Light-dependent magnetoreception in birds: the behaviour of European robins, *Erithacus rubecula*, under monochromatic light of various wavelengths and intensities

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Summary

To investigate how magnetoreception is affected by the wavelength and intensity of light, we tested European robins, *Erithacus rubecula*, under monochromatic lights of various wavelengths at two intensities using oriented behaviour as an indicator of whether the birds could derive directional information from the geomagnetic field. At a quantal flux of 7×10^{15} quanta s^{-1} m^{-2}, the birds were well oriented in their migratory direction east of North under 424 nm blue, 510 nm turquoise and 565 nm green light, whereas they were disoriented under 590 nm yellow light. Increasing the intensity of light at the same wavelengths more than sixfold to 43×10^{15} quanta s^{-1} m^{-2} resulted in a change in behaviour: under bright blue and green light, the birds now showed a preference for the East–West axis, with the majority of headings at the western end; under bright turquoise light, they oriented unimodally towards a direction slightly west of North. Under bright yellow light, the birds continued to be disoriented.

These findings suggest a rather complex relationship between the receptors involved in magnetoreception. Magnetoreception appears to follow rules that are different from those of vision, suggesting that light-dependent magnetoreception may involve receptors and neuronal pathways of its own.

Key words: magnetic compass, magnetoreception, radical-pair mechanism, photopigment, migratory orientation, European robin, *Erithacus rubecula*.

Introduction

A current hypothesis of avian magnetoreception proposes that magnetic compass information is mediated by a radical-pair mechanism. This model, first suggested by Schulten et al. (Schulten et al., 1978), assumes that macromolecules are raised by photon absorption to excited singlet states, at which radical pairs are generated. By hyperfine interactions, singlet pairs may be converted into triplet pairs, with the yield depending on the alignment of the macromolecules to the axis of the magnetic field lines. Since triplet products are different from singlet products, they could be used to detect the triplet yield and, as a consequence, could indicate the direction of the magnetic field if the triplet yields obtained in different directions are compared (Schulten and Windemuth, 1986; Ritz et al., 2000). Because of their hemispherical shape, with photopigments oriented in various spatial directions, the eyes have been favoured as the location of magnetoreception. The processes leading to magnetoreception would result in characteristic patterns that are symmetrical to magnetic North and South (for details, see Ritz et al., 2000), and birds could obtain directional information by simultaneously sampling and integrating the output of numerous receptors spaced out across the retina.

Because the initial step in magnetoreception is assumed to be photon absorption, magnetoreception should be light-dependent. Behavioural experiments using migratory orientation as a criterion of a bird's ability to derive directional information from the geomagnetic field showed that this is indeed the case. Migratory species, such as Australian silvereyes, *Zosterops l. lateralis* (Zosteropidae), European robins, *Erithacus rubecula* (Turdidae), and garden warblers, *Sylvia borin* (Sylviidae), were well oriented under monochromatic 443 nm blue and 565 nm green light, whereas they were disoriented under 590 nm yellow and 630 nm red light (W. Wiltschko et al., 1993; W. Wiltschko and Wiltschko, 1995; W. Wiltschko and Wiltschko, 1999; Rappl et al., 2000). Experiments with young homing pigeons suggest a similar relationship between the wavelength of light and the ability to obtain directional information from the magnetic field (R. Wiltschko and Wiltschko, 1998). In summary, the available data indicate that light from the blue-green part of the visual spectrum is required for magnetoreception in birds.

Recent tests, however, have indicated a more complex relationship between the wavelength of light and

magnetoreception than originally assumed. So far, birds had been tested under monochromatic light at fairly low intensities, with a quantal flux in the range of 6×10^{15} to 9×10^{15} quanta s^{-1} m^{-2}. Australian silvereyes tested under 565 nm green light with an intensity of 22×10^{15} quanta s^{-1} m^{-2} were also well oriented in their seasonally appropriate northerly migratory direction. At an intensity of 44×10^{15} quanta s^{-1} m^{-2}, however, they showed a pronounced northwesterly tendency that was also observed in birds migrating southwards (W. Wiltschko et al., 2000a; W. Wiltschko et al., 2000b). The northwesterly tendency was therefore independent of the migratory direction. It appears to be a fixed response; its nature and significance are unclear.

For a meaningful interpretation of these findings, it seemed important to learn more about the response of birds to monochromatic light of higher intensities at this and other wavelengths. Here, we report first results of a series of such tests with European robins.

Materials and methods

The experiments were performed in Frankfurt a.M. (50°08′N, 8°40′E) from 11 January to 13 February 1999; three test conditions were repeated with different birds from 10 January to 16 February 2000.

Test birds

The test birds were 12 European robins, *Erithacus rubecula* (Turdidae), in both 1999 and 2000. Juveniles born the same year (see Svensson, 1975) had been mist-netted during the autumn migration in September and October 1998 and 1999. They were kept indoors in individual cages with a photoperiod that simulated the gradual decrease in day length at Frankfurt a.M. until L:D 8 h:16 h was reached at the beginning of December. After New Year, the photoperiod was increased to L:D 13 h:11 h, a treatment that advances the robins' annual cycle so that they were exhibiting Zugunruhe a few days later, when testing began.

Test conditions

All tests took place in wooden huts in the garden of the Zoological Institute in the local geomagnetic field (magnetic North, mN=360°, 46 000 nT, 66° inclination).

We used light of four colours: blue, turquoise, green and yellow (Table 1). Green and yellow were produced by the same light-emitting diodes (LEDs) used in earlier tests (W. Wiltschko et al., 1993; W. Wiltschko and Wiltschko, 1999; Rappl et al., 2000). Blue and turquoise were also produced by LEDs; blue, at 424 nm, had a shorter wavelength than the previously used 443 nm blue light produced by a filter (see W. Wiltschko et al., 1993). The lights of four colours were adjusted to be of equal quantal flux and were presented at two intensities: the lower intensity (B, T, G, Y), at approximately 7×10^{15} quanta s^{-1} m^{-2}, was similar to that used in our previous studies with European robins (W. Wiltschko and Wiltschko, 1995; W. Wiltschko and Wiltschko, 1999), while the higher intensity (the 'bright' colours BX, TX, GX, YX),

Table 1. *Test lights used in this study*

Colour	Peak wavelength (nm)	$-\lambda/2, +\lambda/2$ (nm)
Blue	424	403, 459
Turquoise	510	492, 529
Green	565	553, 583
Yellow	590	571, 604

λ, wavelength.

at 43×10^{15} quanta s^{-1} m^{-2}, corresponded approximately to the quantal flux of the XL condition in the studies with Australian silvereyes (W. Wiltschko et al., 2000a; W. Wiltschko et al., 2000b).

In 1999, all birds were tested under these eight test conditions in a pseudo-random sequence until they had produced three evaluable recordings in each. In 2000, the tests under green G, turquoise T and bright turquoise TX were repeated under the same protocol, these tests alternating with tests belonging to a different series. The tests under 565 nm green at 7×10^{15} quanta s^{-1} m^{-2}, in which the birds had always shown excellent orientation in their migratory direction, served as control condition, providing the reference with which the behaviour in the other conditions was compared.

Test apparatus and performance

Orientation behaviour was recorded in funnel cages (Emlen and Emlen, 1966) lined with typewriter correction paper (BIC, Germany; formerly Tipp-Ex), where the birds were tested one at a time (see W. Wiltschko et al., 1993). Each funnel cage was placed in an aluminium cylinder the top of which consisted of the plastic disk carrying the LEDs. The blue, green and yellow test lights were produced by 24 LEDs, mounted in three sets of eight on a disk. The turquoise LEDs were brighter, so only four were used. The light passed through at least two sets of diffusers before it reached the bird. There were four such test units for each colour. The intensity of light was altered by varying the current, the numbers of LEDs activated and/or the number of diffusers. The light intensity in the test cages was measured as irradiance using an Optometer P9710-1 (Gigahertz-Optik, Puchheim, Germany) with the radiometric probe 'Visible' RW-3703-2, a silicium photoelement for the wavelength range 400–800 nm.

Recording began in the evening at about the time when the light went off in the housing cages and lasted for approximately 75 min. When active, the birds left scratch marks on the coating of the inclined walls that documented the distribution of their activity.

Data analysis

After removal from the cage, the coated paper was divided into 24 sectors, and the scratch marks in each sector were counted. Recordings with a total of fewer than 35 scratches were excluded from the analysis because of too little activity (for details, see W. Wiltschko and Wiltschko, 1995).

From the distribution of the activity within the cage, the heading and the concentration of the respective test were calculated. From the three headings of each bird under each condition, we calculated, by vector addition, the mean vector of that bird, with direction α_b and length $\mathbf{r}_b$. The mean directions α_b of the 12 or 24 birds tested made up the grand mean vector for each condition, with direction α_N and length $\mathbf{r}_N$. The grand mean vectors were tested by the Rayleigh test for directional preferences. The orientation in the various conditions was compared by the Mardia–Watson–Wheeler test indicating differences in distribution (Batschelet, 1981).

For two conditions, bright blue BX and bright green GX, this procedure proved inadequate because the headings of the tests were axially distributed, as is indicated by the significant axial vectors calculated from the first, second and third tests of each bird (see Table 5). We therefore modified the analysis and applied the procedures used by Weindler et al. (Weindler et al., 1995): for each bird in BX and GX, we calculated the unimodal vector and, by doubling the angles, the bimodal vector. If the bimodal vector lengths exceeded the unimodal vector by at least 0.1, the bird's behaviour was considered to be axial, and the preferred end of the axis (i.e. the side where two of the three headings lay) was entered into the calculation of the grand mean vector, which was also calculated as a preferred axis by doubling the angles (see Batschelet, 1981).

For activity level m_i (number of scratches) and concentration

a_i, medians were determined. The medians of activity and concentration as well as the vector lengths $\mathbf{r}_b$ per bird were compared with the data of the control condition green G using the Wilcoxon test for matched pairs of data. The same test was also applied to test for a directional shift between TX and G and T.

Results and discussion

Table 2 and Table 3 give the individual birds' vectors under the various test conditions, and Table 4 presents the medians of activity, concentration and vector length per bird, together with the grand mean vectors.

The amount of activity m_i and the distribution of this activity within the cage, as indicated by the concentration a_I, were similar under all eight test conditions; there was no difference from the respective control data in any of the test conditions ($P>0.05$, Wilcoxon test).

Orientation under the blue-green part of the spectrum at lower intensities

The orientation behaviour under a quantal flux of 7×10^{15} quanta s^{-1} m^{-2} (Fig. 1A–C) was in agreement with the results of previous studies in showing seasonally appropriate migratory orientation under light from the blue and green parts of the spectrum. The good orientation under 424 nm blue light
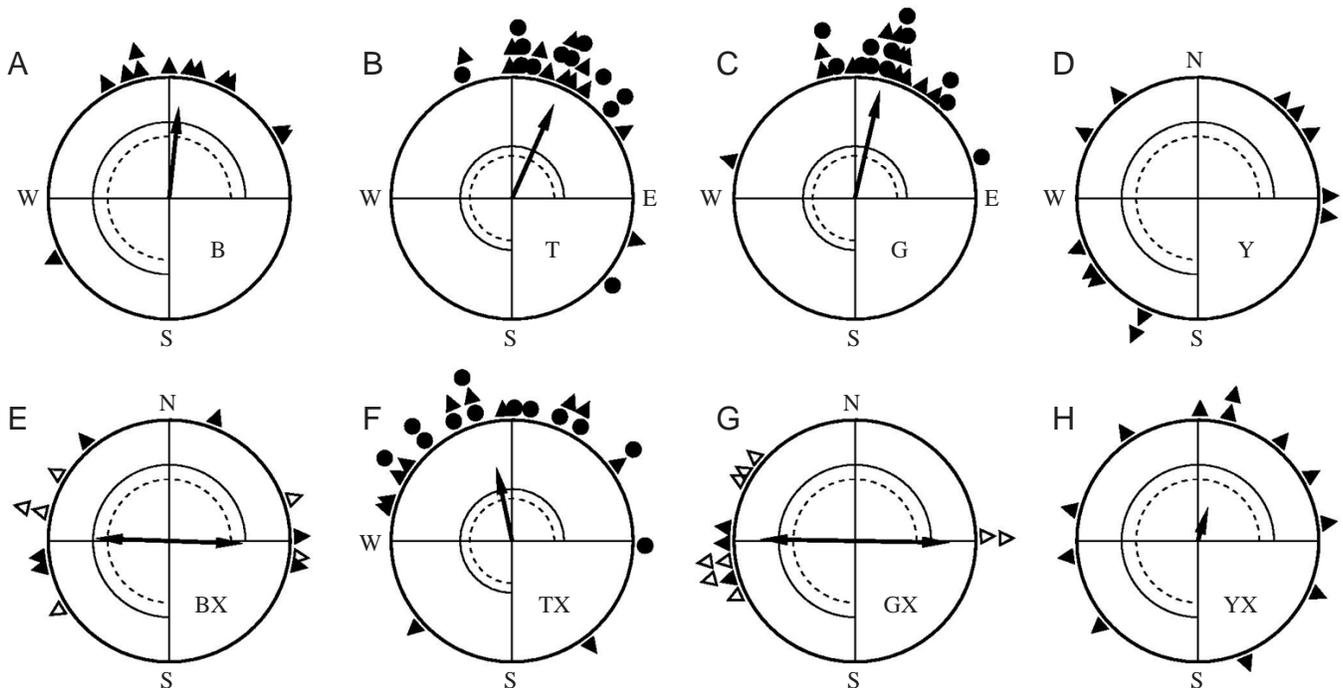

Fig. 1. Orientation behaviour of European robins under monochromatic light of the following wavelengths: (A,E) 424 nm blue; (B,F) 510 nm turquoise; (C,G) 565 nm green; (D,H) 590 nm yellow. (A–D) Quantal flux of 7×10^{15} quanta s^{-1} m^{-2}; (E–H) 'bright' lights, quantal flux of 43×10^{15} quanta s^{-1} m^{-2}. The symbols at the periphery of the circle indicate the mean headings of individual birds. Filled symbols, unimodal means; open symbols, preferred end of an axis (E,G); triangles, data from 1999; circles, data from 2000. The arrow represents the grand mean vector proportional to the radius of the circle. The two inner circles mark the 5 % (broken line) and the 1 % (solid line) significance border of the Rayleigh test (Batschelet, 1981). For numerical data, see Table 2, Table 3 and Table 4. B, blue light; T, turquoise light; G, green light; Y, yellow light; X, bright light.

Table 2. *Orientation behaviour of individual birds (data from spring 1999)*

	Blue (424 nm)		Turquoise (510 nm)		Green (565 nm)		Yellow (590 nm)	
Bird	α (degrees)	r	α (degrees)	r	α (degrees)	r	α (degrees)	r
Quantal flux 7×10^{15} quanta s^{-1} m^{-2}								
R 99-1	341	0.93	29	0.85	20	0.89	205	0.31
R 99-2	242	0.58	359	0.77	38	0.98	300	0.49
R 99-3	346	0.92	21	0.50	19	0.75	98	0.49
R 99-4	13	0.98	24	0.81	18	0.99	49	0.32
R 99-5	331	0.93	16	0.33	11	1.00	231	0.48
R 99-6	61	0.77	341	0.77	31	0.97	41	0.90
R 99-7	25	0.80	109	0.72	346	0.86	247	0.89
R 99-8	9	0.97	11	0.95	347	0.70	205	0.83
R 99-9	347	0.81	59	0.74	15	0.60	322	0.55
R 99-10	59	0.77	34	0.92	23	0.92	84	0.57
R 99-11	360	0.83	360	0.90	359	0.34	60	0.96
R 99-12	30	0.87	27	0.92	287	0.80	235	0.84
Quantal flux 43×10^{15} quanta s^{-1} m^{-2} (bright colours)								
R 99-1	238	0.99[a]	306	0.82	310	0.48[a]	82	0.52
R 99-2	71	0.87[a]	29	0.95	253	0.90	14	0.98
R 99-3	97	0.99[a]	288	0.38	276	0.69	14	0.30
R 99-4	88	0.90	300	0.29	255	0.77[a]	40	0.49
R 99-5	320	0.95	23	0.53	298	0.77[a]	60	0.49
R 99-6	258	0.92	54	0.41	302	0.76[a]	284	0.83
R 99-7	21	0.39	336	0.44	269	0.96	263	0.55
R 99-8	101	0.90	228	0.35	262	0.94[a]	326	0.91
R 99-9	283	0.96[a]	143	0.83	89	0.87[a]	158	0.43
R 99-10	301	0.65[a]	344	0.42	88	0.80[a]	1	0.31
R 99-11	263	0.96	356	0.76	245	0.86[a]	229	0.28
R 99-12	283	0.85[a]	285	0.60	261	0.80[a]	114	0.69

α, r, direction and length of mean vector calculated from three recordings each.
[a]Axial behaviour: preferred end of the axis and axial vector length.

Table 3. *Orientation behaviour of individual birds (data from spring 2000)*

Quantal flux (quanta s^{-1} m^{-2})	Green (565 nm) 7×10^{15}		Turquoise (510 nm) 7×10^{15}		Bright turquoise (510 nm) 43×10^{15}	
Bird	α (degrees)	r	α (degrees)	r	α (degrees)	r
R 00-1	16	0.86	37	0.90	53	0.72
R 00-2	39	0.56	23	0.96	21	0.21
R 00-3	14	0.40	19	0.74	319	0.94
R 00-4	18	0.99	48	0.75	1	0.94
R 00-5	349	0.83	4	0.71	334	0.61
R 00-6	7	0.98	131	0.85	8	0.74
R 00-7	14	0.86	4	0.82	344	0.66
R 00-8	6	0.94	9	0.85	343	0.94
R 00-9	352	0.95	48	0.60	303	0.73
R 00-10	3	1.00	25	0.89	31	0.74
R 00-11	72	0.56	2	0.65	319	0.51
R 00-12	44	0.81	344	0.31	92	0.76

α, r, direction and length of mean vector calculated from three recordings each.

Table 4. *Orientation behaviour of European robins under light of different wavelengths and intensities*

Colour	Wavelength (nm)	N	m_i	a_i	r_b	α_N (degrees)	r_N	ΔC
Quantal flux 7×10^{15} quanta s^{-1} m^{-2}								
Blue	424	12	154	0.24	0.86	6	0.76***	NS
Turquoise	510	24	141	0.34	0.79	24	0.85***	NS
Green (C)	565	24	165	0.28	0.86	13	0.91***	C
Yellow	590	12	208	0.22	0.56	247	0.05^{NS}	***
Quantal flux 43×10^{15} quanta s^{-1} m^{-2}								
Bright blue	424	12	166	0.38	0.91	272–92	0.61*	***
Bright turquoise	510	24	155	0.32	0.69	348	0.62***	***
Bright green	565	12	156	0.35	0.80	271–91	0.78**	***
Bright yellow	590	12	182	0.27	0.51	17	0.29^{NS}	*

N, number of test birds.

m_i, a_i, median number of scratches and median concentration of the recordings.

r_b, median vector length of individual birds.

α_N, r_N, direction and length or axial directions and axial vector length of grand mean vectors, respectively; asterisks indicate significance by the Rayleigh test.

ΔC, statistical differences from the green control are indicated by asterisks: *$P<0.05$; **$P<0.01$; ***$P<0.001$; NS, not significant.

enlarges the known wavelength range in which magnetic orientation is possible by approximately 20 nm towards the short-wavelength end, and the equally well oriented behaviour observed under 510 nm turquoise light bridges the 120 nm gap between the blue and green wavelengths used previously. The birds' mean headings under blue, turquoise and green did not differ from each other. This was true for the long vectors of the individual birds, with medians between 0.79 and 0.86 (see Table 4), which reflect the high consistency of their directional choices ($P>0.05$, Wilcoxon test). Apparently, the entire wavelength range from 424 to 565 nm allows birds to obtain directional information from the geomagnetic field with similar ease.

Table 5. *Orientation behaviour under bright blue and bright green light of 43×10^{15} quanta s^{-1} m^{-2}*

		Unimodal		Axial	
	n	α_1 (degrees)	r_1	α_2–α_2 (degrees)	r_2
Bright blue (424 nm)					
First tests	12	244	0.34^{NS}	272–92	0.70**
Second tests	12	44	0.06^{NS}	266–86	0.40^{NS}
Third tests	12	10	0.32^{NS}	278–98	0.67**
Bright green (565 nm)					
First tests	12	284	0.40^{NS}	282–102	0.52*
Second tests	12	255	0.11^{NS}	265–85	0.58*
Third tests	12	253	0.44^{NS}	266–86	0.67**

n, number of tests.

α_1, r_1, direction and length of unimodal vector.

α_2–α_2, r_2, directions and length of axial vector.

Asterisks at vector length indicate significance by the Rayleigh test: *$P<0.05$; **$P<0.01$; NS, not significant.

Orientation under the blue-green part of the spectrum at higher intensities

In tests under light of the same wavelengths at 43×10^{15} quanta s^{-1} m^{-2}, i.e. at more than six times the quantal flux as under blue, turquoise and green light described above, the birds' behaviour was significantly different from that under the same wavelengths at the lower flux.

Under bright blue BX and bright green GX, the birds showed axial responses (Fig. 1E,G). This becomes obvious when the unimodal and axial vectors of the first, second and third tests of each bird are compared (Table 5). To take the axiality into account, we calculated the birds' individual vectors in the modified way described in the Materials and methods section. In more than half the cases (six in BX and nine in GX), the bird's axial vector was considerably longer than the corresponding unimodal vector, which means that the headings are axially distributed, with two of the three headings at one end of the axis and the third at the other. These birds are marked with 'a' in Table 2. It is unclear, however, whether the longer unimodal vectors of the other birds involve truly unimodal responses because only one of the 12 birds had longer unimodal vectors in both bright blue and bright green light (see Table 2). With only three headings per bird, axiality might not always become obvious. It is possible that all the birds would have produced axial distributions of headings if we had recorded them more often.

Under both bright blue and bright green light, the preferred axes ran East–West, with the majority of headings in the West. Because the migratory direction lies so close to North, it is unclear whether the observed axes are perpendicular to the migratory direction or whether they represent a preference for the (magnetic) East–West axis. The closeness of their ends to East and West, however, suggests the latter. The distributions of headings under bright blue and bright green light were

similar (*P*>0.05, Mardia–Watson–Wheeler test) and significantly different from the distributions under blue and green light (*P*<0.001, both conditions). With medians of 0.91 in bright blue and 0.80 in bright green light, the vector lengths of the individual birds did not differ from those recorded under the control condition green (*P*>0.05, Wilcoxon test), with the axial vectors no shorter than the unimodal vectors (see Table 2).

The intermediate wavelength of 510 nm at bright turquoise TX caused a significantly different (*P*<0.05 compared with BX, *P*<0.01 compared with GX) unimodal preference for a direction slightly west of North (Fig. 1F). As the data from 1999 alone were barely significant, with a vector length of 0.51 towards 333°, we repeated the tests with 12 more birds in 2000, which produced a vector of 0.77 towards 358°. The distribution of the pooled mean headings under bright turquoise was significantly different from that of the control condition green (see Table 4) as well as from that of turquoise (*P*<0.01). Most of this difference is attributable to increased scatter, reflected by the shorter length of the grand mean vector. This, together with the shorter vectors of the individual birds with a median of 0.69, suggests that the birds might have had certain problems with determining directions under this condition.

The interpretation of the behaviour under bright turquoise light is not entirely clear. In both years, the mean direction lies west of the mean heading under green (1999, 8°; 2000, 17°) and turquoise (1999 and 2000, 24°) light. It might represent a preference for the normal spring migratory direction, as was found under green light, but with more scatter so that the mean by chance lies a bit more to the west. However, the mean heading of 17 of the 24 birds lies west of that recorded under green and turquoise light (*P*<0.05, Wilcoxon test). Possibly, the birds preferred a different, more westerly, direction, which may mean that the type of response had changed.

The response of the robins under monochromatic light from the blue-green part of the spectrum at 43×10^{15} quanta s^{-1} m^{-2} was thus not uniform. This implies that the input produced by a narrow band of bright turquoise light in the centre of this range is qualitatively different from that produced by a similarly narrow band of bright blue or bright green light towards the limits of this range, while the input produced by the latter two, judging by the birds' response, appears to be similar. Whether the behaviour of robins under the higher intensities represents fixed responses, such as that described for silvereyes under green light with an intensity of 44×10^{15} quanta s^{-1} m^{-2} (W. Wiltschko et al., 2000a; W. Wiltschko et al., 2000b), is still unclear. The orientation along the East–West axis under bright blue and bright green light shows some resemblance to an alignment response, in contrast to the unimodal, if scattered, preference for slightly west of North observed under bright turquoise light, which cannot yet be classified.

Orientation under 590 nm yellow light

Under 590 nm yellow light, the birds were disoriented at both intensities (Fig. 1D,H). The distributions of headings under yellow and bright yellow did not differ from each other (*P*>0.05, Mardia–Watson–Wheeler test), but both were significantly different from that recorded under control green light (see Table 4). At only 0.56 and 0.51, the median vector lengths of the individual birds under yellow and bright yellow light, respectively, were considerably shorter than those under blue, turquoise and green light. This, too, indicates that the birds were not able to use their magnetic compass properly for identifying their migratory direction when only yellow light was available.

The transition from well-oriented behaviour under 565 nm green light to disoriented behaviour under 590 nm yellow light at intensities of 7×10^{15} quanta s^{-1} m^{-2} confirms an earlier finding (W. Wiltschko and Wiltschko, 1999). This transition is surprisingly abrupt, as the peak wavelength is shifted by only 25 nm and the wavelengths of the two types of LEDs overlap to some extent (see fig. 1 in W. Wiltschko and Wiltschko, 1999). Raising the light level more than sixfold did not alter the response under yellow light: the birds were still disoriented. This implies that disorientation observed under yellow light at 7×10^{15} quanta s^{-1} m^{-2} does not result simply from the stimulus being below threshold, but has other causes.

General discussion

Changes in magnetic orientation caused by different light regimes are also known in amphibians. Phillips and Borland (Phillips and Borland, 1992; Phillips and Borland, 1994) described a wavelength-dependent shift: shoreward-orienting salamanders showed normal orientation up to 450 nm blue light and a counterclockwise shift in direction from 500 nm turquoise onwards. Interestingly, most tests involved light levels of 45×10^{15} quanta s^{-1} m^{-2}, similar to our higher intensity. Since the salamanders have not yet been tested at lower intensities, it must remain open whether their shift in direction is in any way related to the intensity-dependent changes in behaviour we observe in birds. The conditions under which the respective changes are recorded, however, do not support such an assumption, and the simple physiological model proposed by Phillips and Borland (Phillips and Borland, 1992) to explain the wavelength-dependent shift in salamanders (see also Deutschlander et al., 1999b) does not seem to explain our findings with birds adequately. Furthermore, there are fundamental differences concerning the site of magnetoreception between the two groups. A study by Deutschlander et al. (Deutschlander et al., 1999a) showed that magnetic orientation in salamanders is mediated by extraocular receptors, probably located in the pineal gland, whereas the available evidence suggests that avian magnetoreceptors are associated with the eyes (Semm et al., 1984; Semm and Demaine, 1986; Schneider et al., 1994). Hence, magnetoreception in birds and amphibians, although both based on light-dependent processes, appears to involve mechanisms that are rather different in their anatomical and functional details.

Why an increase in intensity should result in a change in

behaviour is difficult to explain. The light level used in the previous studies, between 2 and 4 mW m^{-2}, according to wavelength, was rather low, with an irradiance that occurs in nature during twilight more than 30 min after sunset. The irradiance of our 'bright' lights (GX, approximately 15 mW m^{-2}; BX, approximately 20 mW m^{-2}) corresponds to light levels found well after sunset. A group of robins, tested in 1999 in a parallel series under 'white' light of approximately 24 mW m^{-2}, was excellently oriented in their migratory direction (see Möller et al., 2001), although that intensity exceeds the 'bright' lights used in the present study. This clearly shows that it was not the light level itself that caused the birds to change their behaviour, but the fact that the bright light was monochromatic, consisting of a narrow band of wavelengths only.

The observed change in behaviour implies that the increase in intensity of the monochromatic lights led to a change in the quality of input. In the present situation, with hardly anything known about the photopigments, receptor types or neuronal network involved, we can only speculate about possible reasons. The normal orientation under light at an intensity of 7×10^{15} quanta s^{-1} m^{-2} suggests that one or more basic receptors provide appropriate magnetic information at this light level across the entire range of wavelengths from below 424 nm blue up to 565 nm green light. Other receptors that possibly modify the output of these receptors, or interactions between these receptors, do not become active at low light levels. However, light of a narrow band of wavelengths only, as presented in our tests, is a stimulus not found in nature – natural light is always more-or-less 'white', a combination of wavelengths from all parts of the visual spectrum. Of several receptors, monochromatic light would strongly activate one type, while other receptors that respond to other wavelengths would not be activated. This very unusual activation pattern of receptors might be tolerable as long as the level of activation of the active receptor remains low; at higher intensities, however, it may lead to an inbalance in input, which, for reasons yet unknown, appears to prevent the birds from deriving directional information from the magnetic field in the usual way.

Another possibility is that a receptor providing input to different channels at different light levels is involved. If this were the case, normal magnetoreception would be possible only within a limited intensity range, which appears highly unlikely. The light intensity presented under bright blue, bright turquoise and bright green light was still considerably lower than the intensity of the respective parts of the natural spectrum on a sunny day. For example, while bright green light was presented at 15 mW m^{-2}, the intensity within $\lambda/2$, where λ is wavelength, of our green light on a summer day well exceeds 3000 mW m^{-2}. The unimodal response under bright turquoise light, in contrast to the axial orientation under bright blue and bright green light, suggests that the quality of input from the narrow band of wavelengths near the centre of the range of magnetoreception is different from that of similarly narrow bands nearer the limits of that range. In all three conditions, the behaviour of our birds was non-random, but what exactly caused their specific behaviour under the 'bright' conditions is unclear.

When mentioning 'receptors' in connection with wavelength, as above, we do not necessarily mean the normal colour receptors of the avian visual system. The colour receptors have been thoroughly analyzed in only a few passerine species, among them the Pekin robin *Leiothrix lutea* (Timalidae), in which four types of cone with maxima at 370 nm (ultraviolet), 460 nm (blue), 530 nm (green) and 620 nm (red) have been identified by behavioural means (Maier, 1992). It seems reasonable to assume that the pigments and receptors in robins may be similar. In that case, our blue test lights lie between the peaks of the ultraviolet and the blue receptor, our turquoise light lies between the peaks of the blue and green receptors, and our green and yellow light both lie between the peaks of the green and red receptors. In short, there is no obvious relationship between the maxima of these receptors and the birds' ability to obtain directional information under the respective wavelengths. This is interesting because Ritz et al. (Ritz et al., 2000) discuss magnetoreception as a modulation of visual perception. Yet, although both vision and magnetoreception start out with light-dependent processes, there is no evidence so far for a direct link between them. The rods, with an absorption maximum at 500 nm (Maier and Bowmaker, 1993), would cover the entire range for which oriented behaviour has been recorded under low quantal flux, but the different responses under an intensity of 43×10^{15} quanta s^{-1} m^{-2} are difficult to interpret on the basis of one receptor only. Also, the abrupt transition from oriented behaviour to disorientation, with the wavelengths increasing by only 25 nm, is very different from the gradual decrease in receptor sensitivity with changing wavelengths that is known from photoreceptors in the visual system. When the birds were disoriented under low-intensity yellow light, a wavelength so close to green, one would expect that an increase in intensity might raise the light level above threshold, allowing the birds to regain their ability to orient. This was not the case, however. Here, too, some interaction between different receptors might be involved, and this might actively interfere with the processing of directional information.

Taken together, the responses of European robins to monochromatic lights of higher intensities suggest that the processes leading to magnetoreception, although they appear to be based on photopigments, involve receptors and follow rules that are distinctly different from those involved in the normal visual processes. This need not speak against the Ritz model, however. The basic ideas proposed by Ritz et al. (Ritz et al., 2000) would also apply to a system independent from vision, with receptors and a neuronal network of its own that share the retina with the photoreceptors of the visual system. The number of magnetoreceptors required might not be high, provided that they are spaced out evenly over the avian retina. Ritz et al. (Ritz et al., 2000) point out a possible role for the large displaced ganglion cells, because of their possible association with cryptochromes, a novel type of photopigment for vertebrates (see Cashmore et al., 1999). Being distributed

rather evenly across the retina, the displaced ganglion cells fulfil the important requirement of representing the various spatial directions, and they project into the nucleus of the basal optic root, where electrophysiological responses to changes in magnetic direction have already been recorded (Semm et al., 1984; Semm and Demaine, 1986), so that they might indeed be likely candidates. With respect to the light-dependent processes of avian magnetoreception, we can only hope that it will soon be possible to identify the various photopigments involved, their location and the possible interactions between the respective receptors.

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