Current Biology, Vol. 14, 1946–1949, November 9, 2004, ©2004 Elsevier Ltd. All rights reserved. DOI 10.1016/j.cub.2004.10.025

Migratory Birds Use Head Scans to Detect the Direction of the Earth's Magnetic Field

Henrik Mouritsen,* Gesa Feenders, Miriam Liedvogel, and Wiebke Kropp
Volkswagen Nachwuchsgruppe "Animal Navigation"
Institute of Biology
University of Oldenburg
D-26111 Oldenburg
Germany

Summary

Night-migratory songbirds are known to use a magnetic compass [1–3], but how do they detect the reference direction provided by the geomagnetic field, and where is the sensory organ located? The most prominent characteristic of geomagnetic sensory input, whether based on visual patterns [4–7] or magnetite-mediated forces [8, 9], is the predicted symmetry around the north-south or east-west magnetic axis. Here, we show that caged migratory garden warblers perform head-scanning behavior well suited to detect this magnetic symmetry plane. In the natural geomagnetic field, birds move toward their migratory direction after head scanning. In a zero-magnetic field [10], where no symmetry plane exists, the birds almost triple their head-scanning frequency, and the movement direction after a head scan becomes random. Thus, the magnetic sensory organ is located in the bird's head, and head scans are used to locate the reference direction provided by the geomagnetic field.

Results and Discussion

We observed and recorded the behavior of 35 night-migratory garden warblers, *Sylvia borin*, placed individually in a cylindrical orientation cage (Figure 1A), directly to hard disk and/or to video tape by two infrared (840 nm) video cameras (top and side view, inbuilt IR light sources) at night (indoors, light level 0.04 lux from four diffused white light bulbs not directly visible to the birds) or during the day (indoors, room light level 275 lux). Each bird had a thin line of infrared-reflective tape glued to its head, and they were tested inside a windowless wooden house. Seven birds were tested during the day in the natural geomagnetic field. The other birds were tested while showing migratory restlessness at night in the natural geomagnetic field ($n = 11$), a zero magnetic field [10] ($n = 11$) or a changing magnetic field switching 120° every 5 min ($n = 6$). The birds tested at night in the natural magnetic field (NMF) showed magnetic orientation directed in the normal migratory direction (Figure 1B), whereas the birds tested in the zero-magnetic field (ZMF) oriented randomly (Figure 1C). How did the NMF birds detect the compass direction of the geomagnetic field?

The video recordings suggested that birds, in addition to their migratory restlessness behavior, perform repeated head-scanning behavior (see movies in the Supplemental Data available with this article online). A naïve observer (W.K.) counted the number of head scans performed by each individual bird during a 1 hr period. We defined a head scan as the turn of the bird's head from the body axis position to an angle turned clearly more than 60° to the left or right, followed by the subsequent return of its head to the straight-ahead position while the bird remained at the same spot (Figure 1D). By requiring that the bird must return its head to the body axis position before moving in the cage, we avoided counting head turns, which always precede movement in a new direction. The side-view camera showed that the head-scanning behavior was performed in the horizontal plane. Sometimes a bird makes a head scan to one side only; other times, one head scan is immediately followed by another head scan in the opposite direction. Four pieces of evidence strongly suggest that head-scanning behavior is directly involved in the process of sensing the geomagnetic reference direction needed for magnetic compass orientation.

First, garden warblers exposed to a zero-magnetic field (ZMF) made 141 ± 33 (SD) head scans in 60 min, whereas birds tested under any other magnetic condition only made 52 ± 35 (SD) head scans in 60 min (see Figure 1E). The increased head-scanning frequency observed in the ZMF birds is highly significant (one-way ANOVA followed by Tukey all pair-wise comparison method: the ZMF group differs significantly [$p < 0.001$] from all other groups, whereas all other differences between groups are non-significant [$0.22 < p < 0.99$]). On average, the birds, irrespective of magnetic condition, performed an equal number of head scans to the left and to the right (mean = 50% ± 18% [SD]). We also quantified the number of flights and wing beats performed by each bird during the same 60 min period, but we found no significant differences depending on the magnetic field condition (flights: one-way ANOVA on ranks, $p = 0.99$, wing beats: one-way ANOVA, $p = 0.77$). Thus, differences in head scan frequency are not due to differences in activity level between NMF and ZMF birds.

Second, garden warblers strongly increased their head-scanning frequency before initiating their first migratory restlessness behavior (repeated jumping and wing flapping on the perch). Birds observed in the orientation cages typically sat still for 10–60 min after the lights went off. During the last 10 min before initiating their first migratory restlessness behavior that night, all birds made many repeated head scans. Within this period, the average head scan frequency increased gradually from ~2/min to about ~6/min (Figure 2A). This strong increase in head-scanning frequency suggests that the birds carefully determined the reference direction of the geomagnetic field before starting their orientation behavior. Once migratory restlessness behavior was initiated, birds experiencing the NMF made less than one head scan per minute on average, whereas birds experiencing the ZMF performed two to three head scans

*Correspondence: henrik.mouritsen@uni-oldenburg.de

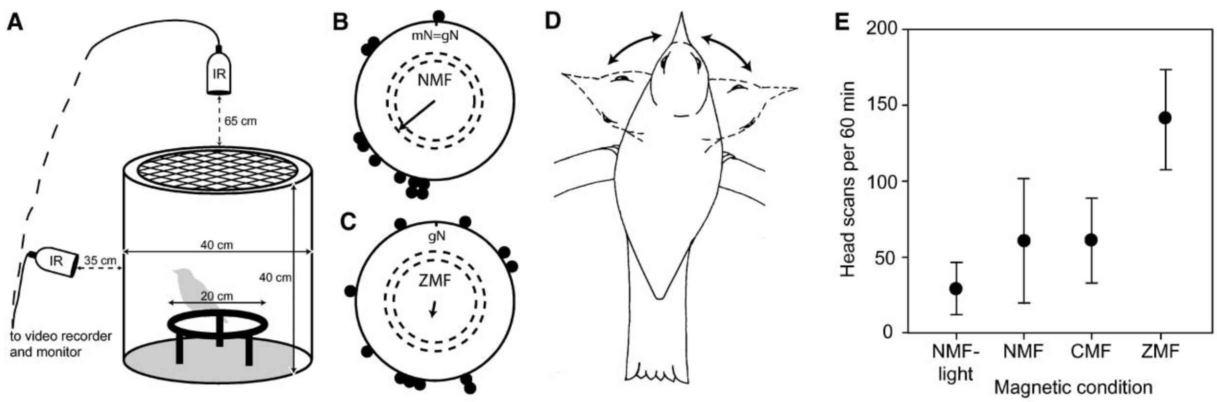

Figure 1. Caged Garden Warblers Perform Head Scan Behavior during Magnetic Orientation

(A) Design of our orientation cage.

(B) Garden warblers tested in the natural magnetic field oriented in their southwesterly migratory direction ($\alpha = 231°$, $r = 0.60$, $p < 0.02$). Each dot indicates the mean orientation of one individual garden warbler (measured as its head's location relative to the center of the cage determined 5 times per s during 45–60 min of constant migratory restlessness behavior). The arrow indicates the group's mean vector length (r). The inner- and outer-dashed circles indicate the length of the group's mean vector needed for significance ($p < 0.05$ and $p < 0.01$, respectively), according to the Rayleigh test. mN = magnetic North; gN = geographic North.

(C) Garden warblers tested in a zero-magnetic field oriented randomly ($\alpha = 187°$, $r = 0.22$, $p = 0.60$).

(D) Schematic drawing of head-scanning behavior.

(E) Number of head scans performed by garden warblers within 60 min under four different conditions: during the day in the natural magnetic field (NMF-light) and while showing migratory restlessness at night in the natural magnetic field (NMF), a changing magnetic field (CMF), or a zero magnetic field (ZMF).

per minute (Figures 1E and 2B). The fact that the birds continued to perform regular head scans throughout the night, even in the natural magnetic field, suggests that they have not transferred magnetic information to other cues in their cage or surroundings.

Third, during migratory restlessness behavior, most garden warblers made occasional flights to the top of the cage followed by fluttering around and landing on the bottom of the cage. After sitting at the bottom of the cage

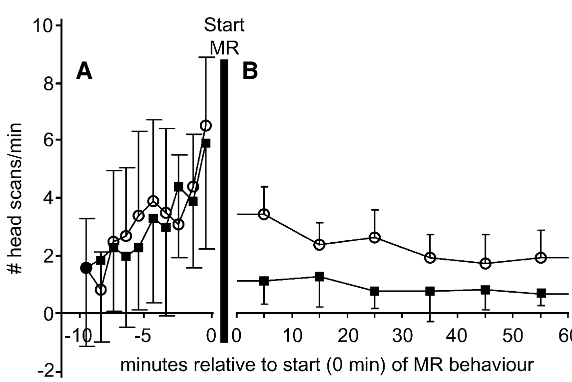

Figure 2. Number of Head Scans Performed per Minute Just before and during Migratory Restlessness Behavior

(A) Just before initiation of their first migratory restlessness behavior at night, garden warblers strongly increase their head-scanning frequency. On the x axis, "0" indicates the time when a bird performed its first migratory restlessness behavior. The symbols are as follows: ■: NMF birds; ○: ZMF birds.

(B) During migratory restlessness behavior, birds experiencing a ZMF continue to show a relatively high head-scanning frequency (two to three head scans per minute), whereas birds experiencing NMF conditions only make about one head scan per minute on average. Error bars indicate (symmetrical) standard deviations.

for a few seconds, most birds returned to the perch, where they usually sat still for 10–60 s before reinitiating migratory restlessness behavior. During this period of sitting still after a flight, the birds seem to reorient themselves before continuing their migratory restlessness behavior. This is evidenced by a highly significant 2-fold increase in head-scanning frequency during the first minute following a flight off the perch compared with any other 1 min period (176 head scans observed in 93 1 min periods immediately after a flight compared to 225 head scans observed in 238 other 1 min periods; chi-square test: $df = 1$, $\chi^2 = 49.5$, $p < 0.001$).

Fourth, if head scans indeed help garden warblers detect the reference compass direction provided by the geomagnetic field, one should expect that the birds in the natural magnetic field move more toward than away from their mean migratory direction after performing a head scan, whereas the direction of movement after a head scan in a zero-magnetic field should be close to random. We tested this by observing the garden warblers' very first move immediately after they performed a head scan. This was done by placing an arrow on the TV monitor pointing in the overall mean direction of the individual bird. Then, if a bird with a mean orientation of 205°, for example, performs a head scan while sitting on the circular perch at 140°, a clockwise move along the perch would be toward the "correct" direction, whereas a counter-clockwise move would be counted as a move in the "wrong" direction. If it performs a head scan at 265°, a counter-clockwise move would be correct and a clockwise move would be wrong. For both the NMF and ZMF condition, we only analyzed birds that showed an overall mean direction oriented in the appropriate, southwesterly mean migratory direction (215° ± 60°) characteristic for garden warblers during autumn migration. Otherwise, no clear correct migratory direction

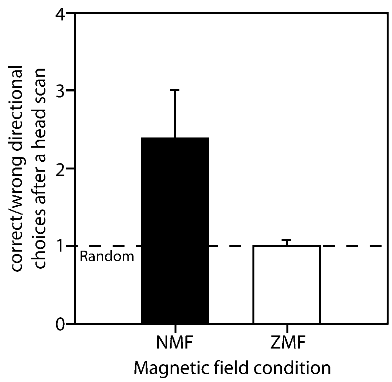

Figure 3. Orientation of NMF and ZMF Birds Immediately Following a Head Scan

Birds experiencing a natural magnetic field move 2.39 ± 0.63 times as often toward their correct migratory direction than away from it after performing a head scan. In contrast, birds experiencing a zero-magnetic field move equally often toward and away from their mean migratory direction following a head scan. Error bars indicate standard deviations.

could be defined. Furthermore, to be reliably analyzed, a bird must have performed most of its migratory restlessness behavior on the perch, where one can clearly determine if the next movement following a head scan is in the correct or wrong direction. All the garden warblers performing migratory restlessness behavior on the perch in the natural magnetic field moved significantly more toward their mean migratory direction after performing a head scan than away from it (number of correct moves/number of wrong moves = 2.39 ± 0.63, Figure 3), whereas the direction of movement following a head scan in a zero-magnetic field was random (number of correct moves/number of wrong moves = 1.01 ± 0.06; difference between NMF and ZMF birds: Mann-Whitney U-test, $p < 0.01$; Figure 3). This difference cannot be explained by a difference in individual directedness (r values) between the ZMF (0.19 ± 0.12) and NMF (0.24 ± 0.18) birds because this difference was nonsignificant (t test, $p = 0.67$).

Based on these converging pieces of evidence, we suggest that caged garden warblers, and possibly night-migratory birds in general, use head movements to detect the reference compass direction of the earth's magnetic field. If magnetoreception in birds is magnetite mediated [8, 9], we suggest that the head movements are designed to scan for the maximum or minimum magnetic field strength direction. If magnetoreception is vision dependent [4–7], we suggest that the purpose of the head scans is to detect the symmetry axis of the magnetically modulated visual patterns that characterize the magnetic-field axis [5] and/or to improve detection of these gradually changing patterns by the visual system, which is more sensitive to them when they move. In fact, due to the predicted graded nature of the magnetically modulated, virtual visual patterns, they may very well be undetectable unless the bird moves its eye relative to the pattern [11]. We also suggest that the strongly increased head-scanning frequency observed in ZMF-birds during migratory restlessness behavior is a result of their repeated, unsuccessful attempts to find a symmetry plane or pattern that does not exist.

The fact that head scanning seems to be used by garden warblers to detect the compass direction of the geomagnetic field confirms that their magnetic sensor must be located in the head. If head scanning is performed by all birds, this will remove an important uncertainty in our search for the avian magnetic sensor and would provide crucial knowledge when designing magnetic-manipulation devices for free-flying birds [12]. Furthermore, virtually all psychophysical experiments designed to elucidate the functional characteristics of the avian magnetic compass have been unsuccessful [13]. We suggest that head scan counts can be used as a much-needed psychophysical measure to determine many unknown functional characteristics of the avian magnetic compass.

Supplemental Data

Supplemental Data including two movies are available at http://www.current-biology.com/cgi/content/full/14/21/1946/DC1/.

Acknowledgments

We thank Nikolaus Troje for writing a key part of the software used to analyze the birds' orientation based on the video images, Tatjana Mouritsen for hand-drawing Figure 1D, Institut für Vogelforschung, Wilhelmshaven & Helgoland, Germany, for help catching and keeping most of the birds, Andreas Sommer for building the orientation cages, and Ole Næsbye Larsen and Thorsten Ritz for constructive commentary on the manuscript. We thank the VolkswagenStiftung and University of Oldenburg for their kind financial support.

Received: July 2, 2004
Revised: September 8, 2004
Accepted: September 13, 2004
Published: November 9, 2004

References

1. Wiltschko, W., and Wiltschko, R. (1972). Magnetic compass of European robins. Science *176*, 62–64.
2. Wiltschko, W., and Wiltschko, R. (1996). Magnetic orientation in birds. J. Exp. Biol. *199*, 29–38.
3. Cochran, W.W., Mouritsen, H., and Wikelski, M. (2004). Migrating songbirds recalibrate their magnetic compass daily from twilight cues. Science *304*, 405–408.
4. Wiltschko, W., Munro, U., Ford, H., and Wiltschko, R. (1993). Red light disrupts magnetic orientation of migratory birds. Nature *364*, 525–527.
5. Ritz, T., Adem, S., and Schulten, K. (2000). A model for photoreceptor-based magnetoreception in birds. Biophys. J. *78*, 707–718.
6. Ritz, T., Thalau, P., Phillips, J.B., Wiltschko, R., and Wiltschko, W. (2004). Resonance effects indicate a radical-pair mechanism for avian magnetic compass. Nature *429*, 177–180.
7. Mouritsen, H., Janssen-Bienhold, U., Liedvogel, M., Feenders, G., Stalleicken, J., Dirks, P., and Weiler, R. (2004). Cryptochromes and neuronal-activity markers colocalize in the retina of migratory birds during magnetic orientation. Proc. Natl. Acad. Sci. USA *101*, 14294–14299.
8. Walker, M.M., Diebel, C.E., Haugh, C., Pankhurst, P.M., Montgomery, J.C., and Green, C.R. (1997). Structure and function of the vertebrate magnetic sense. Nature *390*, 371–376.
9. Fleissner, G., Holtkamp-Rotzler, E., Hanzlik, M., Winklhofer, M., Fleissner, G., Petersen, N., and Wiltschko, W. (2003). Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. J. Comp. Neurol. *458*, 350–360.

10. Mouritsen, H. (1998). Redstarts, *Phoenicurus phoenicurus*, can orient in a true-zero magnetic field. Anim. Behav. *55*, 1311–1324.
11. Metzger, W. (1930). Optische Untersuchungen am Ganzfeld: II. Zur Phanomenologie des homogenen Ganzfelds. Psychol. Forsch. *13*, 6–29.
12. Mouritsen, H., Huyvaert, K.P., Frost, B.J., and Anderson, D.J. (2003). Waved albatrosses can navigate with strong magnets attached to their head. J. Exp. Biol. *206*, 4155–4166.
13. Wiltschko, R., and Wiltschko, W. (1995). Magnetic Orientation in Animals, (Berlin: Springer Verlag).