In brief, after familiarization with the operant box birds had received about 40 training sessions followed by 40 test sessions, each consisting of 12 trials. Sessions were conducted in the local geomagnetic field as well as in experimental fields with magnetic North deflected by 90°, 180° and 270°. At the beginning of the present experiment, pigeons were retrained for three to five sessions in order to make them familiar again with the apparatus and the basic components of the task.

Before sessions, birds were caught from their aviary and placed in wooden containers equipped with water cups where they waited before being placed in the box. Each session consisted of 12 trials. At the beginning of a session the pigeon was placed into the

apparatus, the central light was turned on and the session started. After a randomized waiting delay of 10–20 s all four pecking keys were illuminated for 5 s. The position of the rewarded key always corresponded to the pre-assigned magnetic direction, which was the same for each bird as in the earlier experiment on magnetic compass learning (Wilzeck *et al.* in press). If the animal pecked against that key within the given time of 5 s, access to the feeder was given for 3 s by pneumatically lifting a food bowl close to the opening of the feeder. If an individual chose a wrong direction this was regarded as an error leading to a time-out with 5 s of darkness inside the box. After the randomized intertrial interval, the next trial started. The computer recorded a detailed trial-by-trial protocol of all operations, in particular the number of choices made (success, time-out and error), the position chosen and the exact sequence of choices for each session.

The order of sessions was counterbalanced for the seeing conditions—binocular, monocular right and monocular left—and for the direction of magnetic North. Each animal ran 16 tests in every seeing condition with each geographic direction being tested four times within a condition. Hence, each animal was given a total of 48 sessions.

2.5. Monocular occlusion

After clipping some feathers, a ring of Velcro was attached around each eye with non-toxic, water-soluble glue. The counterpart of this eye-ring was glued to a paperboard disc of 26 mm diameter. The cardboard eye-caps could be bent to adjust them to the shape of the head and the eye-ring to cover the whole eye completely. At least 5 min before each session the animals were fitted with the eye-caps so they could adjust to the condition (see Prior & Güntürkün 2001).

2.6. Data analysis

All birds that completed the predefined number of sessions and showed above chance performance on at least one of the three conditions of viewing were included. Based on this, six birds entered the within-subject comparison between the different conditions of viewing (binocular, left eye, right eye). Two birds did not perform enough test sessions owing to inactivity, two other birds did not perform above chance in any of the experimental conditions.

From the raw data three measures were derived for each condition of viewing. (i) *The number of choices to find the correct direction.* This measure considers all relevant choices within a session. It is a useful and reliable measure in spatial tests with more than two response options (see Clayton 1995). In the present study above chance performance was possible only by using the magnetic cues. In the case with four response options scores can vary between 1 and 4 with a chance level of 2.5. With the conservative assumption that the birds keep perfect track of their orientation, the probability for the four different choice patterns is as follows. For a correct choice in the beginning it is 0.25; for a correct choice on the second try it is the

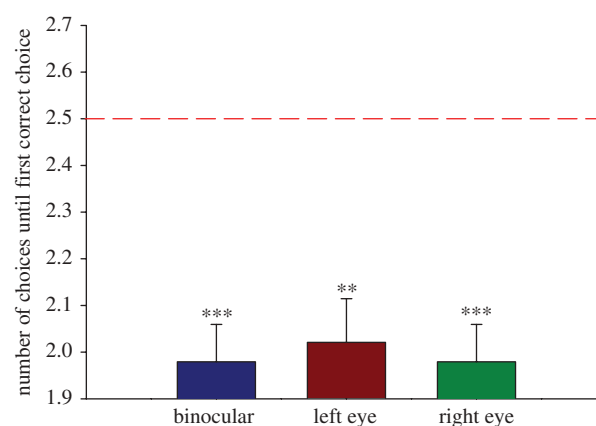


Figure 2. Number of choices to find the correct direction under the different conditions of viewing (group means and s.e.m.). Dashed red line: chance level; asterisks indicate significant deviation from random performance. ** $p < 0.01$; *** $p < 0.001$, one-sample t -tests. Differences between conditions are not significant.

probability of an incorrect choice in the beginning multiplied by the probability for a correct choice after a first incorrect choice = $0.75 \times 0.33 = 0.25$; and so on. (ii) *The direction of the first choice*, classified as correct direction, left, right or opposite to the correct direction, was used to evaluate the pattern of choices and answer the question of whether the birds preferred only the learned direction or whether they also showed some preference for the opposite direction. For a first overall analysis first choices were combined over all individuals and the directional comparisons were tested with χ^2 -tests. Subsequently, the proportion of choices to each direction was calculated for each condition and each individual. These individual parametric values were used to test whether preference for the goal direction or the whole goal-directed axis deviated from chance by means of one-sample t -tests. (iii) *The degree of discrimination along the main axis* was used to test whether the birds preferred the goal direction (unimodal distribution) or whether they preferred both positions along the main axis (axial effect), as found in chicks (e.g. Freire *et al.* 2005) and zebra finches (Voss *et al.* 2007). Therefore, we calculated for each bird the proportion of choices for the correct direction with regard to all choices on this axis ($n_{\text{correct}} / (n_{\text{correct}} + n_{\text{opposite}}) \times 100$). One-sample t -tests served to check whether the scores differed from chance (random = 50%), and between conditions the proportions of goal-directed choices were compared using paired t -tests.

For all tests, a significance level of $\alpha < 0.05$ was selected. All tests are two-tailed.

3. RESULTS

The average performance regarding the number of choices until the first correct choice is given in figure 2. Performance differed significantly from random under all conditions; binocular: $t = 6.523$, d.f. = 5, $p < 0.001$; left eye seeing: $t = 5.121$, d.f. = 5, $p = 0.002$; right eye seeing: $t = 6.488$, d.f. = 5, $p < 0.001$. Thus, pigeons can distinguish magnetic compass

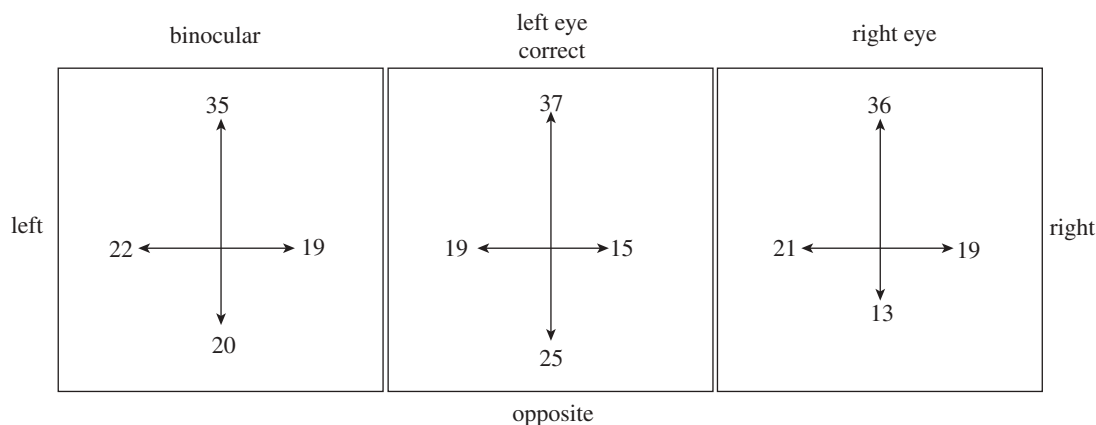


Figure 3. Total number of first choices to the different directions under various conditions of viewing. Pigeons chose the correct side significantly more often than the opposite, left or right side; errors evenly spread among the non-correct sides. With the right eye in use choice behaviour was more specific than with exclusive use of the left eye.

directions with the left hemisphere (right eye) as well as with the right brain hemisphere (left eye).

Although performance with the right eye was slightly better than with the left eye and at the same level as binocular performance, there was no significant difference between the conditions (repeated-measures analysis of variance: $F_{2,10} = 0.094$, $p > 0.9$). With a mean score of 1.98 ± 0.08 (mean + s.e.m.), the binocular performance was comparable to that in a preceding study on magnetic compass learning. In that study (Wilzeck *et al.* in press) birds had a score still close to random in the first block of 20 training trials (2.43 ± 0.10 choices, random 2.5). Performance improved in the second block of training trials (2.23 ± 0.07) and was at 2.17 ± 0.07 choices in a subsequent block of 40 test trials.

In order to analyse the distribution of choices to the different directions, we considered the location of the first choice in each session. In all conditions of viewing there was an overall significant difference between the correct and the other magnetic directions (figure 3; binocular: $\chi^2 = 6.92$, d.f. = 3, $p = 0.038$; left eye: $\chi^2 = 11.50$, d.f. = 3, $p = 0.005$; right eye: $\chi^2 = 12.89$, d.f. = 3, $p = 0.003$). Subsequent tests based on the individuals' proportion of choices for the different directions showed that the goal direction was chosen more often under all conditions of viewing (binocular: $36.5 \pm 3.4\%$, group mean and s.e.m., $t = 3.38$, $p = 0.02$; right eye: $40.7 \pm 3.9\%$, $t = 4.05$, $p = 0.01$; left eye: $38.5 \pm 1.9\%$, $t = 7.05$, $p = 0.001$; all: d.f. = 5). However, while the birds preferred the whole axis (goal direction and its opposite) with the left eye ($t = 4.72$, $p = 0.005$), they did not so with the right eye ($t = 1.25$, $p = 0.27$) or with both eyes ($t = 2.15$, $p = 0.08$).

In order to specify the birds' discrimination along the main axis we calculated for each bird the degree of discrimination. The respective values are shown in figure 4. They differed significantly with the right eye ($t = 2.931$, $p = 0.016$) and marginally with both eyes ($t = 1.923$, $p = 0.056$) from a balanced choice of either direction, but not with the left eye ($t = 1.578$, $p = 0.088$). A direct comparison between conditions of viewing regarding this preference for the goal direction showed a difference between use of the left and the right eye

($t = 2.64$, $p = 0.046$) and no difference between binocular and the right eye ($t = -1.00$, $p = 0.36$) or between binocular and the left eye ($t = 0.33$, $p = 0.75$). Thus, with the right eye (left brain hemisphere) and both eyes (both hemispheres in cooperation) the correct direction could be discriminated, while with the left eye (right hemisphere) mainly the spatial axis was discriminated.

To test whether any external cues could have contributed to choice behaviour we also tested whether the proportion of correct choices differed between the true geographic directions. There was no difference in the proportion of correct choices between the different geographic directions (binocular: $\chi^2 = 2.703$, d.f. = 3, $p > 0.4$; left eye: $\chi^2 = 2.927$, d.f. = 3, $p > 0.4$; right eye: $\chi^2 = 2.363$, d.f. = 3, $p > 0.5$).

4. DISCUSSION

Overall, three main findings emerged. (i) Pigeons can discriminate magnetic compass directions with the left as well as the right eye. This suggests processing of magnetic compass information by either brain hemisphere. (ii) Brain systems associated with the left and the right eye seem to process magnetic cues differently. (iii) Regarding the correct detection of the goal direction, the right eye (left hemisphere) is superior, as in most other cases studied so far.

The first important finding is that pigeons are capable of magnetic compass orientation with the left as well as the right eye and, consequently, with both brain hemispheres. This contrasts with the findings in European robins (Wiltschko *et al.* 2002), silvereyes (Wiltschko *et al.* 2003) and domestic chicks (Rogers *et al.* 2008), but is in line with the recent findings in garden warblers (Hein *et al.* in press). Interestingly, Rogers *et al.* (2008) considered the possibility that either brain hemisphere of chicks might, in principle, be capable of detecting magnetic cues. While in chicks there was orientation along the correct magnetic axis with the right eye only, detailed analysis of response latencies suggested an influence of the magnetic condition also in the left eye condition. Thus, in pigeons as well as in chicks

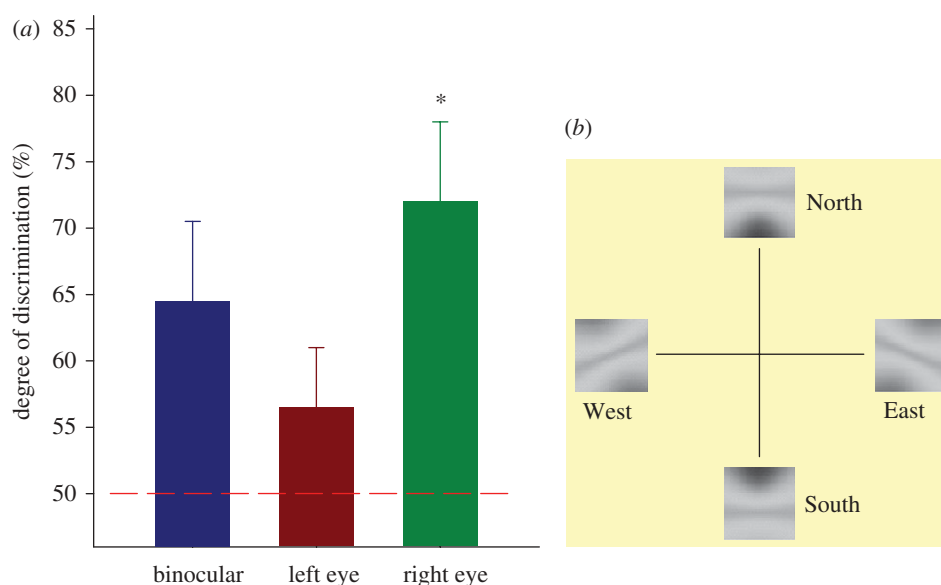


Figure 4. (a) Degree of discrimination along the main axis (means and s.e.m.) calculated as the proportion of choices to the correct direction with regard to all choices along the axis. With the right eye in use the choice behaviour was more specific for the goal direction. See text for statistical values. Dashed red line: chance value; * $p < 0.05$, significant deviation from chance as well as from left eye performance. (b) Modulation of the retinal light perception in different magnetic directions, as suggested by Ritz *et al.* (2000).

(and perhaps in other species) either hemisphere might receive magnetic compass information, but in chicks, European robins and silvereyes this magnetic information might not be used under the conditions of testing.

The second important finding is that, although for either brain hemisphere of the pigeon magnetic compass information is behaviourally relevant, it seems to be processed in a different way. With the right brain hemisphere pigeons mainly discriminated the spatial axis, while they recognized the goal direction with the left brain hemisphere. This direction of lateralization is consistent with the advantage of the right eye and the left brain hemisphere in homing studies (Ulrich *et al.* 1999; Prior *et al.* 2004). In a homing situation it is crucial to discriminate the goal direction from its opposite. Nevertheless, the right hemisphere might support orientation by providing information on the goal-directed axis for following changes in direction, e.g. during path integration.

Finally, with regard to the consistency of lateralization patterns, the question of more general hemispheric differences arises. With the exception of a study in garden warblers (Hein *et al.* 2010), which showed no lateralization, all studies hint at an advantage of the left hemisphere with almost exclusive behavioural control by the left hemisphere or a higher performance in a situation when the right hemisphere also contributes. Answers to this must be preliminary for the moment, but there are several interesting possibilities that can be tested in future studies. Aside from the magnetic compass, all strong lateralizations in navigational components, such as the sun compass- or olfaction-based homing, involved learned behaviours (Wiltschko *et al.* 1976; Papi 1986). In the funnel cage experiments with European robins (Wiltschko *et al.* 2002) and silvereyes (Wiltschko *et al.* 2003) birds that were supposed to return home to their breeding grounds

were tested. Although the direction the birds have to go for is in part a reversal of their innate migratory direction, the return journey is experience-based and might also include map-derived factors (see Perdeck 1983). By contrast, Hein and co-workers (2010) tested birds supposed to leave their breeding ground by means of their innate compass direction alone. In addition, there might be species-specific differences; however, a lateralization in favour of the left brain has been found for several learned spatial behaviours and the possibility should be considered (and tested) that an involvement of learned components in the birds' migratory or homing behaviour might generally favour lateralization towards the left brain hemisphere (e.g. Gagliardo *et al.* 2005*a,b*).

A further possible factor relates to the fact that the left brain hemisphere, which is more specialized for the processing of object-related information in pigeons than the right brain hemisphere, perceives and processes magnetic information like a visual pattern, while the right brain hemisphere uses a different mechanism. For example, Ritz *et al.* (2000) suggested modulations of the activity pattern on the retina that result in rather similar patterns along the main axes (mirror or rotational equivalents, same overall signal strength; see figure 4*b*). If these modulations were summed up over larger parts of the retina or along the horizontal plane, the results for opposite directions (e.g. North and South) were similar, but distinguishable from the directions perpendicular to them (e.g. East and West; see figure 4*b*). Thus, opposite directions on the same cardinal axis might be confused by a gross pattern analysis, while they should be distinguished by a fine-grained analysis. Therefore, a difference in pattern analysis as postulated for the left and right brain hemisphere of pigeons would predict differences in the birds' ability to discriminate the goal direction from its

opposite. Although speculative for the moment, such a difference in information analysis is well in line with general models on processing principles of the avian left and right brain. And it is also consistent with electrophysiological evidence for an involvement of the pigeon's tectofugal system in magnetoreception (Beason & Semm 1996). This system is crucial for object vision (Güntürkün 2003) and lateralized in favour of the right eye and left brain hemisphere (Güntürkün *et al.* 1998).

Overall, our study opens up several new perspectives for the study of spatial orientation in birds. The lateralization pattern for magnetic compass orientation differs from that of the other species studied so far. Therefore, results add novel perspectives to the comparative study of lateralization and to our understanding of magnetic orientation in animals.

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