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Magnetic compass orientation in European robins is dependent on both wavelength and intensity of light

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Summary

Magnetic compass orientation in birds has been shown to be light dependent. Results from behavioural studies indicate that magnetoreception capabilities are disrupted under light of peak wavelengths longer than 565 nm, and shifts in orientation have been observed at higher light intensities (43–44×10^{15} quanta s^{-1} m^{-2}). To investigate further the function of the avian magnetic compass with respect to wavelength and intensity of light, we carried out orientation cage experiments with juvenile European robins, caught during their first autumn migration, exposed to light of 560.5 nm (green), 567.5 nm (green-yellow) and 617 nm (red) wavelengths at three different intensities (1 mW m^{-2}, 5 mW m^{-2} and 10 mW m^{-2}). We used monochromatic light of a narrow wavelength range (half bandwidth of 9–11 nm, compared with half bandwidths ranging between 30 nm and 70 nm used in other studies) and were thereby able to examine the magnetoreception mechanism in the expected transition zone between oriented and disoriented behaviour around 565 nm in more detail. We show (1) that European robins show seasonally appropriate migratory directions under 560.5 nm light, (2) that they are completely disoriented under 567.5 nm light under a broad range of intensities, (3) that they are able to orient under 617 nm light of lower intensities, although into a direction shifted relative to the expected migratory one, and (4) that magnetoreception is intensity dependent, leading to disorientation under higher intensities. Our results support the hypothesis that birds possess a light-dependent magnetoreception system based on magnetically sensitive, antagonistically interacting spectral mechanisms, with at least one high-sensitive short-wavelength mechanism and one low-sensitive long-wavelength mechanism.

Key words: migratory orientation, magnetoreception, magnetic compass, European robin, *Erithacus rubecula*.

Introduction

Magnetic compass orientation of several animals has been shown to be wavelength dependent. So far, the orientation of fruit flies (*Drosophila melanogaster*), Eastern red-spotted newts (*Notophthalmus viridescens*), homing pigeons (*Columba livia domesticus*) and three species of passerine birds – European robins (*Erithacus rubecula*), Australian silvereyes (*Zosterops lateralis lateralis*) and garden warblers (*Sylvia borin*) – has been studied in behavioural experiments under different wavelengths of light (Phillips and Borland, 1992a; Phillips and Sayeed, 1993; Wiltschko et al., 1993; Wiltschko and Wiltschko, 1998, 2001; Deutschlander et al., 1999; Rappl et al., 2000). The wavelength-dependent magnetoreception system studied in most detail is the shoreward orientation of the Eastern red-spotted newt. It has been described as an axial compass mechanism using the inclination angle of the geomagnetic field as the geomagnetic component, with two antagonistic, magnetically sensitive spectral mechanisms suggested to be the underlying magnetoreception system (c.f. Phillips, 1986; Phillips and Borland, 1992a,b). Under short-wavelength light (≤450 nm), newts orient as expected towards a shoreline, but they shift their orientation by 90° relative to the shoreline under long-wavelength light (≥500 nm). When tested under light in the intermediate wavelength of 475 nm, the newts become disoriented (Phillips and Borland, 1992a,b; Deutschlander et al., 1999).

In birds, little is known about the number and possible interactions of the magnetoreception mechanisms. The orientation of birds has been studied under different wavelengths of light between 424 nm (blue) and 635 nm (red) and under different intensities ranging from 0.57×10^{15} quanta s^{-1} m^{-2} to 43×10^{15} quanta s^{-1} m^{-2} (full-spectrum light excluded; see Fig. 5). The experiments showed that both juvenile and adult birds of different species were disoriented under 590 nm (yellow) and 630 nm (red) light but oriented into the seasonally expected migratory directions under full-spectrum (white), 424 nm and 443 nm (blue), 510 nm (turquoise) and 565 nm (green) light (Wiltschko et al., 1993; Wiltschko and Wiltschko, 1995, 1999, 2001; Munro et al., 1997; Rappl et al., 2000). Young inexperienced pigeons were disoriented after being displaced under 630 nm light but oriented towards the home direction after being transported to the release site under 565 nm or full-spectrum light (Wiltschko

and Wiltschko, 1998). These results indicate that magnetoreception capabilities are disrupted under light of peak wavelengths longer than 565 nm. Light-dependent magnetoreception has also been shown to vary between different intensities of light of the same wavelength in the form of directional shifts under higher light intensities ($43–44\times10^{15}$ quanta s^{-1} m^{-2}; Wiltschko et al., 2000a,b; Wiltschko and Wiltschko, 2001). Australian silvereyes oriented during both spring and autumn migration towards NW under high-intensity 565 nm light (Wiltschko et al., 2000a,b). European robins that oriented towards the seasonally appropriate northerly directions under 424 nm, 510 nm and 565 nm light at low intensities (7×10^{15} quanta s^{-1} m^{-2}) in spring showed axial orientation into E–W directions at high light intensities ($43–44\times10^{15}$ quanta s^{-1} m^{-2}) under 424 nm and 565 nm light, but unimodal north-westerly directions under 510 nm light (Wiltschko and Wiltschko, 2001).

Three biophysical magnetoreception models have been proposed to explain the light dependence of the magnetic compass in animals. They all meet the necessary requirements for a magnetic inclination compass by showing axial rather than polar characteristics and by being insensitive to changes in magnetic intensity smaller than 10% of the geomagnetic field (Deutschlander et al., 1999). Leask's optical pumping model (Leask, 1977) is based on a double resonance process that involves the lowest excited triplet state of molecules such as rhodopsin in the retina. The high frequencies (MHz) required for a resonance process to occur probably do not exist in living systems and therefore Leask's model does not seem very likely (Phillips et al., 1999). Schulten (1982) demonstrated that an external magnetic field can influence photon-induced processes that involve bimolecular reactions. In this process, radical pairs are formed by photon excitation through light absorption similar to the photosynthetic reactions. Based on this theory, Schulten and Windemuth (1986) proposed a model for a biophysical magnetic compass with rhodopsin or iodopsin as likely organic reactants. The animals would perceive the magnetic field as an apparent variation in light intensity or colour in their visual field. Recently, this magnetic compass model was refined by Ritz et al. (2000) and a newly discovered class of photoreceptors, the cryptochromes, were proposed as the magnetosensors. It was shown theoretically that magnetic fields with intensities in the range of the geomagnetic field can produce a significant increase of the triplet yield, which also depends on the relative orientation between the magnetic field and the radical pairs (Ritz et al., 2000). Edmonds (1996) developed a model for a sensitive magnetic compass that detects magnetic field information optically through ferro(i)-magnetic crystals, such as magnetite, located in the oil droplets of the avian retina. According to his model, freely moving magnetite particles located in the oil droplets interact with large dye molecules such as β-carotene and align parallel to the geomagnetic field, letting light enter to specialized photoreceptors when the position of the bird's head is oriented parallel or antiparallel to the geomagnetic field lines (Edmonds, 1996).

To study the light dependence of the magnetic compass of passerine birds, we carried out orientation cage experiments with juvenile European robins exposed to 560.5 nm (green), 567.5 nm (green-yellow) and 617 nm (red) light at three different intensities (1 mW m^{-2}, 5 mW m^{-2} and 10 mW m^{-2}). We used lights with a half bandwidth (λ/2) of only 9–11 nm. These wavelength ranges were much narrower than the ones used in previous orientation studies on birds performed under monochromatic light (in other studies, λ/2 ranged from 30 nm to 70 nm). Thus, we could examine in more detail the function of the magnetoreception mechanism in the expected transition zone between oriented and disoriented behaviour around 565 nm light under three different intensities.

Materials and methods

Light equipment and orientation cages

We used two 1000 W ozone-free xenon arc lamps (model no. 6271; Oriel Instruments, Stratford, CT, USA) to produce full-spectrum and monochromatic light (see Fig. 1). From ultraviolet (UV; <350 nm) to above infrared (IR; >700 nm), xenon arc lamps emit light that closely matches the solar spectrum. From each lamp, the light first passed through a column of double-distilled water to reduce the intensity of IR light (>50% reduction above 900 nm). Thereafter, the light entered a trifurcated glass fibre bundle (model no. 77536; Oriel Instruments; <45% transmission below 400 nm, no transmission below 350 nm), which distributed it to the orientation cages. At the end of each of the six fibres, interference filters of different wavelengths (CVI; Oriel Instruments) filtered out all but a narrow bandwidth of light (λ/2=9–11 nm; see Table 1, Fig. 2). We used neutral density (ND) filters (Kodak Wratten 96 gelatine filters) placed in the filter holders at the end of the optic fibres and/or 1–4 opaque Plexiglas sheets placed upon the orientation cages to reduce light intensity. The filtered light always passed through at least one such opaque Plexiglas sheet before entering the orientation cages. The sheet acted as a diffuser and prevented the birds from seeing the light source as a point (see Fig. 1). All external lights were shielded off with wooden walls and black curtains attached to the walls and around the cages, so that no light other than that entering through the desired filters could reach the orientation cages. The xenon lamps were switched on at least 10 min before the birds were let into the orientation cages in order to guarantee that the spectrum and intensity of the emitted light was as homogenous as possible during the entire experiment.

An IL1700 Research Radiometer (International Light, Newburyport, MA, USA) with a detector SHD033 (range $3\times10^{-8}–1\times10^{-2}$ W m^{-2}, spectrum 200–1100 nm) was used to measure overhead light intensity inside the orientation cages, at the level of the birds' head in the middle of the orientation cage at 65 mm height, under the same number of opaque Plexiglas sheets as used during the experiment. The readings were recalculated into radiometric irradiance (mW m^{-2}) and photon quantities (photon irradiance: quanta s^{-1} m^{-2}, log quanta s^{-1} cm^{-2}) for each colour used (Table 1). The light

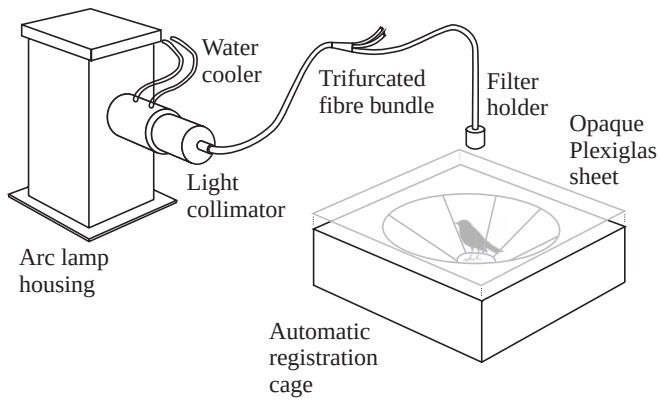

Fig. 1. Setup of the light equipment used in this study to produce full-spectrum and monochromatic light. We used two xenon arc lamps, each lamp distributing light to three orientation cages. The light first passed through a column of double-distilled water and then entered a trifurcated glass fibre bundle, at which end a filter holder contained interference filters and/or neutral density filters to produce monochromatic light and/or to reduce light intensity, respectively. Before entering the orientation cage, the filtered light passed through 1–4 opaque Plexiglas sheets that acted as diffusers and that were placed directly on the top of the orientation cage so that the birds could not see the light source as a point.

intensity was adjusted so that the lights inside the cages had approximately the same radiometric irradiance, regardless of wavelength and bandwidth. With a calibrated S2000 spectrometer (Ocean Optics Inc., Dunedin, FL, USA), we measured the spectrum of the full-spectrum and monochromatic light between 300 nm and 800 nm passing through one opaque Plexiglas sheet. In addition, we measured the full-spectrum light passing through differently strong ND filters and multiple layers of opaque Plexiglas sheets, but we could not find substantial deviations in the spectral composition between the various combinations of diffusers and/or ND filters.

We used six automatic, funnel-shaped registration cages (diameter 30 cm, height approximately 15 cm, overhead view 160°) with eight circularly arranged plates connected to micro-switches, which registered the birds' migratory activity (for one plate, only one activation per second was allowed; Fig. 1). These automatic registration cages give results comparable with data from experiments with funnel cages lined with typewriter correction paper (Emlen and Emlen, 1966) and have extensively been used in orientation experiments with passerine birds (e.g. Sandberg et al., 1988; Åkesson, 1993).

Experimental procedure

A total of 36 juvenile European robins (*Erithacus rubecula* Turdidae) was tested between the beginning of October and the beginning of November 2001. The birds were caught at Ottenby Bird Observatory (56° 12′ N, 16° 24′ E), Sweden during their first autumn migration and were transported to Stensoffa Ecological Field Station (55° 42′ N, 13° 25′ E), Southern Sweden. The birds were kept indoors in individual cages under the natural light regime, but without access to visual cues outdoors, for a maximum of 38 days. The birds were provided with mealworms and vitaminized water *ad libitum*. After an acclimation period of 3–6 days, in which the birds were allowed to adjust to living in a cage, we first recorded the birds' orientation behaviour between one and three times under full-spectrum light (W_{20} bc) at an irradiance of 79×10^{15} quanta s^{-1} m^{-2} (see Table 1) in order to let the birds accustom to the experimental situation. All experiments took place during the evening hours, with the first of a maximum

Table 1. *Properties of light in the orientation cages as experienced by juvenile European robins during the experiments*

Experiment	Peak (nm)	Half bandwidth (nm)	Range of half bandwidth (nm)	Irradiance (mW m^{-2})	Photon quantities ($\times10^{15}$ quanta s^{-1} m^{-2})	Photon quantities (log quanta s^{-1} cm^{-2})
W_1	764.0			1	3.9	11.6
W_{10}	764.0			10	39	12.6
W_{20}	764.0			20	79	12.9
G_1	560.5	9	555.5–564.5	1	2.9	11.5
G_5	560.5	9	555.5–564.5	5	14	12.2
G_{10}	560.5	9	555.5–564.5	10	29	12.5
GY_1	567.5	10	562.5–572.5	1	2.9	11.5
GY_5	567.5	10	562.5–572.5	5	14	12.1
GY_{10}	567.5	10	562.5–572.5	10	29	12.5
R_1	617.0	11	611.0–622.0	1	3.2	11.5
R_5	617.0	11	611.0–622.0	5	16	12.2
R_{10}	617.0	11	611.0–622.0	10	32	12.5

Intensities are given in radiometric irradiance (mW m^{-2}) and photon quantities (photon irradiance: quanta s^{-1} m^{-2}, log quanta s^{-1} cm^{-2}). The intensities that the birds experienced through the different colour filters correspond to natural light levels ranging from values measured at a sun elevation of approximately –2.5° below the horizon (1 mW m^{-2}) to values measured just before the end of civil twilight [sun elevation –6° below horizon, 10 mW m^{-2}; as estimated from spectral irradiance curves measured in nature during twilight (McFarland and Munz, 1975)]. See also Figs 2, 5.

W, full-spectrum light; G, green light; GY, green-yellow light; R, red light.

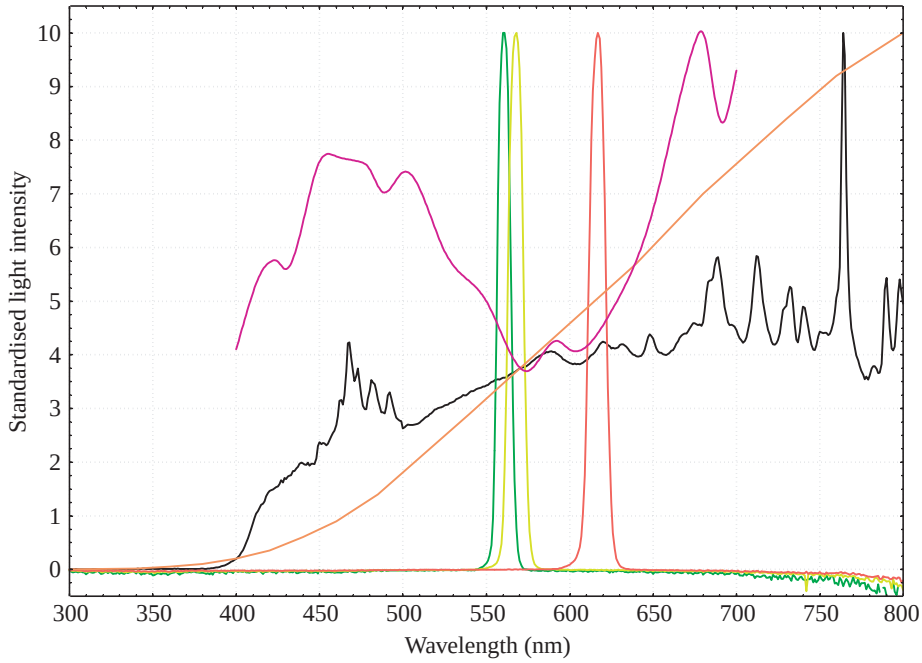

Fig. 2. Spectrometric measurements of the full-spectrum and monochromatic light used in the experiments, and the spectrum of an incandescent light bulb and the natural spectrum at sunset for comparison. The black line indicates the spectrum of the full-spectrum light. The dark green (560.5 nm), yellow-green (567.5 nm) and red (617 nm) lines indicate the spectrum of the monochromatic light as seen by the birds sitting under one opaque Plexiglas sheet. The composition of the measured full-spectrum light passing through neutral density filters of different transmissions and multiple layers of opaque Plexiglas sheets does not deviate substantially from the spectrum shown in black. For comparison, the orange line shows the spectrum of an incandescent light bulb, and the violet line shows the natural spectrum 14 min after sunset (reproduced from McFarland and Munz, 1975; 300–700 nm only). All spectra are standardised by taking the maximum value within the measured wavelength interval as 10.

of three groups starting approximately one hour before sunset. The birds were allowed an adjustment period of 5–10 min after being placed into the orientation cage, before their activity was registered during a period of 60 min. Each bird was tested only once per evening.

After the initial experiments under full-spectrum light, each bird was tested once under each colour and intensity (see Table 1), starting with 5 mW m^{-2} (14–16×10^{15} quanta s^{-1} m^{-2}), continuing with 10 mW m^{-2} (29–32×10^{15} quanta s^{-1} m^{-2}) and 1 mW m^{-2} (2.9–3.2×10^{15} quanta s^{-1} m^{-2}) and ending with a final experiment under 5 mW m^{-2}. The order of colours under which each individual bird was tested was random. Some individuals were tested twice under one experimental condition if the first experiment did not reveal a valid result, mainly due to low activity (see below for conditions). The control experiments under full-spectrum light at an irradiance of 3.9×10^{15} quanta s^{-1} m^{-2} (W_1), 79×10^{15} quanta s^{-1} m^{-2} (W_{20} ac) and 39×10^{15} quanta s^{-1} m^{-2} (W_{10}) were performed at the end of the experimental series in the given order. The experiments took place in the natural geomagnetic field of approximately 50 μT and an inclination of 70° (declination 1.5°; WMM 2000, 15 October 2001).

Statistical analyses

The registrations recorded in the orientation cages were analysed with standard procedures described by Batschelet (1981). For each active bird that activated the micro-switches at least 40 times, we calculated an individual mean direction (α) and an individual mean vector length (**r**). The mean direction was analysed for axiality by using the method of doubling the angles (Batschelet, 1981). If the axial mean vector length ($\mathbf{r}_2$) was larger than the unimodal vector (**r**), the experiment was considered axial and the end of the axis closer to the unimodal direction was included in further analyses. An experiment was considered to be valid when the individual mean vector length corresponded to **r**≥0.05. Only the first valid experiment per bird, colour and intensity was included in further analyses, so each individual was represented only once in each experimental group.

The mean direction of a group was analysed using circular statistics (Batschelet, 1981). Differences in directions between experimental groups were tested for significance using the one-way classification test ($F_{1,df}$; Mardia, 1972). Only groups with unimodal distributions significantly different from random according to the Rayleigh test were compared.

Statistical differences in mean number of registrations and mean individual vector length between the three colour experiments of the same intensity or the three intensities within one colour were analysed using the nonparametric Kruskal–Wallis test. Differences between proportions of valid experiments and unimodal *versus* axial individuals were analysed using the χ^2-test.

Results

The European robins showed a mean orientation towards the expected migratory direction in the southwest under 560.5 nm (green) light at the lowest intensity, G_1, axial orientation towards southwest–northeast under G_5 and almost significant axial orientation into the same directions under the highest intensity, G_{10} (Fig. 3, Table 2). Under 567.5 nm (green-yellow) light, the birds were disoriented as a group under all intensities. Under 617 nm (red) light, the birds oriented towards

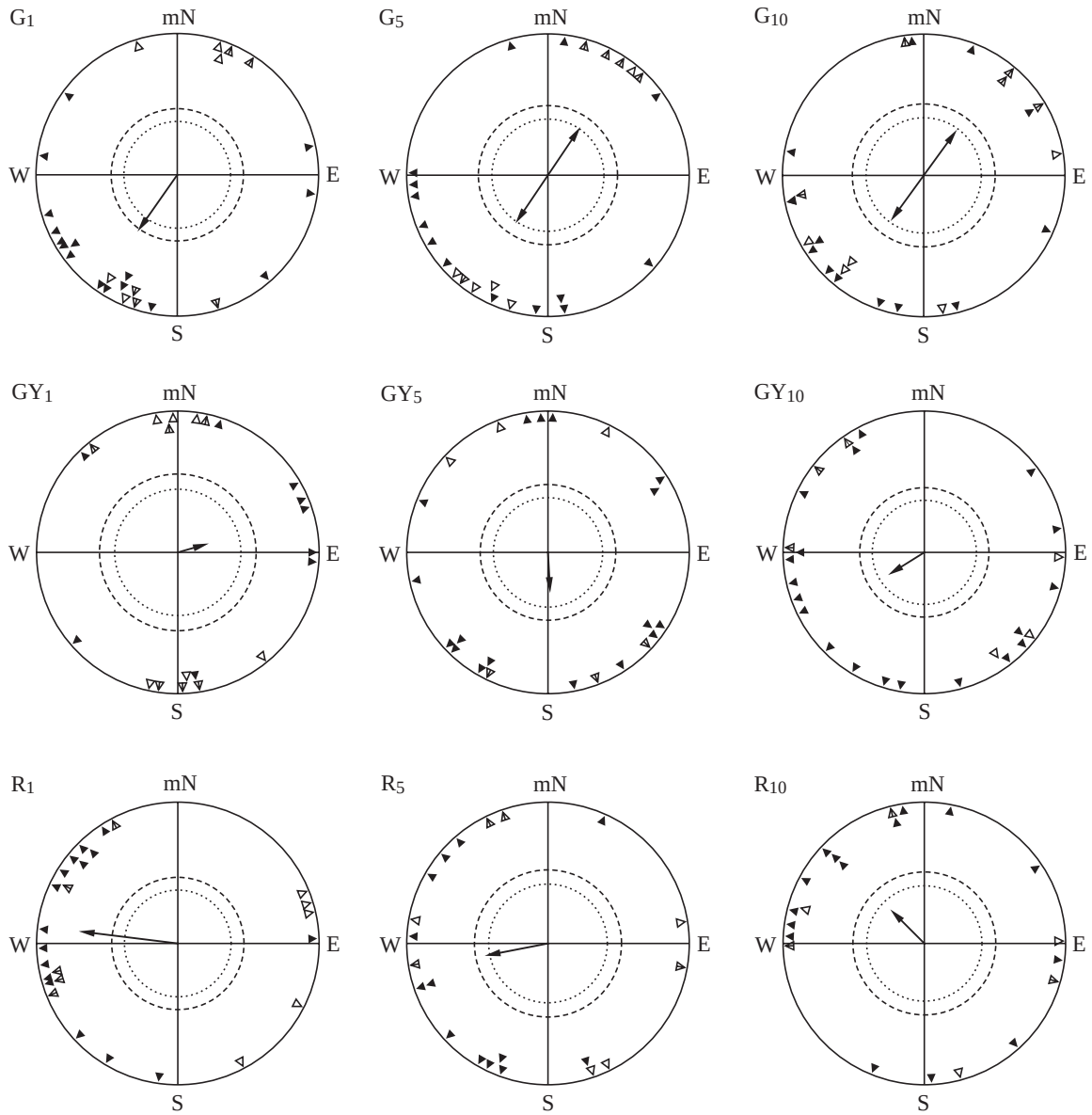

Fig. 3. Orientation behaviour of European robins tested under monochromatic light of different wavelengths and intensities (see Table 1 for details of wavelengths and intensities). Each triangle represents the heading of an individual bird. Filled triangles refer to unimodally directed individuals, and two open triangles denote axially distributed individuals (bisected triangles indicate the direction taken into account in the statistical analyses; unmarked, open triangles represent the other end of the axis). The arrows represent the mean orientation of the group and are drawn relative to the mean vector length (**r**). The inner broken circle gives the 5% significance level, and the outer broken circle gives the 1% significance level according to the Rayleigh test (Batschelet, 1981). See Table 2 for detailed statistical information. G, green light; GY, green-yellow light; R, red light; mN, magnetic north.

west in the lower two intensities, R_1 and R_5, and were disoriented under 32×10^{15} quanta s^{-1} m^{-2} (R_{10}). The westerly direction shown in R_1 was significantly different from the direction under G_1 ($F_{1,40}$=8.1, P=0.007), but R_5 was not different from G_1 ($F_{1,36}$=2.2, P=0.14). Neither the proportion of valid experiments, the mean number of registrations per individual, the mean individual vector lengths nor the percentage of axial individuals differed between the three colours or the three intensities (P>0.05 in all cases).

Under full-spectrum light, our European robins showed mean directions that were significantly different from random only in the first experiment performed before the colour experiments were carried out (W_{20} bc; Fig. 4; Table 2). The westerly direction was significantly different from the southwesterly direction observed under G_1 ($F_{1,48}$=5.3, P=0.026) but not from R_1 ($F_{1,48}$=0.04, P=0.85) or R_5 ($F_{1,44}$=0.6, P=0.46). When tested again under white light (after all colour experiments were performed), the birds' orientation was not significantly different from random. The birds were most active when tested the second time under the highest

Table 2. *Orientation experiments with juvenile European robins tested under different wavelengths and intensities of light during autumn migration*

Experiment	N	α–α_2 (deg.)	95% CI (deg.)	$\mathbf{r}$, $\mathbf{r}_2$	P	Mean number of registrations ± S.D.	Mean individual vector length ± S.D.	Number of axial individuals (% of active and valid experiments)	Total number of experiments/ inactive/invalid experiments
W_1 ac	19	244–64		0.13	0.738	550.6±960.8	0.16±0.10	4 (21)	41/21/1
W_{10} ac	18	41–221		0.34	0.132	1067.2±889.4	0.16±0.10	5 (28)	38/17/3
W_{20} bc	29	282	±43	0.34	0.035	1074.4±782.9	0.16±0.12	6 (21)	50/20/1
W_{20} ac	14	229		0.30	0.298	1383.6±1289.3	0.13±0.07	4 (29)	41/23/4
G_1	21	215	±33	0.49	0.005	1162.5±999.4	0.17±0.12	5 (24)	41/18/2
G_5	19	214–34	±43	0.41	0.037	688.6±916.4	0.18±0.14	5 (26)	42/23/0
G_{10}	18	216–36		0.40	0.054	1130.8±1294.0	0.15±0.10	5 (28)	40/21/1
GY_1	15	74		0.23	0.465	941.1±782.8	0.16±0.14	6 (40)	44/24/5
GY_5	20	177		0.29	0.193	1021.2±993.9	0.18±0.14	3 (15)	43/21/2
GY_{10}	22	238		0.30	0.133	1223.0±1122.6	0.17±0.13	3 (14)	42/20/0
R_1	21	277	±20	0.71	<0.001	951.0±626.8	0.14±0.09	6 (29)	42/20/1
R_5	17	259	±40	0.46	0.026	899.5±670.3	0.16±0.06	4 (24)	44/27/0
R_{10}	18	315		0.34	0.123	1021.0±684.6	0.18±0.08	3 (17)	42/23/1

N, number of active and valid experiments; α–α_2, mean group direction for unimodally (α) and axially (α_2) oriented groups, respectively; 95% CI, 95% confidence interval (directed groups only); $\mathbf{r}$, $\mathbf{r}_2$, mean vector length of the unimodally ($\mathbf{r}$) and axially ($\mathbf{r}_2$) oriented groups; P, level of significance according to the Rayleigh test; bc, before colour experiments; ac, after colour experiments; W, full-spectrum light; G, green light; GY, green-yellow light; R, red light. Also given are the mean number of registrations, mean individual vector length and number of axial individuals per group (valid experiments only), and the total number of experiments performed under each experimental situation and the number of inactive (>40 registrations) and invalid (mean individual vector length <0.05) experiments. See Figs 3, 4.

intensity, W_{20} ac, and were least active under the lowest intensity, W_1 (significant difference in number of registrations in the orientation cages; Kruskal–Wallis test, $H_{3,80}$=12.3, P=0.007; Table 2). The number of valid experiments and mean individual vector length, however, was not significantly different between the four experiments under full-spectrum light (P>0.05).

Discussion

Our experiments with European robins tested under different wavelengths and intensities of light suggest that the birds' magnetic compass orientation is both wavelength and intensity dependent. We could demonstrate that European robins show seasonally appropriate migratory directions under 560.5 nm green light but are disoriented under 567.5 nm green-yellow light at a broad range of intensities. Our data also show that significant mean orientation, although into a direction shifted relative to the expected migratory one, is possible under 617 nm light in European robins, at least at lower intensities. Furthermore, magnetoreception appears to be intensity dependent, but our birds became disoriented at higher intensities rather than showing a shift in orientation as has previously been observed (Wiltschko et al., 2000a,b; Wiltschko and Wiltschko, 2001). We argue that these results strengthen the hypothesis that birds possess a light-dependent magnetoreception system based on two or more magnetically sensitive spectral mechanisms.

A light-dependent magnetoreception system based on antagonistically interacting, magnetically sensitive spectral mechanisms has been described in Eastern red-spotted newts (c.f. Phillips and Borland, 1992a,b). Normal orientation was recorded under wavelengths of ≤450 nm, 90° shifted orientation was recorded under wavelengths of ≥500 nm, and disorientation was recorded under an intermediate wavelength of 475 nm. In conclusion, light-dependent magnetoreception in these newts seems to be mediated by one spectral mechanism in the shorter wavelengths below 450 nm and by another spectral mechanism in the longer wavelengths above 500 nm. An equal excitation of both mechanisms leads to disorientation, suggesting that the two wavelength mechanisms interact antagonistically with each other (for a review, see Deutschlander et al., 1999). There is evidence that the short-wavelength mechanism is more sensitive than the long-wavelength mechanism in amphibians (J. Phillips, personal communication), leading to a system where even a small amount of short-wavelength light can equalize or override the input from the long-wavelength mechanism. Our data support the existence of a similar system in birds, with a short-wavelength mechanism in the blue-green part of the spectrum and a long-wavelength mechanism in the red part of the spectrum.

Seasonally appropriate migratory orientation under 560.5 nm light

Our European robins oriented, directionally very concentrated, towards southwest or axially towards southwest–northeast under 560.5 nm light. The southwesterly

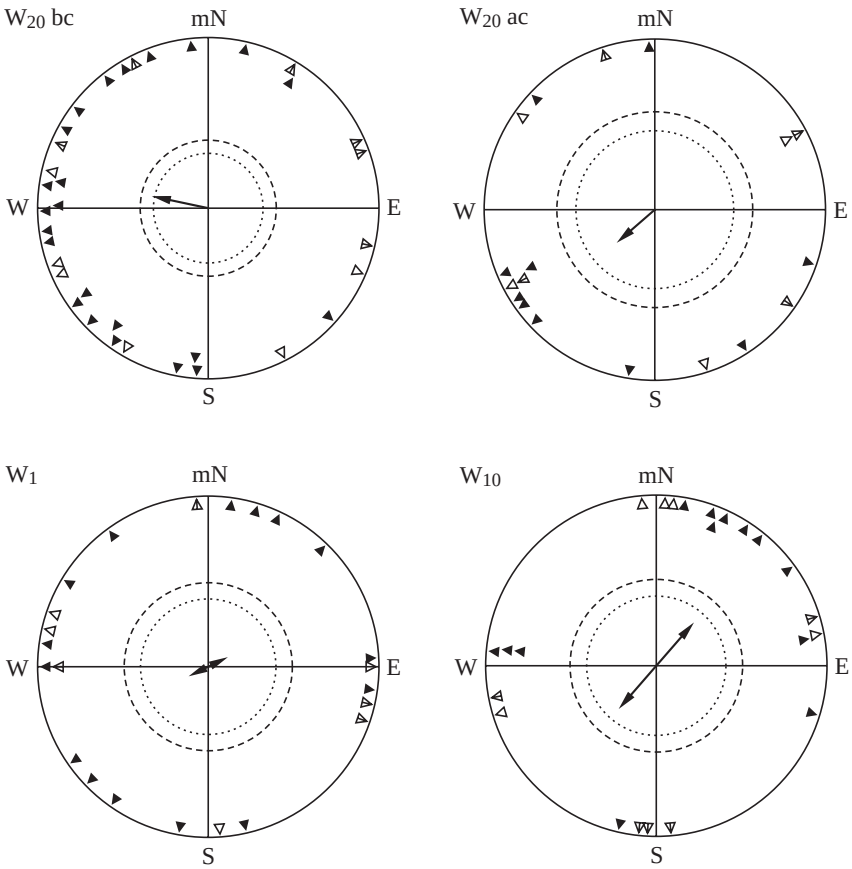

Fig. 4. Orientation behaviour of European robins tested under full-spectrum light of different intensities in autumn. See Table 1 for details on intensities (W_1–W_{20}), Table 2 for detailed statistical information and Fig. 3 for further explanation of the graphs. Abbreviations: ac, after colour experiments; bc, before colour experiments.

direction corresponds to the expected migratory direction. Our birds were in good migratory condition, with high mean fat values (5.7±1.0, mean fat score ± S.D., according to the eight-grade fat scale by Pettersson and Hasselquist, 1995) and high mean body mass (17.9±1.4 g) in the middle of the experimental period. We can therefore assume that the birds exhibited true migratory behaviour. Also, other orientation studies on wavelength-dependent magnetoreception with different species of birds consistently showed oriented behaviour towards the seasonally expected migratory direction under green light (peak wavelength 565 nm) at intensities of approximately 6–8.7×10^{15} quanta s^{-1} m^{-2} and shifts in orientation or axial behaviour under higher light intensities (for a discussion on the effects of light intensities, see below; see Fig. 5 for an overview; Munro et al., 1997; Rappl et al., 2000; Wiltschko et al., 2000a,b). A magnetic inclination compass was shown to be the underlying mechanism because birds reversed their orientation when tested under green light in a magnetic field with an inverted vertical component (Wiltschko et al., 2001). The magnetoreception system of birds thus seems to behave in the same way under green light of approximately 560/565 nm as under natural situations when tested under natural skies during migration. In general, orientation has been shown to be more concentrated under 560/565 nm light than under full-spectrum light (c.f. this study; Wiltschko et al., 1993; Wiltschko and Wiltschko, 1995; Munro et al., 1997; the only exception is the study on garden warblers by Rappl et al., 2000). These observations indicate that green light excites a magnetically sensitive mechanism to a higher degree than other wavelengths or the full spectrum and that the avian magnetoreception system is very sensitive in the short-wavelength region around green.

Disorientation under 567.5 nm light

Our birds were disoriented under light with a peak wavelength of 567.5 nm at all intensities tested. This stresses the observation that magnetoreception is indeed dependent on specific wavelengths of light. The very abrupt transition from significant mean orientation towards the expected migratory direction under 560.5 nm to disorientation under 567.5 nm strongly favours the theory of a magnetoreception system based on two or several antagonistically interacting spectral mechanisms with at least one activity peak in the short-wavelength area below 567.5 nm and one activity peak in the long-wavelength area above 567.5 nm. Equal excitation of two such mechanisms by 567.5 nm light can, in theory, cause the sharp transition from oriented to disoriented behaviour. The involvement of one spectral mechanism alone would result in a more gradual transition between orientation and disorientation over a much broader range of wavelengths due to the characteristics of spectral sensitivity curves. There is a strong parallel between our results and the disorientation found in Eastern red-spotted newts under the intermediate wavelength of 475 nm (Phillips and Borland, 1992a,b), except that the wavelengths involved are shifted to the longer spectrum in our case. In the newt system, equal excitation of both the short-wavelength mechanism revealing normal orientation and the long-wavelength mechanism producing a 90° shift in orientation results in disorientation. So, if the disorientation of our European robins under 567.5 nm is comparable with the disorientation in the newt system, there should be an antagonistic long-wavelength mechanism at wavelengths of >567.5 nm. In conclusion, testing birds under light of >567.5 nm should result in oriented behaviour, shifted by approximately 90° relative to the control direction.

Shifted orientation under 617 nm light

Consistent with these predictions, our European robins were well oriented under 617 nm light at the lower two intensities. Relative to the direction chosen under 560.5 nm, the birds showed a 62° clockwise shift towards west at the lowest

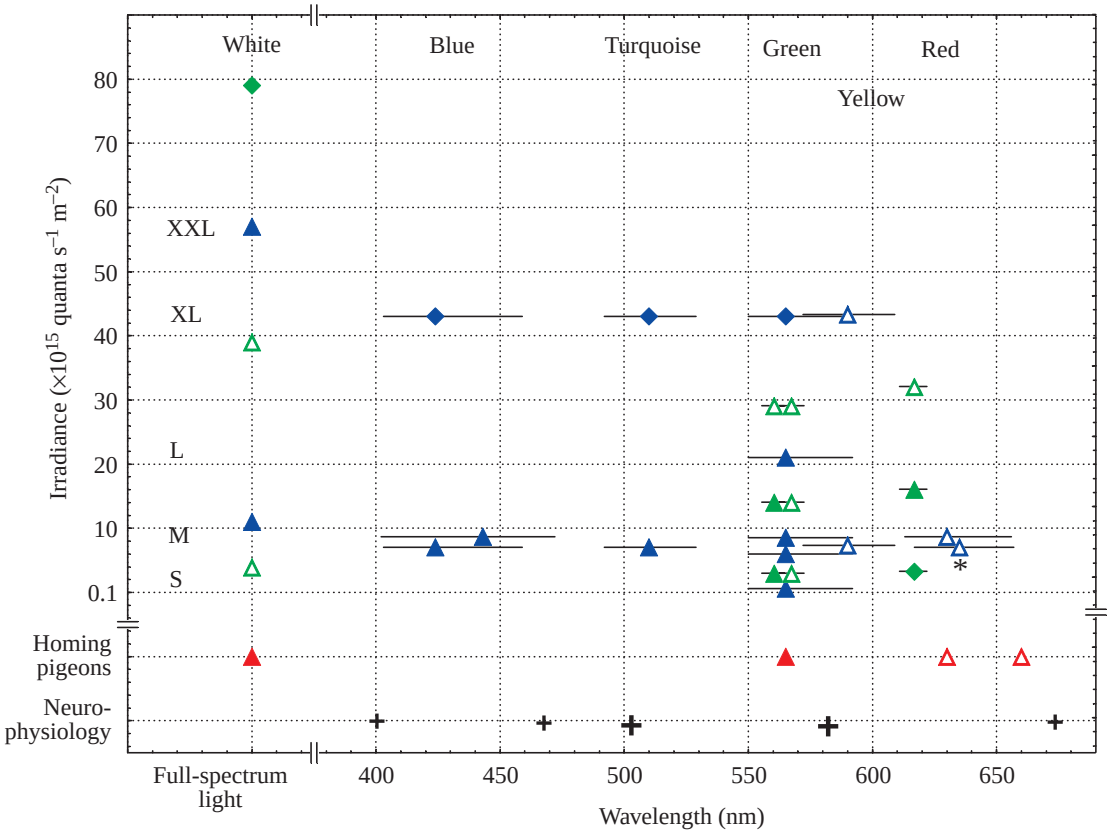

Fig. 5. Summary of orientation experiments (in blue), homing experiments (in red) and neurophysiological studies (in black) examining light-dependent magnetoreception in birds, published until 2001. Also included are the results of the present study (in green). The graph shows the wavelengths and intensities under which birds were tested in orientation experiments and in an electrophysiological study (filled symbols indicate experiments revealing significant orientation, and open symbols indicate experiments revealing disorientation). The triangles indicate the average peak wavelength, and the horizontal bars indicate the half bandwidth ($\lambda/2$) of the spectrum, if available. Diamonds indicate oriented behaviour into directions significantly different from the seasonally expected migratory direction. Magnetic responsiveness of units of the basal optic root (nBOR) in the electrophysiological study on pigeons by Semm and Demaine (1986) is indicated by crosses (larger crosses indicate peak responses). The symbols refer to the following published orientation experiments: full-spectrum light at intensity M (Wiltschko et al., 1993; Wiltschko and Wiltschko, 1995; Munro et al., 1997; Rappl et al., 2000) and intensity XXL (Möller et al., 2001); blue light at intensity M (Wiltschko et al., 1993; Wiltschko and Wiltschko, 1999, 2001; Rappl et al., 2000), and intensity XL (Wiltschko and Wiltschko, 2001); turquoise light at intensity M and intensity XL (Wiltschko and Wiltschko, 2001); green light at intensity S (Wiltschko et al., 2000a), intensity M (Wiltschko et al., 1993, 2000a,b, 2001; Wiltschko and Wiltschko, 1995, 1999, 2001; Munro et al., 1997; Rappl et al., 2000), intensity L (Wiltschko et al., 2000a,b) and intensity XL (Wiltschko et al., 2000a,b; Wiltschko and Wiltschko, 2001); yellow light at intensity M (Wiltschko et al., 1993; Wiltschko and Wiltschko, 1999, 2001; Rappl et al., 2000) and intensity XL (Wiltschko and Wiltschko, 2001); and red light at intensity M (Wiltschko et al., 1993; Wiltschko and Wiltschko, 1995; Munro et al., 1997; Rappl et al., 2000; Möller et al., 2001). The asterisk refers to the study by Möller et al. (2001) where significant mean orientation was found after pre-exposure to red light only. The homing experiments refer to those of Wiltschko and Wiltschko (1998).

intensity, R_1. This shift is smaller than the expected 90° shift (95% interval of the mean direction under 617 nm does not include the expected 90°-shifted direction; see Table 2). We can speculate that the magnetic field provides information on the cardinal directions only under monochromatic light of long wavelengths and that additional information from other cues (for example, celestial cues) would be necessary for fine-tuning in order to be able to identify the seasonally appropriate migratory direction. If this was true, the westerly direction observed under red light (R_1) would correspond to a 90° shift from the magnetic south direction.

Orientation experiments with four species of passerine birds as well as displacement experiments with homing pigeons conducted under 590 nm yellow light and 630–635 nm red light all resulted in disoriented behaviour (one exception was observed by Möller et al., 2001, see below; Fig. 5; Wiltschko et al., 1993; Wiltschko and Wiltschko, 1995, 1998, 1999, 2001; Munro et al., 1997; Rappl et al., 2000). The apparent contradiction between our results and the previous findings can be explained by the difference in the half bandwidth and maybe also in the peak wavelengths of the light that the birds were exposed to. The yellow and red lights produced by light-

emitting diodes (LEDs) and used in previous experiments not only have much broader wavelength spectra at 50% bandwidth ($\lambda/2$=33–43 nm) than the red light we used ($\lambda/2$=9–11 nm) but also become even broader at their bases (bandwidth at 1% peak transmission; Wiltschko et al., 1993; Wiltschko and Wiltschko, 1995, 1998, 1999, 2001; Munro et al., 1997; Rappl et al., 2000; Möller et al., 2001). The spectra of our monochromatic lights have a bandwidth at 1% peak transmission of 21–30 nm; thus, they also have a very small bandwidth at their bases. Light of a broad bandwidth is more likely to excite more than one spectral mechanism, and a sensitive mechanism can become excited by very little light from the outer edges of a spectral curve. Thus, in the case of an antagonistically interacting system between spectral mechanisms with peaks at different wavelengths, disorientation is more likely to occur under broad-spectrum light. As already mentioned, we have indications that the short-wavelength mechanism is more sensitive than the long-wavelength mechanism in European robins. So, the left tail of the spectrum of the broad red LED light could have excited a part of the right tail of the more sensitive short-wavelength mechanism, leading to an equal excitation of both mechanisms and disrupting the magnetoreception capabilities.

Previous orientation experiments under red light revealed significant orientation into the expected migratory direction under one experimental situation (Möller et al., 2001). In that experiment, European robins, pre-exposed to red light in their holding cages before the start of the experiment, were significantly oriented when tested under red light. The control birds that did not experience a red pre-exposure were disoriented when tested under red light. For pre-exposure, red light was added to the normal full-spectrum light in the holding house 2–3 h before the start of the experiment. One hour before the experiments started, the full-spectrum light was switched off and the birds were exposed to the red light only (Möller et al., 2001). These experiments also suggest that birds are, in principle, able to orient under long-wavelength light. Why, in the case of Möller et al. (2001), acclimation seems to be necessary for a successful use of red light for magnetic compass orientation is unclear.

Support for the involvement of a long-wavelength mechanism is also given by neurophysiological studies, as presented in Fig. 5. Extracellular recordings in the nucleus of the basal optic root (nBOR) and in the optic tectum in homing pigeons have resulted in responses to changes in the direction of the magnetic field (Semm et al., 1984) and peak magnetic responsiveness under wavelengths of 503 nm and 582 nm (Semm and Demaine, 1986). The same cells also exhibited a response to magnetic stimuli under 674 nm red light, thus responding to light of longer wavelengths. However, these results have to be considered with some care because of difficulties in repeating the experiment (Deutschlander et al., 1999).

As we carried out our experiments indoors under controlled laboratory conditions, the birds were given access to geomagnetic information only. Further experiments under red light in a shifted or inverted magnetic field will show whether the reactions observed are true compass orientation or non-specific reactions towards a nonsense direction.

Orientation under different light intensities

Changes in orientation behaviour away from the expected migratory direction have been observed at different light intensities in both European robins and Australian silvereyes (Fig. 5; Wiltschko et al., 2000a,b; Wiltschko and Wiltschko, 2001). The observed reactions, however, do not seem to be general, but rather species-specific. Australian silvereyes reacted to higher intensities of 43–44×10^{15} quanta s^{-1} m^{-2} (15 mW m^{-2}) under 565 nm light by showing a shift towards a fixed direction in the northwest during both autumn and spring migration (Wiltschko et al., 2000b). European robins, on the other hand, preferred axial east–west directions under both 424 nm and 565 nm lights, but north to north-westerly directions under 510 nm light at the same high intensity (Wiltschko and Wiltschko, 2001). The reason for the different reactions between Australian silvereyes and European robins under the same intensity level remains unknown. Our experimental birds also showed axial orientation, but at much lower intensities (14×10^{15} quanta s^{-1} m^{-2}) compared with those reported by Wiltschko and Wiltschko (2001). The axial orientation of our European robins was directed along the axis of the expected migratory direction, thus indicating difficulties in identifying the correct axis rather than a shift in orientation as shown in the European robins tested by Wiltschko and Wiltschko (2001). At the highest light intensity of 10 mW m^{-2} (29–32×10^{15} quanta s^{-1} m^{-2}), our birds were disoriented under both 560.5 nm and 617 nm lights, which are the same wavelengths at which they were significantly oriented under the lower two light intensities. Under 560.5 nm light (G_{10}), the disorientation observed is presumably a statistical consequence of small sample size because the mean vector lengths in the higher two intensities, G_5 and G_{10}, are almost identical (**r**=0.41 and **r**=0.40, respectively) and the mean directions of the birds point towards the same direction. Migratory activity and motivation did not seem to be reduced between intensities of the same colour light, as neither the percentage of valid experiments nor the mean number of registrations or individual mean vector lengths were significantly different among the three intensities (P>0.05). So, the ability to perceive useful information for orientation or to interpret information and transfer it into directed orientation behaviour must be impaired in some way.

The disorientation under high-intensity 617 nm light can be explained by the proposed antagonistically working, high-sensitive short-wavelength and low-sensitive long-wavelength mechanisms. The low-intensity light preferentially excited the long-wavelength mechanism and only slightly stimulated the more sensitive short-wavelength mechanism. Increasing light intensity would favour the relative light input to the long-wavelength mechanism, as both our full-spectrum light and the one used by the Wiltschko group emit relatively more energy in the longer than in the shorter wavelengths (Fig. 2).

However, with increasing intensity, the long-wavelength mechanism would become saturated or adapted, resulting in a relative decrease in sensitivity of the long-wavelength mechanism and in a relatively higher input to the short-wavelength mechanism until both mechanisms become excited equally, leading to disorientation.

According to the antagonistic wavelength-dependent magnetoreception mechanism, any transition from directed orientation to shifted orientation involving more than one spectral mechanism includes an intermediate state where disorientation occurs. The relative excitation of a wavelength mechanism revealing directed orientation and a wavelength mechanism revealing shifted orientation, together with the sensitivity of the two mechanisms, decides on whether a bird will be oriented into the expected direction, disoriented or show a shift in orientation. Whether a mechanism becomes excited by a light stimulus depends on whether the light spectrum of the stimulus overlaps with the sensitivity spectrum of the mechanism. The magnitude of the excitation is dependent on the number of photons received by the spectral mechanism, which increases with increasing intensity. Thus, the discrepancies found between our study and those of the Wiltschko group (Wiltschko et al., 2000a; Wiltschko and Wiltschko, 2001) can be explained by the different intensity levels and half bandwidths used in the respective studies (see Fig. 5 for comparison).

Disorientation under full-spectrum light

In view of an avian magnetoreception system with antagonistically interacting wavelength mechanisms, our full-spectrum light experiments allow some very interesting conclusions. Our European robins were significantly oriented only in the very first experiments under full-spectrum light at a very high intensity (W_{20} bc). The westerly direction was significantly different from G_1 and does not coincide with the expected migratory direction but is directed into the same direction as under R_1. The birds were disoriented in all the experiments under full-spectrum light that were performed after the colour experiments.

The full-spectrum light we used in our experiments is supposed to reflect a spectrum that is very close to natural outdoor conditions, and birds are therefore expected to behave most naturally under full-spectrum light. A spectral analysis of our full-spectrum light showed that the birds received very little light from the UV spectrum below 400 nm and maximal light inputs from approximately 760 nm in the near IR when tested under full-spectrum white light (Fig. 2). Compared with the spectrum of incandescent light bulbs used by others (e.g. Wiltschko et al., 1993; Munro et al., 1997; Rappl et al., 2000; Möller et al., 2001), the full-spectrum light emitted by xenon arc lamps matches the natural spectrum better, and the emission of violet-blue light between 400 nm and 500 nm is much higher (Fig. 2). So, it is unlikely that our results are a methodological artefact. Contrary to this, there are indications about the existence of a third spectral mechanism in the UV-blue area at 400–450 nm, which could in our case have interfered with the magnetoreception system in an antagonistic way. Directed orientation under 424 nm and 443 nm blue light has been reported by Wiltschko et al. (1993), Wiltschko and Wiltschko (1999, 2001) and Rappl et al. (2000). Such an additional spectral mechanism would have been activated to a much higher degree under the full spectrum used by us than under a full-spectrum light produced by an incandescent light bulb. Alternatively, the intensity peak measured in the near IR around 760 nm of our full spectrum could have resulted in an inappropriately high activation of the long-wavelength mechanism. Either one could have resulted in an imbalance between the different, antagonistically interacting spectral mechanisms (c.f. Deutschlander et al., 1999), causing shifted orientation or disorientation in the same manner as argued earlier, thus explaining the observed behaviour of our birds under full-spectrum white light.

Our European robins were disoriented in all the experiments under full-spectrum light that were performed after the colour experiments. The significantly lower activity of the birds in the orientation cages might explain the very bad orientation at the lowest intensity, W_1, but we would then also expect a lower proportion of active individuals and a shorter mean individual vector length compared with the other experiments performed under full-spectrum light. But why did our birds show shifted orientation in the first experiment under full-spectrum light before the start of the experiments under monochromatic light, but disorientation when tested after the colour experiments? A possible explanation might be that changing the spectral composition of light that the birds are exposed to could disturb their ability to orient. This could be compared with the reactions observed when changing the intensity of the ambient magnetic field (Wiltschko, 1978). Orientation experiments under magnetic fields of unfamiliar field intensity resulted in disorientation until the birds adapted to the new situation after a few days and learned to use the magnetic field information of unfamiliar field intensity for orientation. In our case, a change of light conditions from monochromatic to full spectrum rather than *vice versa* could have confused the birds. This could explain why we got directed orientation under full-spectrum light in our first experiments before the colour experiments only.

In summary, in view of the idea of an avian magnetoreception system with antagonistically interacting wavelength mechanisms, the results obtained under full-spectrum white light are extremely interesting and they do not, in our opinion, disturb or reduce the importance of the results and conclusions from the colour experiments.

Biophysical processes of magnetoreception

Two theories are currently under discussion to explain the biophysical processes of magnetoreception. The theory forwarded by Schulten and Windemuth (1986) and Ritz et al. (2000) is based on radical pairs, while the theory proposed by Edmonds (1996) is based on magnetite in the birds' oil droplets. Both theories can theoretically build the physiological basis for a magnetoreception system with two or more spectral

mechanisms. Directed orientation under red light seems to contradict the magnetoreception model proposed by Ritz et al. (2000), as it assumes that light of a specific minimum energy is needed to activate the biophysical processes necessary for the detection of magnetic information. Cryptochromes, a class of photoreceptors found in the avian retina and pineal gland (Bailey et al., 2002), with an absorption spectrum in the blue and green wavelength range, were proposed to be involved in light-dependent magnetoreception (Ritz et al., 2000). This, however, does not exclude the possibility that other receptors with different properties are involved in light-dependent magnetoreception. Molecules with absorption spectra in the longer wavelengths of the spectrum could form a long-wavelength mechanism, and antagonistic behaviour between the two wavelength mechanisms could explain the abrupt cut-off between 560.5 nm and 567.5 nm light. Edmonds' model suggesting light-dependent magnetoreception in combination with magnetite particles in the oil droplets of specialized photoreceptors in the avian retina (Edmonds, 1996) can theoretically also explain both the orientation under red light and the abrupt behavioural change between 560.5 nm and 567.5 nm light. The cut-off filtering effect of the oil droplets in the medium- and long-wavelength-sensitive photoreceptors shifts the wavelength of peak absorbance of these photoreceptors towards longer wavelengths (for example, 540 nm and 615 nm in the canary, *Serinus canaria*, and 530–540 nm and 600–610 nm in the Pekin robin, *Leiothrix lutea*) and also causes the effective spectral sensitivity curves to fall off very steeply (Maier and Bowmaker, 1993; Das et al., 1999). We can assume that the effective sensitivity spectra in European robins are similar. Thus, photoreceptors exist that are sensitive in the medium- and long-wavelengths, and, if inputs from such green and red photoreceptors are processed as antagonistic signals, disorientation could occur at intermediate wavelengths.

Ecological considerations

The question arises as to whether the observed properties of the birds' orientation behaviour under different wavelengths and intensities of light have an ecological explanation or whether the different reactions are based on purely physiological reasons. Night-migrating birds are thought to select their migratory direction at the time around sunset. Spectral irradiance measurements at dusk show a relative increase of blue (peak at 450–500 nm) and red (peak at 680 nm) light and a reduction in green, yellow and orange (550–620 nm) light from daytime to twilight (see Fig. 2. for comparison; McFarland and Munz, 1975). Thus, access to yellow-orange light is reduced during twilight, whereas blue and red light is more intense. We can only speculate whether the limited access to green light might be one reason for a higher sensitivity of the short-wavelength mechanism in the green wavelength area compared with the less sensitive long-wavelength mechanism in the red wavelengths and the possible UV-blue mechanism. The disorientation of our birds under 567.5 nm light, however, does not seem to be connected to the natural wavelength spectrum during twilight. The light intensity levels used for the monochromatic light in the various studies seem to cover a large range ($0.57–43\times10^{15}$ quanta s^{-1} m^{-2}; see Fig. 5), but they all lie within the intensities experienced under the natural twilight period for the different wavelengths, as estimated from spectral irradiance curves measured in nature during twilight (McFarland and Munz, 1975). McFarland and Munz (1975) performed their spectral measurements in winter (30 January) and it is likely that the spectrum and intensity of the light of an autumn sky is composed slightly differently. Furthermore, differences in weather conditions, such as fog or cloud cover, can have a large influence on the visible spectrum of the sky. So, currently, it is difficult to find an ecological explanation for the different reactions of the birds under different light intensities.

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