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Migratory orientation of European Robins is affected by the wavelength of light as well as by a magnetic pulse

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Abstract The object of this study was to test the alternative hypotheses of magnetoreception by photopigments and magnetoreception based on magnetite. Migratory European Robins, *Erithacus rubecula*, were tested under light of different wavelengths; after these tests, they were subjected to a brief, strong magnetic pulse designed to alter the magnetization of single domain magnetite. In control tests under "white" light, the birds preferred the normal, seasonally appropriate migratory direction. Under 571 nm green light, they continued to be well oriented in the migratory direction, whereas under 633 nm red light, their behaviour was not different from random. The magnetic pulse had a significant effect on migratory orientation, but the response varied between individuals: some showed a persistent directional shift, while others exhibited a change in scatter; one bird was seemingly unaffected.

These findings indicate a light-dependent process and, at the same time, suggest an involvement of magnetizable material in migratory orientation. They are in agreement with the model of a light-dependent compass and a magnetite-based 'map', even if some questions concerning the effect of the pulse remain open.

Key words Bird migration · Magnetic compass · Photopigments · Magnetite European robin · *Erithacus rubecula*

Introduction

Magnetic orientation responses have been reported from all major groups of animals (for summary, see Kirschvink et al. 1985; Wiltschko 1993), suggesting that the use of magnetic information is fairly widespread in the animal kingdom. However, the physiological basis of magnetoreception is still largely unclear, in spite of considerable research efforts to identify transducer mechanisms and sensory structures. In terrestrial vertebrates, the discussion focuses mainly on two mechanisms which have been proposed on theoretical grounds, namely (1) biochemical bi-radical reactions of excited state macromolecules in connection with light-dependent processes (Leask 1977; Schulten and Windemuth 1986) and (2) processes involving small particles of magnetite (Gould et al. 1978; Yorke 1979; for summary, see Kirschvink et al. 1985). Data from electrophysiological studies on several avian species seem to suggest the presence of both types of mechanisms in birds: Recordings from the visual system produced light-dependent responses to magnetic stimuli which reflect the direction of the magnetic field (e.g. Semm et al. 1984; Semm and Demaine 1986): recordings from the nervus ophthalmicus (which innervates the region where magnetite particles were repeatedly found, comp. Walcott and Walcott 1982; Beason 1989) produced responses to changes in magnetic intensity regardless of the direction of the ambient field (Semm and Beason 1990). The nature of these responses led to the hypothesis that birds might possess a light-dependent magnetic compass providing information on *direction*, while magnetite-depending mechanisms might be used to perceive magnetic 'map'-factors providing information on *position* (e.g. Beason and Semm 1991).

Behavioral data with pigeons are in accordance with this assumption: Very young and inexperienced pigeons determine their homeward course using magnetic compass information obtained during the outward journey (Wiltschko and Wiltschko 1978): such birds were disoriented after displacement while in total darkness (Wiltschko and Wiltschko 1981). Older pigeons establish their home course by help of the navigational 'map' (see Wallraff 1974; Wiltschko 1991 for details): such birds deviated from controls after being treated with an ultra-strong magnetic field

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Table 1 Orientation behavior under various test conditions. *N*, number of test birds; α_N r_N vector based of the mean headings of the individual birds, with asterisks indicating significance by the Rayleigh test. ΔC, Δ green, indicates significant differences to the respective samples as defined under 'condition'

Condition	*N*	α_N	r_N	ΔC	Δgreen
Tests under various colors of light:					
"White" light (C):	12	24°	0.78***		
571 nm green:	12	13°	0.89***	n.s.	
633 nm red:	12	162°	0.32$^{\text{n.s.}}$	**	**
Treatment with a strong magnetic pulse:					
Before treatment (C):	12	18°	0.94***		
After treatment:	12	53°	0.30$^{\text{n.s.}}$	**	

Significance levels: * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, and *n.s.* = not significant

(Kiepenheuer et al. 1986) or with a strong, short magnetic pulse (Wiltschko and Beason 1990). Other types of treatment designed to affect the magnetization of magnetite (e.g. Walcott et al. 1988) proved less effective; the reasons may lie in the treatments themselves or in the general variability of magnetic effects on homing, which often proved site-specific (see Wiltschko and Wiltschko 1988).

Recently, experiments testing the two hypotheses have been extended to migratory birds. Australian Silvereyes, *Zosterops lateralis* (Zosteropidae), were found to be well oriented under 443 nm blue light and 571 nm green light, but failed to show any directional preferences under long wavelength of 633 nm in the red (Wiltschko et al. 1993). This is in agreement with a light-dependent compass mechanism. A brief, strong magnetic pulse of 0.5 T caused a ca. 90° clock wise deflection on the day of application; in the course of the following week, the birds returned to their original headings (Wiltschko et al. 1994). American Bobolinks, *Dolichonyx oryzivorus* (Icteridae), treated with the same pulse, showed similar deflections (Beason et al., 1995). The last mentioned findings suggest that magnetite is also involved in migratory orientation. At the first glimpse, this appears to be at variance with the hypothesis of a light-dependent magnetic compass. However, the experiments described above involved adult birds that had migrated in the wild so that navigation and an involvement of a 'map' cannot be excluded (see Perdeck 1958), even if the general role of navigational processes in migratory orientation is not yet clear.

In view of these findings, it seemed desirable to study the effects of the two treatments in other species and in birds with different migratory experience. Here we report first results of tests with European Robins, *Erithacus rubecula* (Muscicapidae, Turdinae).

Material and methods

Test birds

The northern populations of European Robins are migratory and winter in the Mediterranean countries. They migrate at night; previous experiments revealed that they can use the magnetic field for orientation and that their magnetic compass works as an inclination compass (Wiltschko and Wiltschko 1972).

The test birds were 12 robins caught as transmigrants in Frankfurt a.M (50°08'N, 8°40'E) between 4 and 27 October 1993. Aging according to Svensson (1975) showed that all were juveniles, i.e. birds on their first migration. They were housed indoors in individual cages under photoperiodic conditions which simulated the natural one until mid-December, when L:D 8:16 was reached. On 26 December 1993, the photoperiod was increased to L:D 13:11. This treatment advanced the birds' annual cycle and promoted early spring *Zugunruhe* so that testing could begin in advance of natural spring migration season (comp. Wiltschko 1968). The tests described here were performed between 3 January and 25 February 1994.

Testing procedure and experimental treatment

The orientation tests took place indoors in the local geomagnetic field (46,000 nT, + 66° incl.). They started shortly after the onset of the dark period and lasted for approx. 1 h. The birds were tested one at a time in funnel cages (see Emlen and Emlen 1966) lined with typewriter correction paper (see Beck and Wiltschko 1981 for details).

The first series subjected the birds to light of different wavelengths. Tests under "white" light produced by a Tungsten light bulb served as controls in order to establish the normal directional preference of the test birds. Alternately, the birds were tested under 571 nm green light and under 633 nm red light produced by LEDs, with the levels adjusted to be of equal quantal flux. The arrangement was the same as used in a previous study with Silvereyes (see Wiltschko et al. 1993, Table 1 for details). The assignment of the test condition followed a pseudo-random sequence.

The second series involved an experimental treatment consisting of a magnetic pulse of about 0.5 T and approx. 4 ms duration, produced by a solenoid with 7700 μF capacitors charged to 250 V DC and discharged through a silicon controlled rectifier. It was the same pulse previously used on Silvereyes (for a more detailed description, see Wiltschko et al. 1994). The physical north pole of the induced field was directed towards the end of the coil where the head of the test birds was placed. After treatment with the pulse, the birds were tested under "white" light conditions only. The first such test for each individual began immediately after the bird had been subjected to the pulse; from then on, it was regularly tested every second night. The pulses were applied between 19 January and 5 February.

Data analysis and statistics

From the distribution of the marks left by the bird, the heading of each recording was calculated. Recordings with fewer than 35 scratches were excluded from the analysis.

Table 2 Orientation of individual birds under light of various wavelengths (n_b, number of tests per bird; r_b, α_b, length and direction of mean vectors of the individual birds, with *asterisks* indicating significance by the Rayleigh test. The *summary line* gives the median value of r_b and the center of distribution of the respective vectors. *Symbols* as in Table 1)

bird	"white" control n_b	r_b	α_b	571 nm green n_b	r_b	α_b	633 nm red n_b	r_b	α_b
R 22	4	0.93*	16°	3	0.90	26°	3	0.93	331°
R 23	4	0.88*	360°	4	0.93*	17°	4	0.44	254°
R 24	6	0.67	26°	4	0.80*	17°	4	0.34	146°
R 25	4	0.52	71°	3	0.32	347°	3	0.53	186°
R 26	9	0.15	203°	5	0.68	352°	4	0.30	102°
R 27	6	0.75*	30°	4	0.94	2°	4	0.32	87°
R 28	4	0.99*	19°	3	0.97	18°	4	0.21	50°
R 29	8	0.40	355°	4	0.86*	357°	4	0.44	219°
R 30	8	0.25	33°	4	0.25	71°	3	0.46	216°
R 31	6	0.78*	24°	6	0.65	57°	6	0.50	214°
R 32	4	0.94*	22°	3	0.98	323°	4	0.50	162°
R 33	5	0.92*	43°	5	0.85	20°	4	0.32	63°
$N = 12$		0.77	24°,0.63		0.86	11°,0.69		0.44	193°,0.13

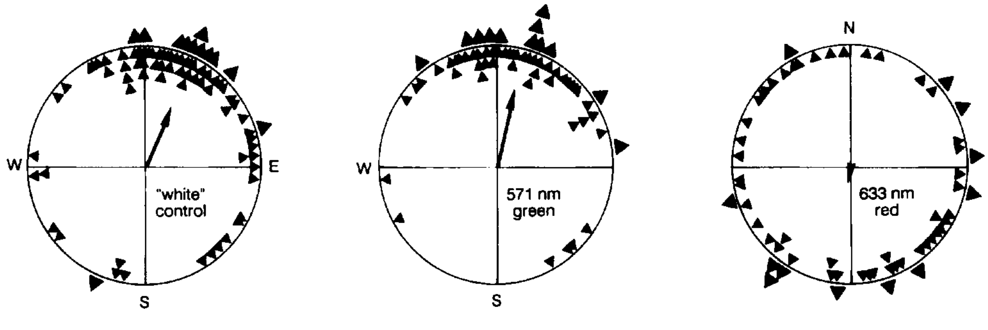

Fig. 1 Orientation of European Robins during spring migration under light of various wavelengths. The *symbols inside the circle* represent the headings recorded in the various test periods; the *triangles* at the periphery indicate the mean headings of the 12 individual birds. The *arrows* represent the mean vectors. For numerical data, see Table 1

From these headings, mean vectors for each individual bird under each condition were calculated by vector addition. The vectors were tested with the Rayleigh test for directional preferences (Batschelet 1981). For each test condition, we calculated the center of distribution of these vectors as well as a mean vector based on their mean directions. The latter was tested for a common directional tendency with the Rayleigh test. Two distributions were compared with the Mardia Watson Wheeler test (Batschelet 1981). The Mann-Whitney *U*-test served to test for differences in scatter, and the Wilcoxon test compared the activity of the birds in the various conditions.

The headings recorded after treatment with the magnetic pulse were analysed (1) with respect to day after treatment (the day of treatment counting as "day 1") and (2) with respect to the individual birds. As reference samples to see whether the behaviour had changed, we used control samples consisting (1) of the first tests of each bird under "white" light, and (2) of all tests of the individual under "white" *and* green light before treatment, respectively.

Results

Table 1 summarizes the data by presenting the vectors based on the mean directions of the 12 individual birds recorded under the various test conditions; differences between samples are indicated.

Orientation under light of various wavelengths

The behaviour of the birds under the different colors of light are presented in Fig. 1 and Table 2. Under "white" light, the robins significantly preferred northerly directions, which are in good agreement with their spring migratory direction. The same was true under 571 nm green light; here, the orientation did not differ from that under "white" light in any aspect. Under 633 nm red light, in contrast, no directional preference was found. The distribution of data recorded under red light is significantly different from the one under "white" light and under green light ($P < 0.01$, Mardia Test).

The difference in behavior under red light evokes the question whether the robins were able to perceive light of 633 nm wavelength. In view of this, we compared the activity under the various test conditions. The median number of scratches (with the first and third quartile in parentheses) was 122 (69; 144) under white light, and 74 (67; 181) under 571 nm green, compared to 102 (70; 162) under red light. There is no difference in activity between any of the test conditions ($P > 0.05$, Wilcoxon test). Since migratory birds tend to become inactive in the dark (Gwinner 1974), the normal level of activity indicates that 633 nm red light was visible to the birds, even if it did not allow orientation.

Orientation after treatment with a strong magnetic pulse

Treatment with a short, strong magnetic pulse led to a significant change in the birds' behaviour. After

Table 3 Orientation on various days after treatment with a magnetic pulse (n_d, number of tests per day; r_d α_d length and direction of mean vectors of the days, with *asterisks* indicating significance by the Rayleigh test. The *summary line* gives the median value of r_d and the center of distribution of the vectors of the 11 test days. The *last column* gives the difference between the various days after treatment and the control tests (first test of each bird under "white"), with *asterisks* indicating significant differences. *Symbols* as in Table 1)

day	n_d	r_d	α_d	ΔC
Control:	12	0.70**	16°	
day 1:	12	0.11	97°	+ 81°*
day 3:	12	0.14	103°	+ 87°*
day 5:	12	0.25	40°	+ 24°
day 7:	11	0.14	36°	+ 20°
day 9:	12	0.40	33°	+ 17°
day 11:	10	0.39	36°	+ 20°
day 13:	11	0.23	33°	+ 17°
day 15:	11	0.55*	54°	+ 38°
day 17:	11	0.34	66°	+ 50°
day 19:	9	0.58*	35°	+ 19°
day 21:	10	0.48	47°	+ 31°
$N = 11$		0.34	47°, 0.31	+ 35°

treatment, the birds did not show a homogeneous response, but each bird headed in its individual preferred direction.

The vectors based on the data of each day (Table 3) are mostly non-significant, i.e. the birds did not show common tendencies. The analysis based on the data of each bird reveals that the individual birds were by no means disoriented, even if their responses showed a great diversity (Fig. 2). Table 4 compares the vectors of the individuals before and after the magnetic pulse. In 11 of the 12 birds, the headings show a significant difference in distribution. The response to the pulse was either (1) a significant deviation from the previous mean heading (birds R 31, R 32, R 33), (2) a significant change in scatter (birds R 22, R 26, R 29, R 30) or (3) a combination of both (birds R 23, R 24, R 27, R 28). Scatter either increased leading to non-oriented behavior (e.g. bird R 22); more often, however, the scatter decreased. In summary, the robins were affected by the treatment with the short, strong magnetic pulse, but each bird responded in its own, individual way. – The oriented behavior of the majority of birds as well as the fact that the mean headings of the various days after treatment lay mostly in the NE sector indicate that the behavior after the pulse remained constant from day to day, at least within the next three weeks.

Discussion

In view of the hypotheses on magnetoreception in birds, data on migratory orientation are of particular interest. In contrast to homing pigeons, migratory birds are normally tested in situations where they have to rely on the magnetic field alone, being more or less isolated from other environmental factors which may provide additional information or serve as back-up systems. Hence observed effects are normally attributed to effects on magnetoreception.

Comparison with previous findings

Under the lights of different colors, European Robins oriented in the same manner as did the Silvereyes in previous tests (Wiltschko et al. 1993) : good orientation under "white" and 571 nm green light, disorientation under 633 nm red light. This suggests that light-dependent processes may be wide-spread among birds. Whether they are similar between species, however, is yet unclear. Beason (1994) reported that Bobolinks, *Dolichonyx oryzivorus* (Icteridae) were poorly oriented under 585 nm light, i.e., under a wavelength which differs only by 14 nm from the one where Robins as well as Silvereyes showed excellent orientation. He also

Table 4 Effect of a magnetic pulse on the orientation of individual birds (n_b, number of tests per bird; r_b, α_b, length and direction of mean vectors of the individual birds, with *asterisks* indicating significance by the Rayleigh test. The *summary line* gives the median value of r_b and the center of distribution of the vectors of the 12 birds. The *last column* gives the difference between the orientation before ("white" and green combined) and after treatment with the magnetic pulse, with *asterisks* indicating significant differences in distribution by the Mardia Watson Wheeler test. Symbols as in Table 1)

	Before treatment			After treatment			Change in direction	
Bird	n_b	r_b	α_b	n_b	r_b	α_b		
R 22	7	0.91***	20°	11	0.38	8°	– 12°	*
R 23	8	0.89***	9°	8	0.46	175°	+ 166°	**
R 24	10	0.75**	21°	7	0.51	202°	– 179°	**
R 25	7	0.34	47°	13	0.69**	28°	– 19°	n.s.
R 26	14	0.17	335°	10	0.69**	294°	– 41°	*
R 27	10	0.76**	18°	11	0.23	120°	+ 102°	**
R 28	7	0.98***	19°	11	0.49	325°	– 54°	*
R 29	12	0.55*	356°	11	0.98***	345°	– 11°	*
R 30	12	0.24	46°	11	0.79***	46°	± 0°	*
R 31	12	0.67**	34°	11	0.98***	111°	+ 77°	***
R 32	7	0.84**	357°	12	0.65**	108°	+ 111°	**
R 33	10	0.85**	32°	11	0.91***	60°	+ 29°	*
$N = 12$		0.76	18°, 0.64		0.67	47°, 0.24	+ 34°,	

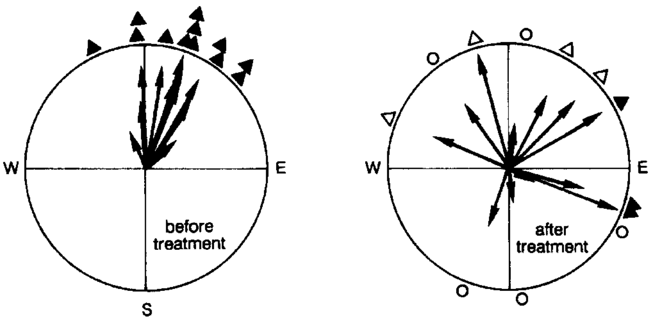

Fig. 2 Orientation of European Robins during spring migration *before* (*left*; control vectors based on headings recorded under "white" and green) and *after* (*right*) treatment with a short, strong magnetic pulse. – The *arrows* represent the vectors of the 12 individual birds drawn proportional to the radius of the circle; the *symbols at the periphery* give the respective mean headings. In the *right diagram*, different symbols indicate differences to the control sample: *solid triangles*: significant deviation from control, open *triangles*, significant samples that do not differ from the control sample in direction; *open dots*: significant increase in scatter. For numerical data, see Table 4

mentioned a directional shift under 450 nm blue light, which had not been observed in Silvereyes. Very different responses to light of various wavelengths have been described for amphibians (Phillips and Borland 1992, 1994). Taken together, evidence suggesting light-dependent mechanisms of magnetoreception in vertebrates continues to accumulate, but at the same time, a considerable variability in the relationship between wavelength and response is suggested. More species have to be studied before orientation as a function of light wavelength can be described.

The responses of European Robins to the magnetic pulse differed markedly from the ones observed in Silvereyes. Birds of the latter species had shown an initial 90° clockwise deviation and had returned to their original heading roughly within one week (Wiltschko et al. 1994). Robins, in contrast, exhibited individually different responses, and their behavior remained constant at least over the next three weeks. The fact that the headings of the first two tests lie nominally about 90° clockwise from the mean of controls, and thus seem to suggest a parallel to the deviation observed in Silvereyes, does not mean very much in view of the very short vectors (comp. Table 3). However, it is interesting to note that two birds which were significantly oriented before and after the pulse (R 31 and R 32, comp. Table 4) showed a roughly + 90° shift.

Treatments acting on different mechanisms?

As in the previous studies with Silvereyes, long wavelength light as well as a strong magnetic pulse affected migratory orientation. This indicates that both treatments interfere with magnetoreception, but the nature of this interference is different. Lights of different wavelengths would solely influence light-dependent processes. Hence the disoriented behavior observed under red light points out a light-dependent magnetoreception mechanism, suggesting that light of 633 nm wavelength may not be sufficient to elicit the processes required for detecting magnetic fields. Electrophysiological responses from the nBOR and the tectum opticum (Semm et al. 1984: Semm and Demaine 1986) as well as behavioral studies (Wiltschko and Wiltschko 1981; Phillips and Borland 1992) indicate that light-dependent processes mediate compass information. The homogeneous response under red light is in agreement with a compass effect; in this respect, our findings are in accordance with the current model.

The individual differences in behavior after treatment with the magnetic pulse are more difficult to explain. The pulse was designed to alter the magnetization of single domain magnetite particles as they were found in the ethmoid region of birds (Beason and Nichols 1984: Beason 1969); thus the fact that there was a change in behavior is in agreement with the magnetite-hypothesis. The specific nature of the effect is unclear, however. The robins were not disoriented after treatment, but preferred individually different directions. The majority of birds produced significant vectors. This argues against a non-specific effect.

Considerations on the question what part of the orientation system – the 'map' or the compass – was affected may start from the assumption that birds on migration mainly rely on innate directional information (see Helbig 1991, 1992 for details). In this case, the 'map' would not be involved. Yet attempts to explain the effect of the pulse as an interference with compass orientation meets certain problems. A magnetite-based compass is not consistent with what is known about the magnetic compass of birds, which is an inclination compass based on the axial course of the field lines (Wiltschko and Wiltschko 1972). Normally, particles can be magnetized only along their long axis; hence any change must be expected to reverse their magnetization. It is unclear how this should affect a mechanism which ignores the polarity of the magnetic field anyhow. Also, a compass response would not be expected to be different among individuals.

This leaves an effect on magnetic components of the 'map'. Since the tests were performed during spring migratory restlessness, the birds were heading towards their breeding area. Young birds possess some 'map' of their home region, acquired during the period between fledging and the onset of migration (Löhrl 1959; Sokolov et al. 1984). On return migration to the familiar breeding ground, navigational processes play an important role (Perdeck 1974, 1983). Thus an effect on a magnetic 'map' seems to be possible, with the pulse maybe simulating some kind of 'displacement'.

Attributing the effect of the pulse to some interference with the navigational 'map' provides an explanation for the diversity of responses observed in European Robins as well as for the differences between robins and Silvereyes. Since our experimental birds had been caught as transmigrants, their background and the extent of their previous spatial experience is not known. Especially their familiarity with 'map' factors at the test site would depend on the length of stay in the region before they were captured; hence it may vary considerably between individuals. In view of this, the diversity of responses to the pulse treatment might reflect individual differences in the development and the size of the 'map', in particular, to what extent the navigational factors of the test site were included. The Silvereyes previously tested, in contrast, had all been caught and tested in their wintering area (Wiltschko et al. 1994). This makes their experience more similar among each other and thus may have led to the more homogeneous response.

A final note of caution: all interpretations of our findings must remain tentative as long as details on the processes of magnetoreception are largely unknown. Light of different wavelengths would only affect mechanisms based on photopigments; in case of the magnetic pulse, however, the situation is more complex. We do not know what side-effects the treatment might have. None of the other postulated magnetic transducer mechanisms would be expected to show effects lasting longer than the treatment; hence after-effects per se might be taken to indicate magnetite-based receptors. Yet effects of a different nature cannot be entirely excluded. For example, in pigeons, short-term after-effects of alternating fields were described (e.g. Papi et al. 1983; Ioalè and Teyssèdre 1989). These effects are still unexplained as the applied fields were too weak to affect the magnetization of magnetite particles; their clear correlation with the frequency of the applied field, on the other hand, argues against mere non-specific effects (see Wiltschko and Wiltschko 1988 for discussion). In view of this, the possibility that the magnetic pulse affected a non-magnetite-based receptor, even if it appears rather unlikely, cannot be completely ruled out.

At the moment, it cannot yet be finally decided whether the two treatments applied – long wavelength light and a strong magnetic pulse – affect different orientation mechanisms, like compass and 'map', or whether they affect different components of one complex mechanism. However, it should be possible to decide whether or not the 'map' is involved – for example, by testing handraised young birds, i.e., birds which have never flown freely and thus had little opportunity to establish a 'map'.

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