

Book Chapter

Lateralization of the Avian Magnetic Compass: Development and Analysis of its Early Plasticity

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Abstract

In European Robins, *Erithacus rubecula*, the magnetic compass was found to be lateralized in favor of the right eye/left hemisphere of the brain, as indicated by cage experiments with migratory birds. This lateralization does not yet exist during the first autumn migration, but develops during the first winter and initially shows a great plasticity. During first spring migration, it can be temporarily removed by covering the right eye. Analyzing the circumstances under which the lateralization can be undone, we found that a period of 1½ h being monocularly left-eyed before tests began already proved sufficient to restore the ability to use the left eye for magnetic orientation. Yet this effect was rather short-lived, as lateralization recurred again within the next 1½ h. Interpretable magnetic information mediated by the left eye was necessary for removing the lateralization. In addition, monocularly left eyed robins could adjust to magnetic intensities outside the normal functional window of the magnetic compass, but this ability was not transferred to the 'right-eye system'. During second autumn migration, when the birds were about 15-16 months old, the lateralization proved more strongly fixed, and covering the right eye for 6 h could not remove it any longer. The origin of the compass course – an innate directional preference or one determined by a navigational process – did not affect the lateralization. Our results clearly show that during the initial phase, asymmetry of magnetic compass perception is amenable to short-term changes, depending on lateralized stimulation. This could mean that the left hemispheric dominance for the analysis of magnetic compass information

depends on lateralized interhemispheric interactions that in young birds can swiftly be altered by environmental effects. As the birds get older, the lateralization becomes more strongly fixed. This change from a bilateral to a lateralized magnetic compass via a flexible phase appears to be a maturation process, the first such case known so far in birds. Since both eyes mediate identical information about the geomagnetic field, brain asymmetry for the magnetic compass would increase efficiency by setting the right hemisphere free for other processes.

Keywords

Avian Magnetic Compass; Lateralization; Right Eye/Left Brain System; Plasticity; Commissures; Cryptochrome 1a

Introduction

Cerebral lateralization refers to the division of functional processing between both hemispheres of the brain. In most vertebrates studied up to now, several perceptual, cognitive, and motor systems display a left-right difference of neural processing [1-3]. This ubiquity of functional brain asymmetries is probably the result of some fundamental benefits. Indeed, various studies could demonstrate in several species ranging from fish to humans that those individuals that are stronger lateralized in a certain function also display higher performances when this function is tested [4-6]. This is possibly due to three mechanisms. First, asymmetries can selectively increase the perceptual or motor learning effect in one hemisphere. This is the case for, e.g., birds where the eyes are so laterally placed that most of the visual input derives from monocular vision. Thus, increased perceptual training of one eye can result in higher discrimination ability with this side [7]. The second mechanism for an advantage of asymmetry is directly related: Increased learning with one perceptual or motor system also decreases reaction times, resulting in a time advantage of the dominant side [8,9]. The third mechanism of advantage is parallel and complementary processing during task execution. If, for example, lateralized and non-lateralized chicks are tested in a foraging task that requires them to find grains scattered among

grit and, at the same time, monitor overhead for a flying model predator, the strongly lateralized birds can conduct both tasks efficiently and in parallel [10]. Thus, hemispheric specialization seems to increase parallel processing by enabling separate processing of complementary information into the two hemispheres [11] or by reducing cognitive redundancies [12].

An important function that has been found to be lateralized is the avian magnetic compass [13]. It is an inclination compass, that is, birds do not rely on the polarity of the magnetic field, but derive directions from the (axial) course of the field lines and their inclination in space [14]. This unusual functional mode arises from the underlying physical processes: the avian magnetic compass is based on a radical pair mechanism [15,16] in the eye, where Cryptochrome 1a, the most likely candidate receptor molecule for mediating directional information, is located along the disks of the outer segments of the UV-receptors [17].

The reception of magnetic directional information is thus associated with the visual system. With only their right eye open, birds could use their magnetic compass in the normal way and were just as well oriented as with both eyes open, whereas monocularly left-eyed birds with the right eye covered were disoriented. That is, the avian magnetic compass is lateralized in favor of the right eye: Directional information from the magnetic field is received by the right eye and processed by the left hemisphere of the brain. This was first demonstrated in migrating European robins, *Erithacus rubecula* (Turdidae) [13,18], yet the same lateralization was also found in subsequent studies with migrating Australian silvereyes, *Zosterops l. lateralis* [19] and is also indicated in homing pigeons [20,21] and domestic chickens [22].

Here we analyze the development of the lateralization of avian magnetic compass, based on migratory orientation of captive European Robins.

Material and Methods

The experiments were performed during autumn migration 2010 and 2011 and during spring migration of the years 2011 to 2013 in the garden of the Zoological Institute of the University of Frankfurt am Main (50°08'N, 8°40'E).

Experimental Birds

The test birds were European Robins, a passerine species that is distributed all over Europe. The northern populations are nocturnal migrants and spend the winter in the Mediterranean region. In September, juvenile birds were caught using mist nets in the Botanical Garden of Frankfurt am Main right next to the test sites and were identified as trans migrants of Scandinavian origin by their wing lengths. They were housed in individual cages in a photoperiod simulating the natural one until early December, when it was decreased to L:D 8:16. Around New Year, it was increased in two steps to L:D 13:11. This induced premature migratory activity and allowed us to conduct spring experiments already in January and February (testing period: 7.1. – 17.2.). One group of robins was caught during return migration to the breeding ground in March and April 2011. These birds and 11 of the birds caught during autumn 2010 were kept over the summer in a photoperiod simulating northward migration to 62°N, a stay there and then again southward migration. At the end of August, the photoperiod was reduced to L:D 11.5:12.5 to promote autumn migratory activity (testing period 31.8. - 19.9. 2011) - After the end of the experiments, the birds were released in the Botanical Garden in the beginning of April when the photoperiod outside had reached 13 h; the birds tested in second autumn were released immediately after the tests.

Covering one Eye

With all experimental test series, we ran control tests with the same individual birds, testing them binocularly (Bi) without any treatment, because previous tests had proven any unspecific effects from covering one eye to be negligible [13]. The methods used to cover one eye for monocular testing was identical with

those used in earlier studies with migratory birds [13,19,23]: a small non-magnetic aluminum cap was placed over the eye to be covered, fixed with adhesive tape (Leukoplast), as shown in Figure 1. If not indicated otherwise, this was done immediately before the tests started; in other test conditions, the eye was covered at pre-determined intervals before tests began to allow a period of pre-exposure to the monocular situation. For some treatments, the right eye-cover was removed before tests started and the left eye was covered instead. The various test conditions and their abbreviations are listed in Table 1. – Immediately after each test the eye cover was removed and the birds were returned to their housing cages.



Figure 1: European Robin monocularly left-eyed

Test Performance

Testing followed our standard procedure, see e.g. [13,16,19,23]: The test sites were wooden houses in the garden of the Zoological Institute where the geomagnetic field ($46 \mu\text{T}$, 66° Inclination) was largely undisturbed. The birds were tested individually once per day in funnel-shaped cages lined with thermo-paper where they left scratches as they moved [24]. The cage was dimly lit with 565 nm green light, our standard control light. Each test lasted about 1 hour. The individual birds were mostly tested three times in each test condition, in some conditions two or four times (see Data Tables in Supplemental Material).

Table 1: Definition of the test conditions and their abbreviations

Test condition	Abbreviation
binocularly tested, Control	Bi
monocularly left-eyed (right eye cover put on immediately before the tests)	L
6 h pre-exposed monocularly left-eyed, tested left-eyed	6peL-L
as above, but tested in a magnetiv field with the vertical component inverted	6peL-Lvi
6 h pre-exposed monocularly left-eyed, tested right-eyed	6peL-R
1 ½ h pre-exposed monocularly left-eyed, tested left-eyed,	1.5peL-L
1 ½ h pre-exposed monocularly left-eyed, then 1 ½ h without eye cover, tested left-eyed	1.5peL/1.5-L
3 h binocularly pre-exposed in a RF field (1.314 MHz, 480 nT), tested binocularly	3peRFBi-Bi
3 h monocularly left-eyed pre-exposed in a RF field(1.314 MHz, 480 nT), tested left-eyed	3peRFL-L
3 h left-eyed pre-exposed in a 92 µT field, tested left-eyed in the 92 µT field	3pe92L-92L
3 h left-eyed pre-exposed in a 92 µT field, tested right-eyed in the 92 µT field	3pe92L-92R
3 h right-eyed pre-exposed in a 92 µT field, tested right-eyed in the 92 µT field	3pe92R-92R

If not indicated otherwise, the birds were pre-exposed and tested in the geomagnetic field

In two test conditions, the birds were pre-exposed to a radio-frequency field of 1.315 MHz (the local Larmor frequency), 480 nT, which was produced by a coil antenna consisting of a single winding of coaxial cable with 2 cm of the screening removed. This antenna was mounted horizontally on a wooden frame and was fed by oscillating currents from a high frequency generator, generating the oscillating field vertically, i.e. at a 24° angle to the vector of the geomagnetic field (for details, see [16,25]). Four birds at a time were pre-exposed in this field in all-plastic housing cages. In another test series, the birds were pre-exposed to, and tested in a magnetic field of 92 µT, twice the strength of the local geomagnetic field. This field was produced by Helmholtz coils (2 m in diameter and 1 m clearance) arranged in the way that the induced field added to the geomagnetic field, increasing the intensity, but not altering magnetic North and inclination (see [26]).

Data Analysis and Statistics

After each test, the thermo-paper was removed from the funnels, virtually divided into 24 uniform sectors and the scratches in these 24 sectors were counted by a person blind to the test condition. Tests with less than a total of 35 scratches were considered to be of too little activity and were discarded; these tests were repeated with the same bird at the end of the test period. From the distribution of the scratches, the heading of the bird in the respective test was determined. The headings of each bird in each test condition were added to calculate a vector for that bird with the heading α_b and the length r_b . From these headings α_b , we calculated second order grand mean vectors for the various test conditions, which were tested for significant directional preference using the Rayleigh test [27]. The data of monocular treatments were compared with the binocular control data and the data from the same birds in different treatments with the Watson Williams test for differences in distribution, and Mann Whitney U-test applied to the differences of the birds' mean bearings from the grand mean for differences in variance [27]. From the individual vector lengths r_b , medians were calculated for each test condition; they reflect the intra-individual variance.

Results and Discussion

In all experiment described below, robins were tested in cages during migratory periods, with the magnetic field as only orienting factor. Since the previous studies had shown that orientation of monocularly right eyed birds was just as good as with both eyes [13,19], we focus on the monocularly left eyed condition, testing birds that had their right eye covered before the tests began.

Development of Lateralization

Some studies had questioned the findings on the lateralization of the avian magnetic compass [13,19], reporting that two species of migratory birds, among them European Robins, were oriented in their migratory direction even if they had to rely on their left

eye alone [28-30]. This raised the question about the reasons for the seemingly contradictory findings.

There were marked differences between these studies, an important one being a difference in season: The tests documenting the lateralization of the magnetic compass had been spring experiments with migrants returning to their breeding grounds, whereas the tests not finding a lateralization were predominantly autumn experiments with mainly young birds heading towards their still unknown wintering area (see [31]). This caused us to start an experimental series where we tested the same birds left-eyed in autumn as well as in spring, and we tested whether covering the right eye for 6 h before the tests began would affect the subsequent orientation. The data are listed in Table 2.

Left-Eyed Orientation in Autumn and Spring

Juvenile migrants caught in first half of September were tested during their first autumn migration to the still unknown wintering area, i.e. when their navigation was controlled by the innate migration program (see [32]). After overwintering in the laboratory, these birds were again tested during spring migration, that is, intending to return to their breeding area.

With both eyes open, the robins were significantly oriented in their seasonal appropriate direction in autumn as well as in spring. When they had to rely on their left eye alone, however, they were significantly oriented in their migratory direction in autumn, but no longer in spring (Figure 2). That is, in autumn, our birds, too, showed no lateralization and could use input from both eyes, whereas in spring, we again found the same strong lateralization in favor of the right eye/left brain hemisphere as in our previous studies with migrants [13,18,19].

Table 2: Orientation of European robins in autumn and spring in the various test conditions.

Group	Season	Condition	N	n	med. r_b	α_N	r_N	Δ Bi	Δ X
Group 1	Autumn 2010	Bi	12	3	0.59	193°	0.68**		
		L	12	3	0.80	185°	0.84***	- 8° n.s.	
	Spring 2011	Bi	12	3	0.93	357°	0.73***		
		L	12	3	0.53	(273°)	0.25 n.s.	(- 83°) **	
Group 2	Spring 2011	Bi	12	3	0.90	347°	0.74***		
		L	12	3	0.60	(53°)	0.33 n.s.	(+66°) n.s.	
		6peL-L	12	3	0.81	21°	0.92***	+ 34° n.s.	X
		6peL-Lvi	12	2	0.97	177°	0.89***	- 170° *** ^d	-177°***
		6peL-R	12	3	0.91	28°	0.66**	+43° n.s.	+7n.s

For the definition of the test conditions, see Table 1. N, number of birds tested; n, number of tests per bird; med. r_b , median of the vector lengths per bird reflecting the intra-individual variance ; α_N , r_N , direction (in parentheses if not significant) and length of the grand mean vector, with asterisks at r_N indicating a significant directional preference (Rayleigh test [27]), Δ Bi, angular difference to the binocular control, Δ X, angular difference to the sample X above (in parentheses if the compared sample is not significantly oriented), with asterisks indicating significance of the difference in directions by the Mardia Watson Wheeler test (indicated by ^d) and in variance by the Mann Whitney U-test (indicated by ^s). Significance level: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; n.s., not significant.

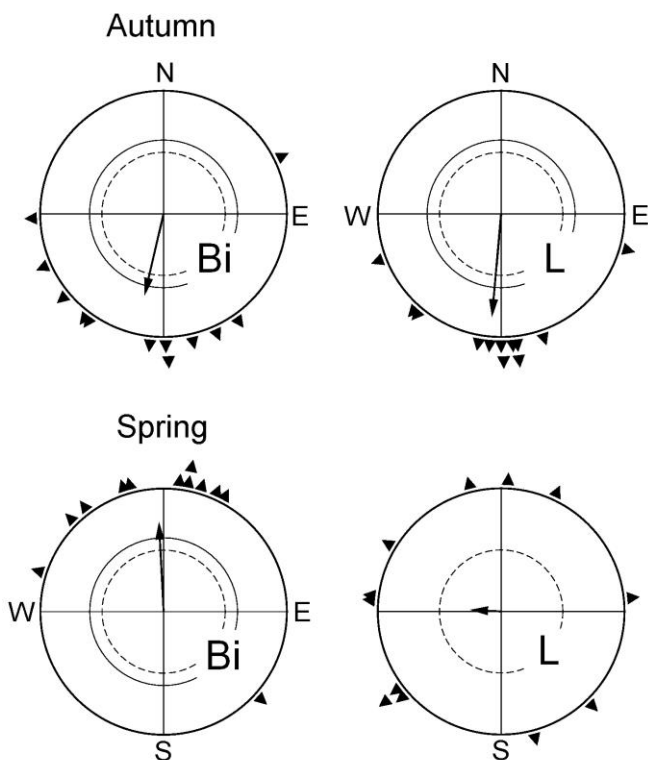


Figure 2: Orientation of the same twelve young robins in their first autumn and in the following spring in the geomagnetic field.

Bi, tested binocularly (control), L, tested monocularly left-eyed. The triangles at the periphery of the circle indicate the mean headings of individual birds, the arrows represent the grand mean vectors in relation to the radius of the circle = 1, with the two inner circles representing the 5% (dotted) and 1% significance border of the Rayleigh test [27]. The numerical data are listed in Table 2.

Lateralization, in particular of the visual system, is widespread among birds [1]. Left-right differences of the brain require a developmental period [33] and in several systems this lateralized maturational process could be shown to correlate with improved behavioral performances [34]. However, a lateralized function that develops only slowly with time has not been known in this class of vertebrates, although similar phenomena have been observed in lateralized systems in the human brain e.g. in connection with handedness or face recognition [33, 34].

A Flexible Phase during First Spring

With another group of robins, we analysed the lateralization of the magnetic compass in spring in more detail, in particular whether it would be affected if the input from the right eye was disrupted. Hence we pre-exposed these birds to the monocularly left-eyed situation by covering their right eye for 6 h prior to testing. Now the left-eyed birds proved significantly oriented in their northerly migratory direction (Figure 3c), and their behaviour was indistinguishable from that recorded under binocular control conditions (Figure 3a). When they were tested in a magnetic field with the vertical components reversed so that the inclination was upward instead of downward, they reversed their headings (Figure 3d), a behaviour demonstrating that this orientation of the left-eyed birds was controlled by the inclination compass as migratory orientation normally is [14].

This raised the question of how this treatment would affect the right eye. After having the right eye covered for 6 h, the robins could orient with their right eye alone as well as with their left eye (Figure 3e). Obviously, disrupting the input from the right eye for 6 hours had no adverse effect on ability of the right eye/left hemisphere to process magnetic compass information; it just seems to remove the lateralization.

Our findings show that during the first spring migration both eyes/hemispheres are in principle able process magnetic compass information. Magnetic directional information could still be provided by the left eye and processed in the right hemisphere, but it appears to be no longer processed as long as corresponding information from the right eye is transmitted to the brain. Yet if this is interrupted, it can be replaced by that from the left eye.

Thus the lateralization during spring migration is still flexible - blocking the input of the dominant right eye abolishes the asymmetry of magnetic compass orientation within six hours. This flexibility suggests that the lateralization does not take place at receptor level, but higher up in the brain where magnetic compass information is processed – information from the left eye appears to be actively suppressed by the left hemisphere (see

[35,36]. This is in agreement with the observation in a histological study that cryptochrome 1a, the most likely receptor molecule, is present in both eyes alike in robins almost a year old, i.e. after spring migration was finished [17].

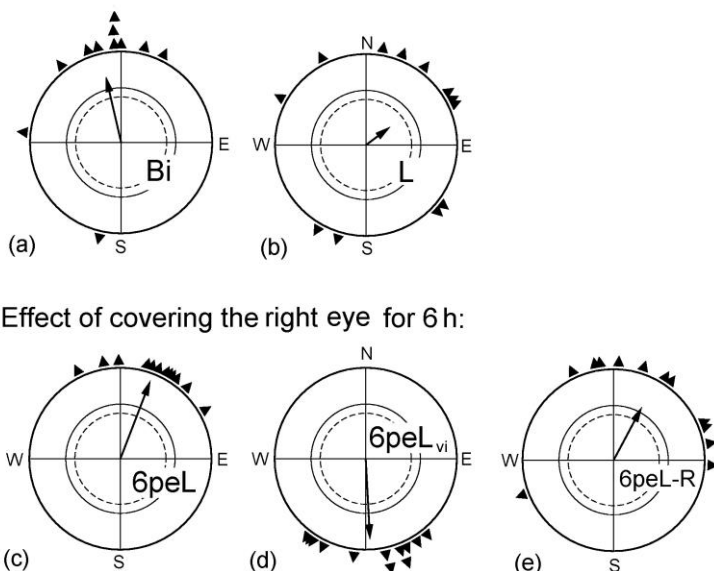


Figure 3: Effect of covering the right eye for 6 h prior to the test.

(a) Untreated binocular birds; (b) monocularly left-eyed birds; (c) birds tested monocularly left-eyed after having the right eye covered for 6 h; (d) same treatment as in (c), but tested in a magnetic field with the vertical component inverted; (e) birds tested monocularly right-eyed after having the right eye covered for 6 h. –Symbols as in Fig. 2; the numerical data are given in Table 2.

Analyzing the Early Plasticity of the Avian Magnetic compass

The flexible phase during spring migration is of particular interest, because it allows some insights into the processes leading to the lateralization of the avian magnetic compass. New behavioral experiments were designed to analyze in more detail the time-span required to restore magnetoreception to the left eye, the extent and the duration of this effect and the circumstances under which it takes place. The data are listed in Table 3.

The Duration of Monocular Pre-Exposure

One question concerned the duration of the interval required to restore the ability to use information from the left eye and how long the effect would last. The data are given in Figure 4. When the right eye was covered immediately before the test, the monocularly left-eyed birds were again disoriented, documenting lateralization in favor of the right eye (Figure 4b). When the birds had been monocularly left-eyed only 1½ h before the tests began, however, they showed normal orientation with their left eye, not different from when they were tested as binocular controls (Figure 4c). Yet this effect of removing the lateralization proved to be rather short-lived: When the birds had been monocularly left-eyed for 1½ h, followed by a binocular period of another 1½ h and were then tested left-eyed immediately afterwards, they were disoriented (Figure 4d) – lateralization had set in again.

Thus, during the first spring migration, the lateralization of the magnetic compass in favor of the right eye/left hemisphere of the brain can be easily undone by covering the right eye for a short time. This re-activation of the left eye/right hemisphere system for sensing magnetic directions is rather fast - a mere 1½ h, possibly even less, of covering the right eye enabled the robins to orient with their left eye. The lateralization of magnetic compass orientation is thus still amenable to changes. 1½ h are probably too short for major anatomical changes within the visual pathway [37]. It is more likely that the causal mechanisms for re-activation of the left eye system are related to the short-term synaptic plasticity of the weights of commissural synapses. As the dominant left hemisphere is able to inhibit the subdominant right [35,36], the functional asymmetry of the magnetic compass could be constituted via asymmetrically organized inhibitory interactions between the two hemispheres. Under normal conditions the dominant left hemisphere (right eye) would inhibit the subdominant right half brain (left eye). This asymmetrical inhibition is abolished after forcing the birds to use the left eye alone for 1½ h. Yet the birds returned to their right eye/left hemispheric dominance after just further 1½ h of binocular vision. Thus, right eye/left hemisphere dominance seems to be

the normal state of the magnetic compass system. In young birds, this condition is subject to plasticity, but it returns to its previous status once the right eye can be used again.

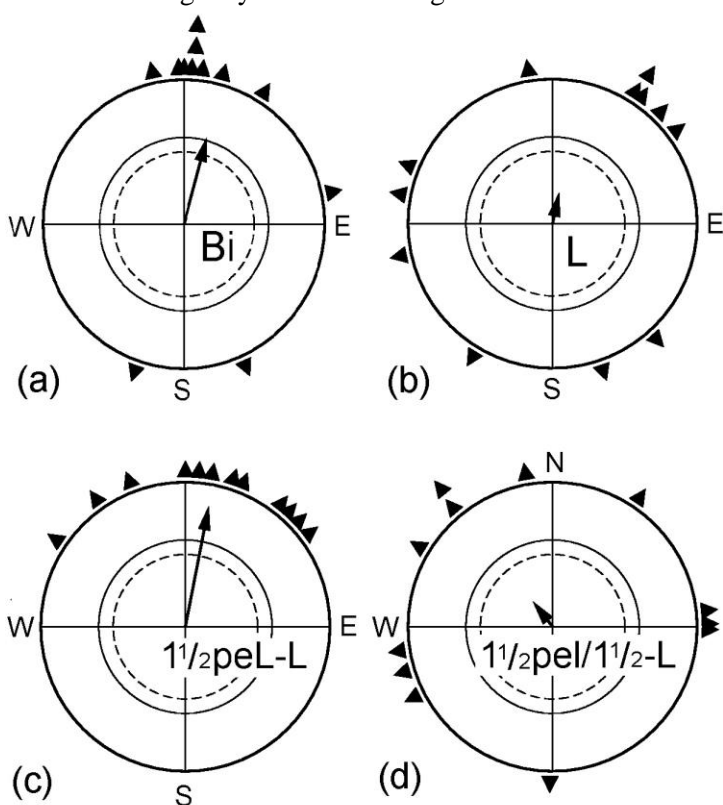


Figure 4: Time required for removing the lateralization in favor of the right eye.

(a) Untreated binocular control; (b) Birds tested monocularly left eyed; their right eye was covered immediately before the tests began, indicating the lateralization in favor of the right eye; (c) Birds tested monocularly left eyed after having the right eye covered 1.5 h before the beginning of the tests; (d) Birds tested monocularly left eyed after having the right eye covered for 1.5 h, then the cover was removed for 1.5 h before the beginning of the tests. – Symbols as in Fig. 2. For the numerical data, see Table 3.

The short time of $1\frac{1}{2}$ h or possibly less required to enable birds to use their left eye during spring migration could also explain some of the seemingly controversial findings in the literature. Engels and colleagues [30] reported that they did not find

lateralization of the magnetic compass in their spring experiments with robins. In their method section, the authors quote previous studies [28,38] which imply that the covering of the right eye occurred at least 2 h before the tests began, often earlier – this would have allowed sufficient time for the neural circuit to process information from the left eye again.

Pre-Exposure without Meaningful Magnetic Information

The previous tests showing a temporary removal of lateralization by covering the right eye had been performed in the local geomagnetic field. Now we subjected birds during pre-exposure period to a radio-frequency field that had been shown to disrupt magnetic orientation [16,25,39,40]. This meant that the birds did not receive interpretable magnetic information during a period of 3 h immediately before the tests began. Immediately after this pre-exposure, birds that had been binocularly exposed were significantly oriented in their migratory direction in the geomagnetic field (see Figure 5b), even if the distribution of their mean headings shows a certain increase in scatter. Birds that were exposed monocularly left-eyed to the radio frequency field for 3 h immediately before they were tested left-eyed, in contrast, were disoriented in the geomagnetic field afterwards (Figure 5c).

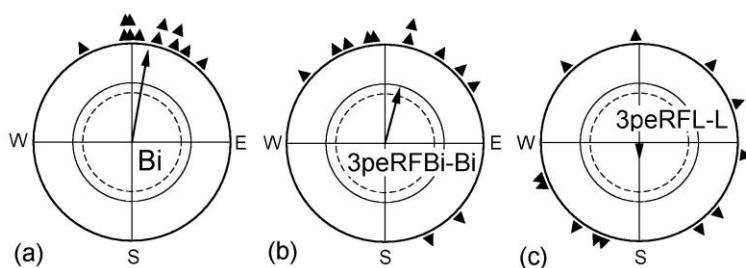


Figure 5: Effect of denying the birds interpretable magnetic information during exposure before the tests.

(a) Untreated binocular control; (b) birds exposed binocularly to a radio frequency field for 3 h prior to being tested binocularly in the local geomagnetic field; (c) birds exposed monocularly left-eyed to the radio frequency field for 3 h prior to being tested monocularly left-eyed in the geomagnetic field. – Symbols as in Fig. 2. For the numerical data, see Table 3.

Covering the right eye for a period of 3 h, twice as long as the one used in the previous tests, should have been sufficient to enable the birds to use their left eye for obtaining magnetic compass information, yet in this case, it did not work. Obviously, removal of light for the right eye and receiving only visual information from the left eye could not remove the lateralization of the avian magnetic compass. The change in asymmetry concerning magnetic compass information is not the result of mere right-eye monocular occlusion; our data clearly show that interpretable directional information from the magnetic field is essential for allowing the processing magnetic information by the left eye again. What is required for this kind of change is sensing interpretable magnetic compass information with the left eye during periods of absence of right eye input - if this specific requirement is not met, the left eye/right hemisphere does not regain the ability to process magnetic information, and the normal right eye/left hemispheric dominance prevails. This seems to indicate that magnetic directional information is processed differently from visual input, with the magnetic stimulus necessary to overcome the normal lateralization in favor of the right eye/left hemisphere system. This suggests that magnetic compass information is a specific kind of input within the visual system and the disruption of this type of input through a radio-frequency field makes it impossible to the left eye/right hemisphere system to regain the ability to process of this specific type of input.

Adjusting to Higher Magnetic Intensities

In a next step, we exposed the birds prior to the tests for 3 h to a magnetic field of 92 μT , twice as strong as the local geomagnetic field. Robins cannot spontaneously cope with such field strengths, but become able orient in it if they have a chance to adjust to this intensity before the tests [41]. In a previous study, 1 h pre-exposure to such a strong field had proven sufficient to allow orientation [26]. We tested two different groups of birds: One group was pre-exposed with only the right eye open and subsequently tested monocularly right-eyed; the other group was pre-exposed and tested monocularly left-eyed.

The results are given in Figure 6: Both groups of birds were oriented in the strong magnetic field. However, there was a difference between the groups: While the right-eyed birds were oriented in their migratory direction right away, with the headings of the three tests not different from each other, the left-eyed birds were first disoriented and oriented only from the third test onward, with only the distribution of the fourth headings significantly different from the disoriented first round (see Table 4). The left eye system, when activated, can thus adjust to intensities outside the normal functional window of the magnetic compass, but requires more time to adjust to the stronger field.

The adjustment to higher magnetic intensities means that the birds become able to interpret a slightly different activation pattern on the retina (see [15,26]); it can start only *after* the ability to process magnetic information has been restored to left eye/right hemisphere. However, this alone can probably not account for the longer delay of the left eye system, as our experiments show that it requires only 1½ h, possibly less. It means that the left eye system is indeed considerably slower in performing the adjustment, requiring much longer than the 1 h observed in binocular birds [26].

Birds that had been pre-exposed monocularly left-eyed to the 92 μ T field for 3 h were tested monocularly right-eyed in the same 92 μ T field, and were found to be disoriented (Figure 6c). While covering the left eye *per se* did not interfere with the ability of the right eye to mediate magnetic directional information (see Figure 3c), the right eye/left hemisphere could not cope with the increased intensity if it had not experienced this intensity before. For adjusting to higher intensities, processing of such input in the respective hemisphere seems to be required - there appears to be no transfer from the right to the left hemisphere where the adjustment to higher magnetic intensities is concerned, at least not within a short time.

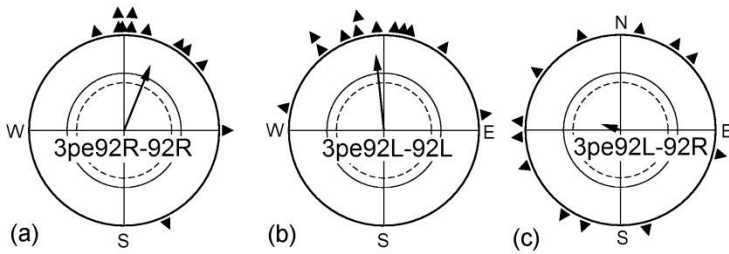


Figure 6: Adjusting to higher magnetic intensities.

(a) Birds of group I pre-exposed monocularly right-eyed for 3 h in a magnetic field of 92 μ T, twice the intensity of the geomagnetic field, then tested in that field. (b) Birds of group II pre-exposed monocularly left-eyed for 3 h in the strong magnetic field then tested in that field; (c) Birds of group II pre-exposed monocularly left-eyed for 3 h in the strong magnetic field then tested monocularly right-eyed in that field. For the orientation of the untreated control birds, see Fig. 5a and Table 3. – Symbols as in Fig.2.

Learning visual discrimination tasks has been observed to take longer with the left eye/right hemisphere than with the right eye, and in several cases of bilateral learning, the right hemisphere did not share the knowledge, but had to be trained separately (e.g [42,43]; for review see [44]). Our findings appear to be in accordance with the results of discrimination studies mentioned above, but it is unclear whether the longer time required for the left eye/right hemisphere to adjust to higher magnetic intensities really represents a parallel case.

Once the left eye system could orient in the stronger magnetic field of 92 μ T, this ability was not directly transferred to the right eye system. This is contrary to the results of most visual discriminations tasks which found a more efficient transfer of visual discrimination from the left eye to the right eye [42,43,45], which is assumed to be due to the more bilateral left hemispheric visual representation in the tectofugal pathway that enables the right eye system to swiftly access left eye information [46]. The fact that our result pattern runs contrary to these data from visual pattern discrimination studies indicates that magnetic compass information is processed differently from visual patterns.

Table 3: Orientation after various lengths and modes of monocular pre-exposure; groups of 12 birds tested

Year	Condition	test magnetic field	n	med. r_b	α_N	r_N	ΔBi	ΔX
2012	Bi	geomagnetic field ^a	3	0.45	15°	0.62**		
“	L	“	3	0.48	(12°)	0.22 ^{n.s.}	(-3°)* ^s	X ₂
“	1.5peL-L	“	3	0.77	11°	0.85***	- 4° n.s.	(-11°)* ^s
“	1.5peL/1.5-L	“	3	0.60	(322°)	0.22 ^{n.s.}	(-53°)* ^d	(-50°n.s.)
2013 I	Bi	“	3	0.82	10°	0.95***		
“	3peRFBi-Bi	“	3	0.44	15°	0.59*	+ 5°* ^s	X ₃
“	3peRFL-L	“	3	0.41	(180°)	0.18 ^{n.s.}	(+170°)** ^s	(-165°)* ^s
“	3pe92L-92L	92 nT	4	0.50	354°	0.80***	-16° n.s.	X ₄
“	3pe92L-92R	92 nT ^a	3	0.83	(287°)	0.21 ^{n.s.}	(-103°)**	(-67°)* ^s
2013 II	Bi	geomagnetic field	3	0.92	351°	0.65**		
“	3pe92R-92R	92 nT	3	0.90	22°	0.74***	+31° n.s.	

For the definition of the test conditions, see Table 1. Symbols and abbreviations as in Table 2.

Table 4: Orientation of Robins pre-exposed and tested in the 92 μ T-field.

Test round	Monocularly right-eyed birds					Monocularly left-eyed birds				
	N	α	r	Δ Round1		N	α	r	Δ Round1	
1	12	8°	0.87***			11	(304°)	0.38 ^{n.s.}		
2	11	(20°)	0.46 ^{n.s.}	+12° n.s.		12	(10°)	0.36 ^{n.s.}	+66° n.s.	
3	10	22°	0.64**	+14°n.s.		11	3°	0.54*	+59° n.s.	
4						12	13°	0.74***	+69°*	

Test round refers to consecutive test in this condition; N, number of birds contributing. The column Δ Round1 gives differences to the behavior in the first test round; other symbols and abbreviations as in Table 2.

Lateralization during Second Autumn Migration

In second autumn, we re-tested the birds that had been tested during first autumn and spring. Being caught in autumn the year before at the beginning of autumn migration and held in captivity, they were unfamiliar with the wintering area. Their behavior was compared with that of a group of robins caught in spring on their return journey from the winter quarters, that is, with birds that had already stayed in the wintering ground and hence were familiar with the goal area.

The results of the respective tests are given in Figure 7; the numerical data in Table 5. There was no difference between the two groups: the birds of both groups were disoriented when they had to rely on their left eye alone, regardless of whether they were familiar with the goal or not. At the same time, covering the right eye for 6 h now failed to remove the lateralization – it seemed to have become more persistent.

These data from the second autumn indicate that the origin of the direction of migration - flying innate courses versus navigation to a familiar goal – does not influence the lateralization of the magnetic compass. Its lateralization in favor of the right eye/left brain hemisphere appears to be the result of a maturation process. Apparently, as the young birds grow older, the neural architecture of the respective brain centers specializes in a way that magnetic directional information is based only on input from the right eye processed in the left hemisphere of the brain.

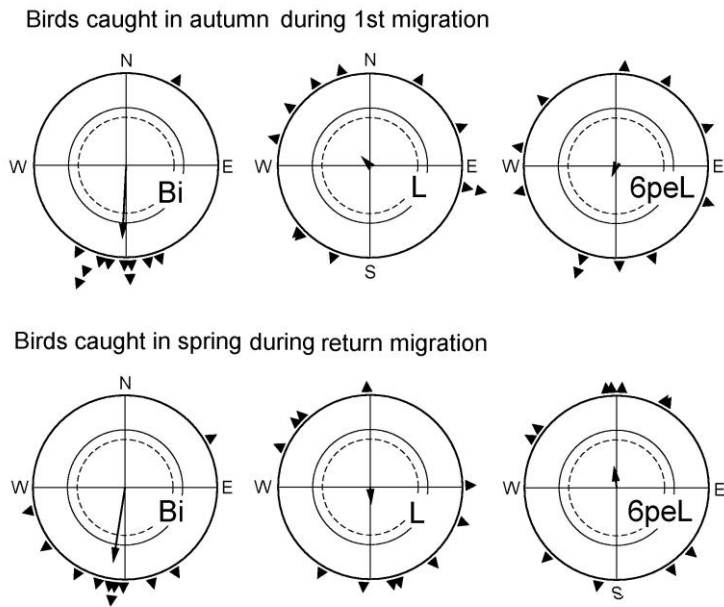


Figure 7: Orientation during second autumn migration.
Birds migrating towards a still unknown wintering ground and birds heading to an area where they had spent the last winter did not show any difference in response. Symbols as in Fig. 2.

Table: 5 Orientation of Robins about 1 ½ years old during second autumn migration.

Condition	N	n	med. r_b	α_N	r_N	Δ Bi
<i>Birds caught in autumn 2010 during their first migration:</i>						
Bi	11	3	0.90	183°	0.80***	
L	11	3	0.58	(317°)	0.14 n.s	(+134°)**
6peL-L	11	3	0.48	(201°)	0.13 n.s.	(+18°)*
Bi final	11	1	-	188°	0.88***	+5° n.s.
<i>Robins caught in spring 2011 during their return migration</i>						
Bi	11	3	0.74	189°	0.73**	
L	11	3	0.53	(177°)	0.19 n.s	(-12°)*
6peL-L	11	3	0.67	(353°)	0.24 n.s	(+164°)*
Bi final	11	1	-	179°	0.81***	-10° n.s.

Conditions as defined in Table1; abbreviations and Symbols as in Table 2.

General Discussion

The directional information from the magnetic field originates in the retina and is transmitted by the visual nerve to higher centers in the brain (e.g. [47-49]). There are two main ascending visual systems in the bird brain that reach the telencephalon: One is the tectofugal system that runs from the retina via the optic tectum to the thalamic *nucleus rotundus*, which in turn projects to the *entopallium*. The second is the thalamofugal system that ascends from the retina via a thalamic link to a telencephalic area called wulst [50]. Anatomical and physiological studies in pigeons could demonstrate that both systems display asymmetries with a dominance of the left hemisphere. The tectofugal system is characterized by diverse anatomical and physiological asymmetries along its route [46,51-54]. Consequently, left sided tectofugal lesions result in more severe visual deficits than right sided ones [45,55]. In the thalamofugal system, the left but not the right sided wulst is able to importantly modify activity patterns of the tectofugal pathway [56]. Thus, both ascending visual pathways are lateralized with a superiority of the right eye, a phenomenon widespread among birds [1], and constitute a leading role of the left hemisphere e.g. in recognizing and categorizing objects [57,58]. This could also be the reason for the normal dominance of right eye/left hemisphere system in magnetoreception. At the same time, several commissural fibers that run through the tectal and posterior commissures are asymmetrically organized in birds in a way that the left tectum is less inhibited by its right counterpart than vice versa [35]. As a consequence, the dominant left hemisphere is able to inhibit the subdominant right. Inhibitory interactions are possibly crucial when only one function for which one hemisphere is dominant has to be executed [36]. – Against this background, we will discuss our findings.

During the first autumn migration in a young birds' life, the magnetic compass is not yet lateralized, but develops into a lateralized system during first winter before spring migration, with the right eye/left hemisphere of the brain being the dominant one. Our findings show that this asymmetry during first spring is still flexible. Both hemispheres are in principle

able process magnetic compass information, and lateralization can easily be reversed by covering the right eye for just a few hours. This flexibility suggests that the lateralization takes place higher up in the brain where magnetic compass information is processed. In the brain, the left eye/right hemisphere seems to be actively suppressed by the left hemisphere - information from the left eye is no longer processed as long as corresponding information from the right eye is available. However, if this is interrupted, it can be replaced by that from the left eye during this flexible phase. The observation that the right eye system is not affected by being temporarily covered and that the re-gained ability to use the information from the left eye is lost rather quickly when the right eye is open again demonstrates the dominance of the right eye/left hemisphere in processing magnetic directional information already in first spring.

The fact that initially a mere 1½ h of obstructing right eye input can modulate the asymmetry suggests that stimulation-induced modifications of synaptic strengths play a crucial role. Our findings point to the existence of competitive and modifiable synaptic interactions between inputs from both eyes, possibly along the ascending visual system. Synaptic convergence from both eyes takes place in the *nucleus rotundus* of the tectofugal pathway [54,59] and also in the visual Wulst of the thalamofugal system [60], with the latter being discussed as relevant for magnetic compass orientation (e.g. [49], but see [61]). At least in pigeons, the Wulst is known to modify lateralized activity patterns of the tectofugal pathway [54,56] and to thereby affect interhemispheric exchange of information [45]. Thus, monocular obstruction of right eye input for less than 2 h hours could increase the synaptic weight of left eye input at tecto- and thalamofugal convergence zones of both eyes. As a result, the left eye could then successfully feed magnetic compass information into the processing system.

In older birds, roughly 15 to 16 months old, lateralization proved to be less flexible. It seems possible that changes of asymmetry are easier during early ontogeny and less flexible in adult individuals. Indeed, Lesley Rogers [58,62] pioneered studies on the ontogenetic establishment of visual asymmetries in chicks

and could demonstrate that both functional and anatomical lateralized systems can be easily modified in early ontogeny, with a similar effect also observed in young pigeons [63,64]. While our findings indicate a maturation process and that the origin of the migratory direction – innate course vs. course determined by a navigational process – does not play a role, we cannot exclude that differences in hormone state may be additionally involved. Gonadal hormonal levels have been shown to modify lateralization (e.g. [65]), but since we did not test the birds in their second spring, this question must remain open.

The lateralization of the avian magnetic compass becomes more fixed as the birds grow older. We cannot exclude that in robins and other birds, the left eye/right hemisphere system can still be activated in later years, but this appears to require more time than the 6 h (provided, on average, every fourth day) tested during the second autumn migration (see also [23]). Possibly, if a bird is injured and loses its right eye, its brain proves flexible enough to eventually restore magnetoreception to the left eye system. Robins older than 16 months were not examined histologically, but at least in Domestic Chickens, Cry1a was still present in both eyes when they are more than 2 years old (C. Nießner, pers. comm). This suggests that magnetic directional information could still be provided by the left eye and processed in the right hemisphere brain. Studies in humans make it likely that asymmetries that depend on lateralized commissural interactions can retain their plasticity up to late adulthood [66]. In Japanese quails, a life-long potential for plasticity has been observed [8].

Another question concerns the possible advantage of the asymmetry of the magnetic compass system. In contrast to vision and hearing, where the differential input between right and left eyes or ears conveys additional information and changes in input serve to alert the animals, the geomagnetic field never changes rapidly in nature. The input from both eyes is redundant, because both eyes provide absolutely identical information on the direction of the magnetic field. Thus, the right eye superiority of the magnetic compass could serve to free the capacity of circuits

reached by the left eye and could thus increase neural efficiency during tasks that demand the simultaneous but different use of both hemispheres [10].

References

1. Ocklenburg S, Güntürkün O. Hemispheric asymmetries: the comparative view. *Frontiers Comp. Psychol.* 2012; 3: Article 5, 1-9.
2. Ocklenburg S, Ströckens F, Güntürkün O. Lateralisation of conspecific vocalisation in non-human vertebrates. *Laterality.* 2013; 18: 1–31.
3. Ströckens F, Güntürkün O, Ocklenburg S. Limb preferences in non-human vertebrates. *Laterality.* 2013; 18: 536-575.
4. Güntürkün O, Diekamp B, Manns M, Nottelmann F, Prior H, et al. Asymmetry pays: visual lateralization improves discrimination success in pigeons. *Curr. Biol.* 2000; 10 : 1079–1081.
5. Dadda M, Bisazza A. Does brain asymmetry allow efficient performance of simultaneous tasks? *Anim. Behav.* 2006; 72: 523–529.
6. Hirnstein M, Hugdahl K, Hausmann M. How brain asymmetry relates to performance - a large-scale dichotic listening study. *Front. Psychol.* 2014; 4: 997.
7. Ventolini N, Ferrero EA, Sponza S, Della Chiesa A, Zucca P, et al. Laterality in the wild: preferential hemifield use during predatory and sexual behaviour in the black-winged stilt. *Anim. Behav.* 2005; 69: 1077–1084.
8. Gülbetekin E, Güntürkün O, Dural S, Cetinkaya H. Visual asymmetries in Japanese quail *Coturnix japonica*; retain a lifelong potential for plasticity. *Behav. Neurosci.* 2009; 123 : 815–821.
9. Vallortigara G, Chiandetti C, Sovrano VA. Brain asymmetry animal;. *Wiley Interdisc. Rev. Cogn. Sci.* 2011; 2: 146–157.
10. Rogers LJ, Zucca P, Vallortigara G. Advantages of having a lateralized brain. *Proc. Royal Soc. B* 2004; 271: S420-S422.
11. Vallortigara G. The evolutionary psychology of left and right: costs and benefits of lateralization. *Dev. Psychobiol.* 2006; 48: 418-427.

12. Levy J. The mammalian brain and the adaptive advantage of cerebral asymmetry, *Ann. N. Y. Acad. Sci.* 1977; 299: 264-272.
13. Wiltschko W, Traudt J, Güntürkün O, Prior H, Wiltschko R. Lateralisation of magnetic compass orientation in a migratory bird. *Nature*. 2002; 419: 467-470.
14. Wiltschko W, Wiltschko R. Magnetic compass of European Robins. *Science*. 1972; 176: 42-64.
15. Ritz T, Adem S, Schulten K. A model for photoreceptor-based magnetoreception in birds. *Biophys. J.* 2000; 78: 707-718.
16. Ritz T, Thalau P, Phillips JB, Wiltschko R, Wiltschko W. Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature*. 2004; 429: 177-180.
17. Nießner C, Denzau S, Gross JC, Peichl L, Bischof HJ, et al. Avian ultraviolet/violet cones identified as probable magnetoreceptors. *PLoS ONE*. 2011; 6: e20091
18. Stapput K, Güntürkün O, Hoffmann KP, Wiltschko R, Wiltschko W. Magnetoreception of directional information in birds requires non-degraded vision. *Curr. Biol.* 2010; 20: 1259-1262.
19. Wiltschko W, Munro U, Ford H, Wiltschko R. Lateralisation of magnetic compass orientation in silvereyes, *Zosterops lateralis*. *Aust. J. Zool.* 2003; 51: 597-602.
20. Prior H, Wiltschko R, Stapput K, Güntürkün O, Wiltschko W. Visual lateralization and homing in pigeons. *Beh. Brain Res.* 2004; 154: 301-310.
21. Wilzeck C, Wiltschko W, Güntürkün O, Wiltschko R, Prior H. Lateralization of magnetic compass orientation in pigeons. *J. R. Soc. Interface.* 2010; 7: 235-240.
22. Rogers L, Munro U, Freire R, Wiltschko R, Wiltschko W. Lateralized response of chicks to magnetic cues. *Behav. Brain Res.* 2008; 186: 66-71.
23. Gehring D, Wiltschko W, Güntürkün O, Denzau S, Wiltschko R. Development of lateralization of the magnetic compass in a migratory bird. *Proc. R. Soc. B* 2012; 279: 4230-4235.
24. Mouritsen H, Feender G, Hegemann A, Liedvogel M. Thermopaper can replace typewriter correction paper in Emlen funnels. *J. Ornithol.* 2009; 150: 713-715.

25. Thalau P, Ritz T, Stapput K, Wiltshcko R, Wiltshcko W. Magnetic compass orientation of migratory birds in the presence of a 1.315 MHz oscillating field. *Naturwissenschaften*. 2005; 92: 86-90.
26. Wiltshcko W, Stapput K, Thalau P, Wiltshcko R. Avian magnetic compass: fast adjustment to intensities outside the normal functional window. *Naturwissenschaften*. 2006; 93: 300-304.
27. Batschelet E. *Circular Statistics in Biology*. London: Academic Press. 1981.
28. Hein CM, Zapka M, Heyers D, Kurzschauch S, Schneider NL, et al. Night-migratory Garden Warblers can orient with their magnetic compass using the left, the right or both eyes. *J. R. Soc. Interface* 7, Focus. 2010; 2: S227-233.
29. Hein CM, Engels S, Kishkinev D, Mouritsen H. Robins have a magnetic compass in both eye *Nature*. 2011; 271: E11-E12.
30. Engels S, Hein C, Lefeldt N, Prior H, Mouritsen H. Night-migratory songbirds possess a magnetic compass in both eye. *PLoS ONE*. 2012; 7: e43271.
31. Wiltshcko W, Traudt J, Güntürkün O, Prior H, Wiltshcko R. Reply.to Hein et al. *Nature*. 2011; 471: E12-E13.
32. Berthold P. The control of migration in European warblers. In: Ouellet H, editor. *Acta XIX Congr. Intern. Ornithol.* Ottawa. Univ. of Ottawa Press. 1988; 215-249.
33. Bryden PJ, Pryde KM, Roy EA. A developmental analysis of the relationship between hand preference and performance: II. A performance-based method of measuring hand preference in children. *Brain Cogn.* 2000; 43: 60-64.
34. Golarai G, Ghahremani DG, Whitfield-Gabrieli S, Reiss A, Eberhardt JL, et al. Differential development of high-level visual cortex correlates with category-specific recognition memory. *Nat Neurosci*. 2007; 10: 512-522.
35. Keyser C, Diekamp B, Güntürkün O. Evidence for physiological asymmetries in the intertectal connections of the pigeon *Columba livia*; and their potential role in brain lateralisation. *Brain Res*. 2000; 852: 406–413.
36. Genç E, Ocklenburg S, Singer W, Güntürkün O. Abnormal interhemispheric motor interactions in patients with callosal agenesis. *Behav. Brain Res*. 2015; 293: 1–9.

37. Bailey CH, Kandel ER, Harris KM. Structural components of synaptic plasticity and memory consolidation. *Cold Spring Harbor Perspect Biol.* 2015; 7: a021758.
38. Liedvogel M, Feender G, Wada K, Troje NF, Jarvis ED, et al. Lateralized activation of cluster N in the brain of migratory songbird. *Europ. J. Neuroscience.* 2007; 25: 116-1173.
39. Keary N, Roploh T, Voss J, Thalau P, Wiltschko R, et al. Oscillating magnetic field disrupts magnetic orientation in Zebra finches, *Taeniopygia guttata*. *Front. Zool.* 2009; 6: 25.
40. Kavokin K, Chernetsov N, Pakomov A, Bojarinova J, Kobylkov D, et al. Magnetic orientation of garden warblers *Sylvia borin*; under 1.4 MHz radio frequency field. *J. R. Soc. Interface.* 2014; 11: 20140451.
41. Wiltschko R, Wiltschko W. Sensing magnetic directions in birds: radical pair processes involving cryptochrome .*Biosensors.* 2014; 4: 221-242.
42. Nottelmann F, Wohlschläger A, Güntürkün O. Unihemispheric memory in pigeons – knowledge, the left hemisphere is reluctant to share. *Behav. Brain Res.* 2002; 133: 309-315.
43. Xiao Q, Güntürkün O. Natural split brains? Lateralized memory for task contingencies in pigeons. *Neurosci. Lett.* 2009; 458: 75-78.
44. Vallortigara G, Rogers LJ. Survival with an asymmetrical brain: advantages and disadvantages of cerebral lateralization. *Behav Brain Sci.* 2005; 28: 575-589.
45. Valencia-Alfonso CE, Verhaal J, Güntürkün O. Ascending and descending mechanisms of visual lateralization in pigeons. *Philos. Trans. Roy. Soc. B: Biol. Sci.* 2009; 364: 955–963.
46. Güntürkün O, Hellmann B, Melsbach G, Prior H. Asymmetries of representation in the visual system of pigeons. *Neuroreport.* 1998; 9 : 4127–4130.
47. Semm P, Demaine C. Neurophysiological properties of magnetic cells in the pigeon's visual system. *J. Comp. Physiol.* 1986; 159: 619-625.
48. Heyers D, Manns M, Luksch H, Güntürkün O, Mouritsen H. A visual pathway links brain structures active during magnetic compass orientation in migratory birds. *PLoS One.* 2007; 9: 1-6.

49. Zapka M, Heyers D, Hein CM, Engels S, Schneider NL, et al. Visual but not trigeminal mediation of magnetic compass information in a migratory bird. *Nature*. 2009; 461: 1274-1277.
50. Mouritsen H, Heyers D, Güntürkün OT. The Neural Basis of Long-Distance Navigation in Birds. *Ann. Rev. Physiol.* 2016; 78: 133–154.
51. Ströckens F, Freund N, Manns M, Ocklenburg S, Güntürkün O. Visual asymmetries and the ascending thalamofugal pathway in pigeons. *Brain Struct. Funct.* 2013; 218: 1197–1209.
52. Güntürkün O. Morphological asymmetries of the tectum opticum in the pigeon. *Exp. Brain Res.* 1997; 116: 561–566.
53. Manns M, Güntürkün O. 'Natural' and artificial monocular deprivation effects on thalamic soma sizes in pigeons. *Neuroreport*. 1999; 10: 3223–3228.
54. Folta K, Diekamp B, Güntürkün O. Asymmetrical modes of visual bottom-up and top-down integration in the thalamic nucleus rotundus of pigeons, *J. Neurosci.* 2004; 24: 9475-9485.
55. Güntürkün O, Hahmann U. Visual acuity and hemispheric asymmetries in pigeons. *Behav. Brain Res.* 1994; 60: 171–175.
56. Freund N, Valencia-Alfonso CE, Kirsch J, Brodmann K, Manns M, et al. Asymmetric top-down modulation of ascending visual pathways in pigeons. *Neuropsychologia*. 2016; 83: 37–47.
57. Yamazaki Y, Aust U, Huber L, Hausmann M, Güntürkün O. Lateralized cognition: Asymmetrical and complementary strategies of pigeons during discrimination of the “human concept”. *Cognition*. 2007; 104: 315–344.
58. Rogers LJ. Asymmetry of brain and behavior in animals: Its development, function, and human relevance. *Genesis*. 2014; 52: 555–571.
59. Schmidt A, Bischof HJ. Integration of information from both eyes by single neurons of nucleus rotundus, ectostriatum and lateral neostriatum in the zebra finch *Taeniopygia guttata castanotis* Gould. *Brain Res.* 2001; 923: 20–31.

60. Pettigrew JD, Konishi M. Neurons selective for orientation and binocular disparity in the visual Wulst of the barn owl *Tyto alba*. *Science*. 1976; 193: 675–678.
61. Zapka M, Heyers D, Liedvogel M, Jarvis ED, Mouritsen H. Night-time neuronal activation of cluster N in a day- and night-migration songbird. *Europ. J. Neuroscience*. 2010; 32: 619-624.
62. Rogers LJ. Light input and the reversal of functional lateralization in the chicken brain. *Behav. Brain Res*. 1990; 38: 211–221.
63. Manns M, Güntürkün O. Monocular deprivation alters the direction of functional and morphological asymmetries in the pigeon's visual system. *Behav. Neurosci*. 1999; 113: 1-10.
64. Skiba M, Diekamp B, Güntürkün O. Embryonic light stimulation induces different asymmetries in visuoperceptual and visuomotor pathways of pigeons. *Behav. Brain Res*. 2002; 134: 149-156.
65. Hausmann M, Güntürkün O. Steroid fluctuations modify functional cerebral asymmetries: The hypothesis of progesterone-mediated interhemispheric decoupling. *Neuropsychologia*. 2000; 38: 1362-1374.
66. Hausmann M. Why sex hormones matter for neuroscience: A very short review on sex, sex hormones, and functional brain asymmetries. *J. Neurosci. Res*. 2017; 95: 40-49.

Supplementary Material:

Orientation behaviour of the individual birds

For the abbreviations of the test conditions, see Table 1 in the main text

n, number of tests per bird, α_b , mean direction of the bird; r_b , vector length of the bird

Table S1: Mean vectors of the 12 birds caught in autumn 2010 tested in the geomagnetic field.

Bird	Autumn 2010						Spring 2011					
	Bi (Control)			L			Bi			L		
	n	α_b	r_b	n	α_b	r_b	n	α_b	r_b	n	α_b	r_b
10-1	3	230°	0.82	3	106°	0.45	3	342°	0.79	3	136°	0.54
10-2	3	179°	0.92	3	222°	0.28	3	24°	0.94	3	3°	0.40
10-3	3	167°	0.33	3	220°	0.95	2	315°	0.03	2	229°	0.79
10-4	3	178°	0.81	3	161°	0.78	3	17°	0.98	3	233°	0.62
10-5	3	217°	0.40	3	173°	0.77	3	28°	0.93	3	84°	0.86
10-6	3	268°	0.46	3	173°	0.98	3	11°	0.98	3	165°	0.42
10-7	3	156°	0.38	3	185°	0.70	3	11°	0.93	3	275°	0.31
10-8	3	246°	0.55	3	249°	0.44	3	132°	0.56	3	25°	0.52
10-9	3	186°	0.67	3	175°	0.81	3	7°	1.00	3	277°	0.61
10-10	3	64°	0.63	3	179°	0.91	3	345°	0.99	3	346°	0.10
10-11	3	145°	0.14	3	180°	0.83	3	288°	0.47	3	301°	0.87
10-12	3	215°	0.86	3	190°	1.00	3	323°	0.55	3	232°	0.33

Table S2: Spring 2011.

	Bi				L				6 peL-L				6peL-L				6 peL-R		
Bird	geomagnetic field				geomagnetic field				geomagnetic field				vertical component inverted				geomagnetic field		
	n	α_b	r_b		n	α_b	r_b		n	α_b	r_b		n	α_b	r_b		n	α_b	r_b
10-13	3	26°	0.88		3	57°	0.75		3	334°	0.79		2	148°	0.99		2	3°	0.77
10-14	3	322°	0.93		3	197°	0.95		3	43°	0.83		2	168°	0.79		2	335°	1.00
10-15	3	276°	0.75		3	333°	0.37		3	16°	0.89		2	187°	1.00		2	249°	0.77
10-16	3	346°	0.22		3	62°	0.37		3	60°	0.58		2	158°	0.65		2	70°	0.87
10-17	3	357°	0.92		3	37°	0.53		3	23°	1.00		2	167°	0.98		2	352°	0.93
10-18	3	340°	0.92		3	10°	0.88		3	28°	0.95		2	213°	0.87		2	32°	0.90
10-19	3	193°	0.26		3	133°	0.18		3	350°	0.22		2	215°	0.96		2	349°	1.00
10-20	3	360°	0.91		3	65°	0.25		3	19°	0.94		2	155°	1.00		2	80°	1.00
10-21	3	356°	0.70		3	22°	0.71		3	30°	0.36		2	206°	0.81		2	67°	0.18
10-22	3	356°	0.93		3	128°	0.66		3	32°	0.87		2	217°	0.98		2	36°	0.99
10-23	3	14°	0.99		3	299°	0.68		3	359°	0.33		2	141°	0.58		2	18°	0.93
10-24	3	360°	0.93		3	210°	0.51		3	35°	0.45		2	159°	0.99		2	93°	0.40

Table S3: Spring 2012.

Bird	Bi (Control)				L				1½ peL-L				1½ peL,½Bi-L		
	n	α_b	r_b		n	α_b	r_b		n	α_b	r_b		n	α_b	r_b
11-1	3	4°	0.51		3	351°	0.35		3	325°	0.70		3	91°	0.94
11-2	3	78°	0.37		3	35°	0.39		3	5°	1.00		3	320°	0.58
11-3	3	199°	0.30		3	292°	0.66		3	360°	0.84		3	243°	0.47
11-4	3	360°	0.98		3	53°	0.94		3	10°	0.97		3	89°	0.27
11-5	3	156°	0.39		3	258°	0.51		3	47°	0.48		3	34°	0.36
11-6	3	3°	0.32		3	211°	0.75		3	304°	0.42		3	253°	0.83
11-26	3	4°	0.95		3	281°	0.22		3	42°	0.87		3	350°	0.72
11-8	3	15°	1.00		3	138°	0.31		3	22°	0.69		3	261°	0.55
11-9	2	358°	0.64		3	33°	0.18		2	53°	0.44		2	84°	0.97
11-10	3	348°	0.23		3	32°	0.44		3	339°	0.85		3	182°	0.66
11-11	3	32°	0.37		3	161°	0.60		3	38°	0.26		3	301°	0.33
11-12	3	7°	0.94		3	44°	0.97		3	18°	0.98		3	321°	0.62

Table S4: Spring 2013, birds of group I.

Bird	Bi				3 peRFBi- Bi				3peRFL-L				3 pe92L-92L				3 pe92L-92R		
	n	α_b	r_b		n	α_b	r_b		n	α_b	r_b		n	α_b	r_b		n	α_b	r_b
12-1	3	23°	0.98		3	135°	0.24		3	250°	0.17		4	322°	0.11		3	33°	0.91
12-2	3	4°	0.92		3	310°	0.45		3	217°	0.84		4	283°	0.51		3	311°	0.91
12-4	3	42°	0.44		3	13°	0.89		3	68°	0.77		4	81°	0.49		3	201°	0.17
12-5	3	359°	0.71		3	354°	0.98		3	97°	0.32		4	35°	0.39		3	45°	0.89
12-6	3	31°	0.45		3	339°	0.38		3	145°	0.41		4	356°	0.97		3	214°	0.04
12-7	3	14°	0.81		3	13°	0.33		3	132°	0.59		4	323°	0.98		3	305°	0.95
12-8	3	359°	1.00		3	57°	0.42		3	358°	0.87		4	346°	0.51		3	337°	0.33
12-9	3	356°	0.83		3	32°	0.41		3	204°	0.21		3	347°	0.36		3	165°	0.95
12-25	3	357°	0.89		3	46°	0.34		3	43°	0.40		4	11°	0.55		3	249°	0.34
12-16	3	24°	0.84		3	332°	0.96		3	246°	0.41		4	15°	0.94		3	104°	0.64
12-27	3	15°	0.59		3	155°	0.69		3	200°	0.24		4	337°	0.45		3	266°	0.77
12-19	3	332°	0.36		3	351°	0.81		3	316°	0.80		3	6°	0.32		3	275°	0.95

Table S5: Spring 2013, birds of group II.

Bird	Bi (Control)				3 pe92R-92R		
	n	α_b	r_b		n	α_b	r_b
12-13	3	269°	0.40		2	4°	0.94
12-14	3	335°	0.92		3	357°	0.98
12-15	3	71°	0.36		3	359°	0.90
12-17	1	3°	(1.00)		1	4°	(1.00)
12-18	3	9°	0.93		3	344°	0.85
12-24	3	293°	0.81		3	33°	0.96
12-30	3	226°	0.35		3	155°	0.21
12-31	3	347°	0.97		3	357°	0.91
12-32	3	1°	0.99		3	38°	0.60
12-33	3	26°	0.33		3	13°	0.99
12-34	3	28°	1.00		3	50°	0.63
12-35	3	358°	0.98		3	92°	0.46

Table S6: Autumn 2011; bird caught in autumn 2010.

Bird	Bi				L				6 peL-L		
	n	α_b	r_b		n	α_b	r_b		n	α_b	r_b
10-1	3	202°	0.96		3	67°	0.91		3	112°	0.56
10-2	3	160°	0.86		3	202°	0.92		3	31°	0.49
10-3	3	167°	0.90		3	225°	0.31		3	67°	0.36
10-4	3	201°	0.83		3	103°	0.58		3	178°	0.32
10-5	3	190°	0.90		3	30°	0.27		3	158°	0.47
10-6	3	195°	0.98		3	326°	0.32		3	312°	0.48
10-7	3	181°	0.65		3	286°	0.25		3	5°	0.25
10-8	3	209°	0.96		3	227°	0.57		3	281°	0.65
10-9	3	177°	0.95		3	103°	0.84		3	200°	0.93
10-10	3	178°	0.90		3	306°	0.88		3	255°	0.63
10-11	3	31°	0.51		3	343°	0.77		3	200°	0.43

Table S7: Autumn 2011; bird caught in spring 2011.

Bird	Bi				L				6 peL-L		
	n	α_b	r_b		n	α_b	r_b		n	α_b	r_b
1-11	3	196°	0.95		3	167°	0.91		3	359°	0.85
2-11	3	233°	0.79		3	140°	0.60		3	354°	0.38
3-11	3	186°	0.33		3	210°	0.62		3	307°	0.67
4-11	3	149°	0.96		3	358°	0.66		3	29°	0.32
5-11	3	181°	0.93		3	316°	0.42		3	300°	0.96
6-11	3	189°	0.99		3	294°	0.39		3	225°	0.38
7-11	3	187°	0.74		3	111°	0.49		3	3°	0.36
8-11	3	209°	0.60		3	184°	0.57		2	146°	0.54
9-11	3	60°	0.14		3	163°	0.16		3	31°	0.79
10-11	3	164°	0.34		3	89°	0.22		3	191°	0.91
11-11	3	256°	0.29		3	311°	0.53		3	131°	0.75