

Magnetoreception of Directional Information in Birds Requires Nondegraded Vision

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Summary

The magnetic compass orientation of birds is light dependent [1, 2]. The respective directional information, originating in radical pair processes [3–5], is mediated by the right eye [6]. These findings suggest possible interactions between magnetoreception and vision, in particular with the perception of contours, because the right eye has been found to be dominant in discrimination tasks requiring object vision [7–9]. Here we report tests in the local geomagnetic field with European robins wearing goggles equipped with a clear and a frosted foil of equal translucence of 70%. Robins with a clear foil on the right eye and a frosted foil on the left eye oriented in the migratory direction as well as birds using both eyes. Birds with a frosted foil that blurred vision on the right eye and a clear foil on the left eye, in contrast, were disoriented. These findings are the first to show that avian magnetoreception requires, in addition to light, a nondegraded image formation along the projectional streams of the right retina. This suggests crucial interactions between the processing of visual pattern information and the conversion of magnetic input into directional information.

Results and Discussion

Migratory birds can locate their migratory direction with the help of the geomagnetic field. Behavioral studies using migratory orientation as a criterion for the function of the magnetic compass identified this mechanism as an “inclination compass” [10] based on radical pair processes [3–5] and revealed its light dependency ([1]; see [2] for summary). The right eye system was previously identified as the site of magnetoreception by testing birds monocularly [6]. European robins, *Erithacus rubecula*, with their left eye covered by an eye cap so that they had to rely on their right eye alone were just as well oriented in their migratory direction as birds with both eyes uncovered. Tested with only the left eye open and the right eye covered, however, the same birds were disoriented [6]. This indicated a strong lateralization of the magnetic compass in favor of the right eye. Together, these previous

findings suggest that perception of the geomagnetic field for compass orientation is associated with the visual system of the right eye. In consequence of the almost complete cross-over of the optic fibers in birds and few interhemispheric commissures, the visual input of the right eye is predominantly processed in the left hemisphere of the brain. Interestingly, earlier studies had revealed a functional division between the two brain hemispheres, with the right eye/left hemisphere dominant in discrimination tasks requiring object vision [7–9]. This raised the question of whether these two functions—object vision and magnetoreception—could possibly be interrelated.

To test this hypothesis, we studied the effect of blurring vision on magnetoreception, again using migratory orientation as an indicator. Our test birds, European robins, were made to wear special goggles that consisted of a clear foil on one side and a frosted foil on the other (Figure 1). Both foils were of equal translucence, allowing 70% of the light to pass, but whereas the clear foil allowed object vision, the frosted foil disrupted it completely. We used the same funnel-shaped test cages as in previous experiments [1–6], but in order to enhance the visual features for the birds, the cages were modified by adding radial lines running from the top to the bottom of the funnel walls (see Experimental Procedures). The tests took place in the local geomagnetic field at a light level of 2 mW/m².

The mean headings of the individual birds and the resulting grand mean vectors are presented in Figure 2, with Table 1 giving the numerical results and indicating statistical differences between the test conditions. (For the mean vectors of the individual birds, see Table S1 available online.) When tested binocularly with both eyes open in the geomagnetic field, the birds significantly preferred their seasonally appropriate northerly migratory direction (Figure 2A). Their disorientation when exposed to a radio frequency field of 1.315 MHz, 480 nT (Figure 2B) indicates that their orientation is based on radical pair processes [11], with the visual stimuli of the radial lines in the cage not affecting the behavior. When the birds wore goggles with the right eye covered by a clear foil and the left eye covered by a frosted foil, the birds headed northward as in the control condition (Figure 2C), whereas the reversal of the foils, with the frosted foil now on the right eye, led to disorientation (Figure 2D). These findings clearly show the importance of vision in the birds' right eye: covering it with a foil that blurs vision and prevents the detection of contours has a strong disorienting effect, suggesting an interference with the reception of the magnetic field, the only source of directional information in the test situation.

Comparison with Earlier Studies

In previous studies with monocular birds [6, 12], covering the right eye with an aluminum cap led to disorientation, an effect that we had attributed to the lack of light suppressing the crucial radical pair processes. In the case of the present study, about 70% of the light still reached the eye, roughly corresponding to a light level of 1.4 mW/m². This seems sufficient to allow the radical pair mechanism to function—birds have been able to orient in their migratory direction at the much lower light level of 0.2 mW/m² [13]. Nevertheless, the robins

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Figure 1. A Robin Wearing Goggles

in the present study were disoriented when wearing the frosted foil on their right eye, indicating that they lacked directional information. This suggests that degrading image formation in the right eye deprives birds of the means to translate magnetic information into a meaningful direction.

In view of this, it may seem surprising that it was possible to observe excellent orientation in the earlier experiments by using unstructured funnels with blank paper. In the present study with the radial lines, the median of individual vector lengths reflecting intraindividual variance was 0.92 and 0.93 in the two oriented samples (see Table 1); the respective data for spring tests with robins in blank funnels during the last nine years varied between 0.81 and 0.96 (median 0.93)—a difference in the accuracy of orientation is not suggested. The same is true for the distribution of the birds' activity in the cage—here, too, the radial lines did not seem to have an effect. However, even the cages with the blank paper were not completely featureless. There was the sharp border between the cover of the cage lit from above and the darker inclined walls and, probably less pronounced, between the four or five paper clips that held the coated paper in place and the overlap of that paper. Together, these features seem to have provided enough visual background information for recognizing the direction of the magnetic field.

Interaction of Object Vision and Magnetoreception

How is the interaction between object vision and magnetoreception to be explained? One possibility is that detection of contours is an integrated component of magnetoreception itself. Based on theoretical considerations, Ritz and colleagues [14] proposed that magnetic input would lead to specific activation patterns in the retina, centrally symmetric to the magnetic vector. These patterns might be manifested as a modulation of the visual input, depending on the direction in which the bird is looking with respect to the magnetic field lines. With the maximum on the order of magnitude of about 20%, the expected differences in magnetic modulation are not very large. The regular activation pattern that Ritz and colleagues illustrated in their paper [14] reflects the magnetic modulation for a completely homogeneous distribution of light within the eye, an unrealistic assumption. Under natural conditions, the visual field is inhomogeneously illuminated, with the sky brighter than the ground and parts of the visual field additionally shaded, other parts in the sun, etc. Hence the pattern of magnetic modulation is superimposed on a very inhomogeneously contrastful pattern of activation resulting from visual input. As a consequence, birds face the neural processing

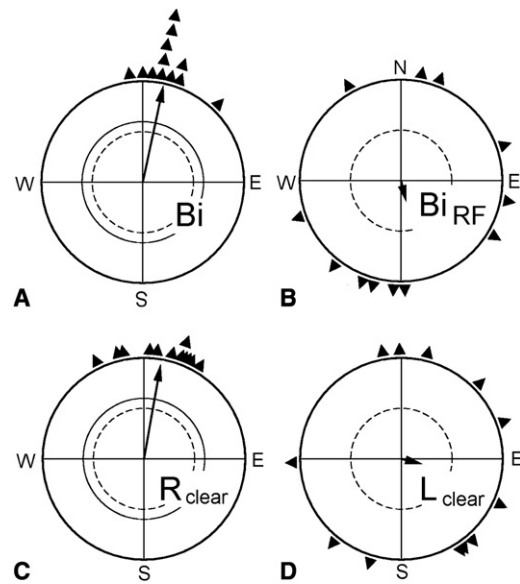


Figure 2. Orientation of European Robins during Spring Migration with the Local Geomagnetic Field as the Only Cue

(A) In the binocular control tests without goggles (Bi), the birds preferred their normal northerly migratory direction. (B) Birds tested binocularly in a radio frequency field (Bi_{RF}) were disoriented, indicating that the orientation was based on radical pair processes. (C) When the right eye was covered with a clear foil and the left eye covered with a frosted one (R_{clear}), the birds were oriented in their normal migratory direction. (D) When the left eye was covered with a clear foil and the right eye covered with a frosted one (L_{clear}), the birds were no longer oriented. The triangles at the periphery of the circles indicate mean headings calculated from three tests of the individual birds; the arrows originating from the center represent the grand mean vector drawn proportional to the radius of the circle = 1 (for numerical data, see Table 1). The two inner circles are the 5% (dashed circle) and 1% (solid circle) significance borders of the Rayleigh test [28].

task of distinguishing the modulations arising from the receptors' alignment to the magnetic field from those caused by light variations in the visual field. The modulation from the magnetic field is smooth, gradually changing as the angle to the field lines increases or decreases, whereas visual patterns are mostly fast changing and characterized by sharper transitions, such as lines or edges. Nondegraded object vision might be involved in separating magnetic from visual effects by identifying sharp transitions as visually caused, thus helping to discern the proper pattern indicating magnetic compass direction. With the frosted lens in place, the input of that eye will be dominated by low spatial frequencies. Because magnetic and visual spatial information would in this case overlap in the frequency domain, distinguishing these two sources of information would be rather difficult. Indeed, in the human visual system, high-spatial-frequency input enabling visualization of contours has proven considerably more salient and important for direction discrimination [15].

In addition, the eye transmitting blurred vision has an important disadvantage when competing against the input from the eye with clear vision. Studies in mammals have shown that degrading image formation on the retina via blur-inducing lenses replaces well-correlated ganglion cell responses with poorly correlated spontaneous activity [16]. This rapidly shifts visual dominance toward the nondegraded ocular input side [17, 18].

Table 1. Orientation of European Robins in the Local Geomagnetic Field with and without Goggles

Test Condition	n	Median r_b	α_n	r_n	ΔC
Bi: binocular, both eyes open (control)	12	0.92	12°	0.98***	
Bi _{RF} : binocular with radio frequency field (1.315 MHz, 480 nT) added	12	0.49	(166°)	0.22 ^{NS}	(+154°)***S
R _{clear} : right eye with clear foil, left eye with frosted	12	0.93	10°	0.95***	-2° ^{NS}
L _{clear} : left eye with clear foil, right eye with frosted	12	0.47	(104°)	0.21 ^{NS}	(+92°)* ^S

The following data are shown: n, number of birds tested; median r_b , median length of the individual birds' mean vectors based on three recordings, indicating the intraindividual variance; α_n and r_n , direction and length of the grand mean vectors, respectively, with asterisks indicating a significant directional preference by the Rayleigh test [28] and nonsignificant mean directions given in parentheses; ΔC , angular difference to the binocular control data, with asterisks indicating significant differences in direction by the Watson-Williams test, asterisks with "S" indicating significant differences in scatter by the Mann-Whitney U test [28], and values in parentheses indicating difference between significant and nonsignificant vector. *p < 0.05; **p < 0.01; ***p < 0.001; NS, not significant (p > 0.05).

This effect is caused not by reduction of light but by the loss of correlated activity due to the absence of high-contrast patterns [19]. It results from the competition between inputs from the two eyes, a competition that the impeded eye system loses because of the low cross-correlations between its neuronal spike trains [20]. If the principal scenario in birds is similar, the observed loss of ability to locate the migratory direction with the help of the magnetic field might also involve a shift of dominance toward the left eye system, which has only limited ability to distinguish object-related visual patterns from magnetic field-related patterns and transform the latter into directional information. This implies that this transformation requires neural structures downstream of the first point of synaptic convergence of the ascending visual pathways. In birds, synaptic convergence from both eyes takes place in the thalamic nucleus rotundus of the tectofugal system and the visual Wulst of the thalamofugal system. In birds, similar to in mammals, projections of the two eyes converge at these forebrain levels on single neurons. For both the nucleus rotundus [21, 22] and the Wulst [23], a structure recently discussed in connection with magnetic orientation [24], single cells have been shown to receive input from both eyes via upstream neural structures [25]. In addition, both the tectofugal system in pigeons [26] and the thalamofugal system in chicks [27] are asymmetrically organized with a dominance of the right eye/left hemisphere for various aspects of object vision. Thus, if magnetoreception is processed at forebrain level, degrading the dominant right eye input might rapidly shift the dominance toward the nondominant side and thereby impede magnetic orientation.

Conclusions

Our experiments with goggles thus confirm the important role of the right eye in detecting magnetic directions and demonstrate a crucial interaction between magnetoreception and vision. This interaction involves not only color vision [2] but also detecting contours to an extent not previously recognized.

Experimental Procedures

The experiments were performed in the spring of 2007 with European robins. All experiments were performed in accordance with the animal welfare laws and regulations of Germany.

Test Birds and Housing Conditions

Robins breed in most parts of Europe; the northern populations are nocturnal migrants and winter in the Mediterranean countries. The test birds were juveniles believed to be of Scandinavian origin because of their wing length. The 12 birds tested had been caught as transmigrants in September 2006 in the botanical garden near the Zoological Institute in Frankfurt am Main

and were kept over the winter in individual cages. The photoperiod simulated the natural one until the beginning of December, when it was reduced to light:dark 8:16. At the beginning of January, the photoperiod was increased to light:dark 13:11 to induce preseasonal spring Zugunruhe (migratory restlessness) that allowed us to begin the spring tests on January 12, 2007.

Goggles

The goggles consisted of a plastic frame upon which the two types of foils (clear and frosted) were fixed symmetrically. Because the frosted foil allowed 70% of light to pass, we covered the clear side with a -0.3 occlusion foil (Ryser Optik, St. Gallen, Switzerland). Hence, both types of foil were of equal translucence so that the amount of light reaching each eye was equal, the only difference being that the clear foil permitted the perception of contours, whereas the frosted one did not. The goggles were fixed on the robin's head with elastic adhesive tape (Leukoplast, BSN Medical, Hamburg, Germany; see Figure 1) in the bird room before the birds were brought into the test cages, and they were removed again immediately after the test was finished when the birds were returned to their housing cages.

To check for possible effects of the goggles on the birds' behavior, we observed single robins wearing the goggles in their housing cages with the help of a video camera. The birds moved around freely, hopping from perch to perch in a normal manner.

Test Apparatus and Test performance

All tests took place in wooden houses in the garden of the Zoological Institute where the local geomagnetic field (46 μ T, 66° inclination) was largely undisturbed. Orientation behavior was recorded in modified funnel cages (Figure 3) lined with coated paper (BIC, formerly Tipp-Ex), where the birds, tested one at a time, left scratches as they moved (see [1-6]). In contrast to previous experiments, where we had used blank coated paper, this time we applied a regular pattern of radial lines inside the inclined walls of each cage to provide visual features for the birds (see Figure 3). The cage was placed in a light-proof cylinder. For the tests in the geomagnetic field, cage and cylinder were made from aluminum; for the tests involving the oscillating field (see below), all test cages and cylinders were metal-free and made from PVC.



Figure 3. Funnel Cage Lined with Coated Paper Carrying Radial Lines to Provide Visual Features

All tests were performed under monochromatic green light with a peak wavelength of 565 nm (half bandwidth 553–583 nm) produced by light-emitting diodes (LEDs). The light intensity was 2 W/m^2 , corresponding to the brightness more than 45 min before sunrise or after sunset. In previous studies, we used this green light as control condition or as background light in tests with magnetic and other manipulations [3–6]; the robins always showed excellent orientation in their migratory direction under this light. The LEDs were mounted on the plastic disk covering the cylinder. The light passed two sets of diffusers until it reached the bird in the cage.

In some tests, we added an oscillating field of 1.315 MHz with an intensity of 480 nT to the local geomagnetic field. A weak radio frequency field is a useful diagnostic tool for identifying the nature of the mechanism underlying magnetoreception, because it is only expected to interfere with the birds' orientation if this orientation is based on radical pair processes [11]. The radio frequency field was produced by a coil antenna consisting of a single winding of coaxial cable with 2 cm of the screening removed opposite the feed. The antenna was mounted on a horizontal wooden frame surrounding a group of four test cages so that the axis of the oscillating field formed an angle of 24° with the local magnetic vector. For details of the equipment used, see [3].

Testing began in the evening when the light went off in the housing cages and lasted about 75 min. Each bird was tested in each condition three times, following a pseudorandom sequence.

Data Analysis and Statistical Treatment

For data analysis, the coated paper was removed and divided into 24 sectors, and the scratch marks in each sector were counted by a person blinded to the test condition. Recordings with a total of fewer than 35 scratches were excluded from the analysis because of too little activity and were repeated.

From the distribution of the activity within the cage, we calculated the heading of the respective test by vector addition, and from the three headings of a bird under each condition, we calculated the mean vector of that bird. The mean headings of the 12 test birds were then comprised in the grand mean vector for each condition, with the direction α_n and the length r_n .

The grand mean vectors were tested via the Rayleigh test for significant directional preferences [28]. The data of different test conditions were compared via the Watson-Williams test to look for differences in direction (if $r_n > 0.65$) and via the nonparametric Mardia-Watson-Wheeler test, applied to the angular difference of the birds' mean headings from the grand mean of the respective sample, to look for differences in distribution when an oriented and a nonoriented sample were compared [28].

Supplemental Information

Supplemental Information includes one table and can be found with this article online at [doi:10.1016/j.cub.2010.05.070](https://doi.org/10.1016/j.cub.2010.05.070).

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