Magnetic orientation in birds: non-compass responses under monochromatic light of increased intensity

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Migratory Australian silvereyes (*Zosterops lateralis*) were tested under monochromatic light at wavelengths of 424 nm blue and 565 nm green. At a low light level of 7×10^{15} quanta $m^{-2} s^{-1}$ in the local geomagnetic field, the birds preferred their seasonally appropriate southern migratory direction under both wavelengths. Their reversal of headings when the vertical component of the magnetic field was inverted indicated normal use of the avian inclination compass. A higher light intensity of 43×10^{15} quanta $m^{-2} s^{-1}$, however, caused a fundamental change in behaviour: under bright blue, the silvereyes showed an axial tendency along the east–west axis; under bright green, they showed a unimodal preference of a west–northwesterly direction that followed a shift in magnetic north, but was not reversed by inverting the vertical component of the magnetic field. Hence it is not based on the inclination compass. The change in behaviour at higher light intensities suggests a complex interaction between at least two receptors. The polar nature of the response under bright green cannot be explained by the current models of light-dependent magnetoreception and will lead to new considerations on these receptive processes.

Keywords: magnetic field; inclination compass; magnetoreception; monochromatic light;
migratory orientation; *Zosterops lateralis*

1. INTRODUCTION

The geomagnetic field is an important source of directional information for migratory birds. A magnetic compass has been demonstrated in numerous species of passerines (see R. Wiltschko & Wiltschko 1995, 1999) and recently also in a non-passerine migrant (Gudmundsson & Sandberg 2000). However, little is known about how birds obtain the relevant information from the magnetic field. Three types of model have been proposed: one is based on small particles of magnetite, which have been found in the upper beak of pigeons (e.g. Williams & Wild 2001; Fleissner *et al.* 2003), with various possible transducer mechanisms discussed (e.g. Yorke 1979; Kirschvink & Walker 1985; Winklhofer *et al.* 2001); the other two focus on magnetoreception by specialized photoreceptors. The model of Schulten & Windemuth (1986) involves macromolecules that by photon absorption reach the excited singlet state; by hyperfine coupling, they are transferred into the excited triplet state forming radical pairs. The triplet yield depends on the alignment of molecules in the ambient magnetic field and can thus be used for magnetoreception (for details see Ritz *et al.* 2000). In the other model, Edmonds (1996) suggested that small free-moving ferrimagnetic crystals associated with light-absorbing molecules in the oil-droplets may align parallel to the magnetic vector and thus allow magnetoreception by modulating the amount of light reaching the receptors. In both, the radical pair model and the Edmonds model, magnetoreception involves axial rather than polar processes, which is in agreement with the birds' magnetic

compass being an 'inclination compass', not using the polarity of the field (Wiltschko & Wiltschko 1972), and both models assume that magnetoreception is initiated by light-dependent processes.

This prediction was tested in migratory Australian silvereyes, *Zosterops lateralis*, by exposing them to near-monochromatic light of various wavelengths, and the ability to orient in their migratory direction served as a criterion whether or not they could detect magnetic directions under the test conditions. Normal migratory orientation was observed only under light from the blue–green part of the visual spectrum; under longer wavelengths from *ca.* 590 nm yellow onwards, the birds were disoriented (W. Wiltschko *et al.* 1993). Meanwhile, additional species like European robins, *Erithacus rubecula* (W. Wiltschko & Wiltschko 1995, 1999; Muheim *et al.* 2002), and garden warblers, *Sylvia borin* (Rappl *et al.* 2000), as well as homing pigeons (R. Wiltschko & Wiltschko 1998) have been tested; and all of them showed the same pattern of response that might be typical for birds (W. Wiltschko & Wiltschko 2002). This wavelength dependency of avian magnetoreception is different from the one described for amphibians, the only other group in which a light-dependent magnetic compass has been demonstrated (Phillips & Borland 1992, 1994).

Because the passerine species tested migrate either during twilight or at night, the light intensities used in the early studies were rather low, corresponding to a quantal flux of *ca.* $6–9 \times 10^{15}$ quanta $m^{-2} s^{-1}$. First tests at 565 nm green light of higher intensities produced a very surprising result: when the quantal flux was raised sixfold to *ca.* 43×10^{15} quanta $m^{-2} s^{-1}$, silvereyes showed a strong directional tendency towards west–northwest. The observation that the same west–northwesterly preference was

observed in autumn as well as in spring (W. Wiltschko *et al.* 2000*a,b*) indicated that this tendency was independent of the migratory direction: it no longer reflects migratory orientation, but appears to be some fixed direction, possibly related to alignment responses (see Wiltschko *et al.* 2000*b*).

This unexpected finding raised several crucial questions, the most important ones being: (i) do birds use their normal magnetic inclination compass for this fixed direction? and (ii) does bright light of corresponding intensities at other wavelengths produce similar effects? Here, we report the results of a new test series with Australian silvereyes designed to answer these questions.

2. MATERIAL AND METHODS

The experiments were performed in Armidale, NSW, Australia (30°30′ S, 151°40′ E), during Southern Hemisphere spring from 24 September to 18 October 2001.

(a) *Test birds*
The test birds were 24 Australian silvereyes of the migratory Tasmanian and Victorian population that had been mist netted on the campus of the University of New England in Armidale between 9 and 13 September 2001. They were kept indoors in groups of four in large cages (80 cm × 40 cm × 40 cm) under a photoperiod that simulated the natural one of Armidale. On the day after the tests were completed, the birds were set free at the site of capture.

(b) *Test conditions*
For testing, the birds were subdivided into two groups: 12 birds were tested under blue light with a peak wavelength of 424 nm ($\lambda/2$ at 403 and 459 nm, respectively) and the other 12 under green light with a peak wavelength of 565 nm ($\lambda/2$ at 553 and 583 nm). The test lights were produced by the same light-emitting diodes (LEDs) used in earlier studies (e.g. W. Wiltschko & Wiltschko 2001); they were adjusted by modulating the current to be of equal quantal flux and presented at two intensities: the lower, with *ca.* 7×10^{15} quanta m^{-2} s^{-1} (blue and green) was in the range where birds had shown excellent migratory orientation in previous studies (e.g. W. Wiltschko *et al.* 1993; W. Wiltschko & Wiltschko 1995; R. Wiltschko & Wiltschko 1999), while the higher intensity (the 'bright' colours: bright blue and bright green), with 43×10^{15} quanta m^{-2} s^{-1} was the same as the one where silvereyes had previously shown the odd west–northwesterly tendency not related to their migratory direction (W. Wiltschko *et al.* 2000*a,b*). In terms of radiation, this meant 2.8 and 20 mW m^{-2} for blue and 2.1 and 15 mW m^{-2} for green light.

The test rooms were located in a wooden building on the university campus, where the local geomagnetic field was unchanged with an intensity of 56 000 nT, and $-62°$ inclination, i.e. the magnetic vector was pointing upwards. Birds were tested under three magnetic conditions: (i) under each light regime in the local geomagnetic field; (ii) under blue, green and bright green also in a magnetic field where the vertical component was inverted so that the inclination was now pointing downward instead of upward: birds using their normal magnetic inclination compass should reverse their headings in this field; and (iii) under bright green also in a magnetic field with magnetic north turned by 120° counterclockwise towards west–

southwest. The two experimental fields were produced by battery-operated Helmholtz coils (2 m diameter, 1 m clearance).

The birds were tested under the assigned test conditions until they had produced three recordings with sufficient activity (see below) in each. Tests under 424 nm blue and 565 nm green at 7×10^{15} quanta m^{-2} s^{-1}, where birds had always shown excellent orientation in their migratory direction, served as a control and provided the reference for the birds' behaviour in the other conditions.

(c) *Test apparatus and performance*
Orientation behaviour was recorded in funnel cages (Emlen & Emlen 1966) lined with typewriter correction paper (BIC, Germany; formerly Tipp-Ex), where the birds were tested one at a time (see Wiltschko *et al.* 1993). Each funnel cage was placed in an aluminium cylinder, which isolated the cages against each other. The top of the cylinder consisted of the plastic disc carrying the LEDs. For tests in experimentally altered magnetic fields, four of these units were placed in the centre of a Helmholtz coil. The intensity of light was altered by varying current and number of LEDs activated. The light passed through two sets of diffusers before it reached the bird. It was measured in the test cages as irradiance using Optometer P9710-1 (Gigahertz-Optik, Puchheim, Germany) with the radiometric probe 'Visible' RW-3703-2, a silicium photoelement for the wavelength range of 400–800 nm.

Recording the birds' orientation began in the evening at about the time when the light went off in the housing cages and lasted for *ca.* 1 h 15 min. When active, the birds left scratch marks on the coating of the inclined walls, which documented the distribution of their activity.

(d) *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 insufficient activity.

From the distribution of the activity within the cage, the bird's heading and the concentration of activity of the respective test were calculated. In condition bright blue, we observed an unusual behaviour: the scratches within the cage were often bimodally distributed along an axis, indicated by a higher concentration (longer vector) obtained when the angles were doubled (modulo 360°) so that opposite sectors added. In these cases, we used the preferred end of the axis as heading for further calculations.

From the three headings of each bird, we calculated the mean vector of this bird under each condition, with direction α_b and length r_b (for the birds B6 and B12 under blue, the respective vector is based on only two recordings). Under bright blue, the headings of most birds were axially distributed; in these cases, we calculated the axial vector (indicated in table 3), with its preferred end used in the same way as the mean direction of unimodal vectors (see W. Wiltschko & Wiltschko 2001). The mean directions α_b of the 12 birds were comprised in the grand mean vector for each condition, with the direction α_N and the length r_N; for bright blue, we also calculated the grand preferred axis by doubling the angles (Batschelet 1981). The grand mean vectors (or grand axis) were tested by the Rayleigh test for directional preferences. The orientation in the various conditions was compared with the parametric Watson Williams test for differences in direction and with the non-parametric Mardia Watson Wheeler test for differences in distribution (Batschelet 1981).

Table 1. *Orientation of Australian silvereyes under 424 nm blue light.*

(α_b, r_b direction and length of the bird's mean vector based on three recordings under the respective test condition.)

light	7×10^{15} quanta m^{-2} s^{-1}		7×10^{15} quanta m^{-2} s^{-1}		43×10^{15} quanta m^{-2} s^{-1}	
magnetic condition	geomagnetic field		vertical component inverted		geomagnetic field	
bird	α_b (deg)	r_b	α_b (deg)	r_b	α_b (deg)	r_b
B1	173	0.32	296	0.97	357[a]	0.80
B2	190	0.97	13	0.98	237[a]	0.55
B3	195	0.80	318	0.81	277	0.99
B4	169	0.77	6	0.95	98[a]	0.53
B5	218	1.00	299	0.54	82[a]	0.78
B6	200	0.67	55	0.75	39	0.75
B7	199	0.86	24	0.33	314	0.93
B8	193	1.00	4	1.00	292[a]	0.83
B9	170	0.32	14	0.93	81	0.90
B10	195	0.96	358	0.87	277[a]	0.74
B11	169	0.94	357	0.93	96[a]	0.95
B12	233	0.95	343	0.99	277	0.98

[a] At 43×10^{15} quanta m^{-2} s^{-1} indicates axial vectors α_b.

Table 2. *Orientation of Australian silvereyes under 565 nm green light.*

(α_b, r_b direction and length of the bird's mean vector based on three recordings under the respective test condition.)

light	7×10^{15} quanta m^{-2} s^{-1}				43×10^{15} quanta m^{-2} s^{-1}					
magnetic condition	geomagnetic field		vertical component inverted		geomagnetic field		vertical component inverted		magnetic north = 240°	
bird	α_b (deg)	r_b	α_b (deg)	r_b	α_b (deg)	r_b	α_b (deg)	r_b	α_b (deg)	r_b
G1	178	0.94	22	0.94	268	0.82	99	0.31	159	0.96
G2	211	0.84	356	0.95	268	0.87	1	0.56	147	0.95
G3	150	0.41	144	0.31	298	0.68	304	0.34	185	0.59
G4	166	0.94	2	1.00	258	0.97	214	0.39	184	0.34
G5	204	0.93	16	0.93	279	0.34	331	0.96	109	0.34
G6	228	0.97	353	0.96	262	0.97	320	0.96	151	0.98
G7	218	0.99	346	0.89	273	0.99	283	0.38	121	0.94
G8	177	0.96	36	0.97	308	0.36	222	0.35	110	0.86
G9	180	0.69	307	0.56	18	0.37	299	0.86	129	0.72
G10	184	1.00	346	0.66	317	0.98	279	0.97	152	0.72
G11	132	0.93	302	0.91	247	0.82	287	0.89	139	0.98
G12	229	0.29	29	0.92	281	0.96	290	0.94	135	0.83

From the activity level (number of scratches) and concentration, we determined the median for each bird, and from these 12 medians the grand medians were determined. The medians of activity and concentration as well as the vector lengths r_b per bird were compared with the data of the green and blue control condition, respectively, using the Wilcoxon test for matched pairs of data.

3. RESULTS

The birds' vectors under the various test conditions are listed in tables 1 and 2; figures 1 and 2 give the mean headings of each bird, together with the grand mean vectors. Table 3 summarizes the data of the second-order analysis, including activity and concentration.

Under 424 nm blue and 565 nm green light of 7×10^{15} quanta m^{-2} s^{-1} in the local geomagnetic field, the silvereyes showed a strong preference for their seasonally appropriate southerly migratory direction (figures 1a and 2a); there is no difference between the two groups ($p > 0.05$, Watson Williams test). When tested in a magnetic field with the vertical component inverted, both groups of birds reversed their headings (figures 1b and 2b), indicating that they located their direction with the help of an inclination compass.

When light intensity at the same wavelength was increased about sixfold, the behaviour changed significantly. Under bright blue of 43×10^{15} quanta m^{-2} s^{-1}, the birds often showed axially bimodal behaviour, with this axiality observed at all levels of analysis. About one-third

Table 3. Orientation under blue and green light at two intensities.

(Asterisks at r_N indicate significance by the Rayleigh test; C indicates the respective control condition; ΔC, difference to controls; asterisks at ΔC indicate significance of the difference by the Watson Williams test and, between blue control and bright blue, by the Mardia Watson Wheeler Test. n.s., not significant.)

| light intensity (quanta m^{-2} s^{-1})	magnetic condition	N	median activity	median concentration	median vector length r_b	grand mean vector α_N (deg)	r_N	ΔC (deg)
424 nm blue light								
7×10^{15}	geomagnetic field	12	86	0.37	0.90	192	0.95***	C
	vertical component inverted	12	87	0.38	0.93	355	0.84***	+163***
43×10^{15}	geomagnetic field	12	186	0.26	0.82	341	0.24$^{n.s.}$	+149***
					axial:	93–273	0.56*	−99,+81
565 nm green light								
7×10^{15}	geomagnetic field	12	92	0.35	0.94	188	0.87***	C
	vertical component inverted	12	74	0.34	0.93	360	0.74***	+172***
43×10^{15}	geomagnetic field	12	138	0.32	0.85	283	0.85***	+95***
	vertical component inverted	12	128	0.35	0.71	293	0.63**	+105***
	magnetic north = 240	12	194	0.31	0.85	143	0.92***	−45***
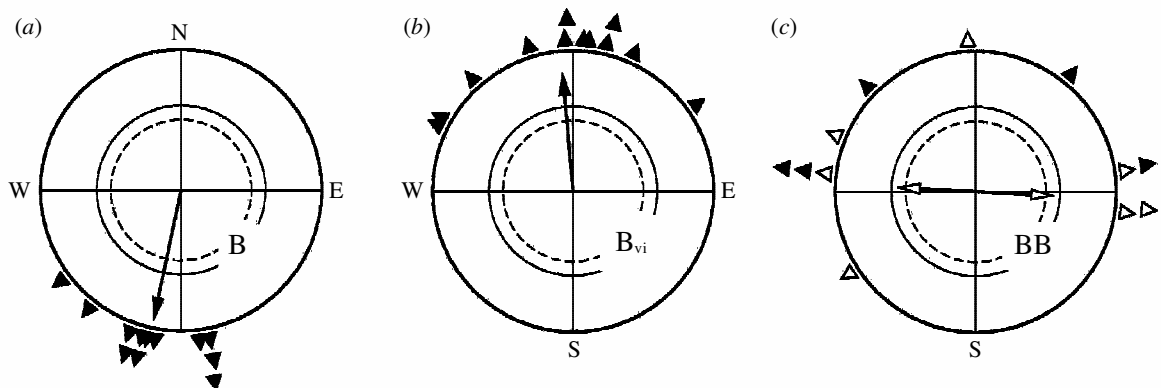
Figure 1. Orientation behaviour under 424 nm blue (B) light with the magnetic field as the only cue. (*a*) Tests under blue with an intensity of 7×10^{15} quanta m^{-2} s^{-1} in the local geomagnetic field; (*b*) under the same blue in a magnetic field with the vertical component inverted (B$_{vi}$) and (*c*) tests under bright blue (BB) with an intensity of 43×10^{15} quanta m^{-2} s^{-1}. The mean headings of the 12 birds are indicated by solid triangles at the periphery of the circle; the grand mean vector is represented by an arrow proportional to the radius of the circle (for numerical values, see table 3); in (*c*) open triangles indicate preferred ends of axial vectors (see text). The inner circles are the 5% (dotted) and the 1% significance border of the Rayleigh test.

of the individual recordings are characterized by an axial distribution of activity. Seven out of the 12 birds had their headings distributed along an axis, with two on one side and the third roughly opposite. The preferred ends of these axes together with the unimodal means of the five other birds indicate an axial preference of the east–west axis (figure 1*c*). Possibly, silvereyes generally show axial responses under bright blue light of the given intensity, but this did not become evident in all of our test birds with only three tests per bird.

Under bright green light of 43×10^{15} quanta m^{-2} s^{-1}, the silvereyes also changed their headings, but in a different way. In the geomagnetic field, they again preferred a west–northwesterly direction (figure 2*c*), that is, the mean direction shifted 95° clockwise with respect to the green

control. Although the present mean heading is about 20° south of the one observed in the two earlier studies under the same light regime (Wiltschko *et al.* 2000*a*,*b*), there is no statistical difference between the three samples ($p > 0.05$, Watson Williams test). Under the same bright green light in a magnetic field with the vertical component inverted, the birds did not change their headings, but continued in west–northwesterly directions (figure 2*d*); the 10° difference in mean between these tests and the ones in the local geomagnetic field is far from significant ($p > 0.05$, Watson Williams test). A change in inclination thus did not affect the birds' directional tendencies. However, when magnetic north was turned by 120° to 240° west–southwest, the birds responded with a corresponding 140° counterclockwise change in direction (figure 2*e*),
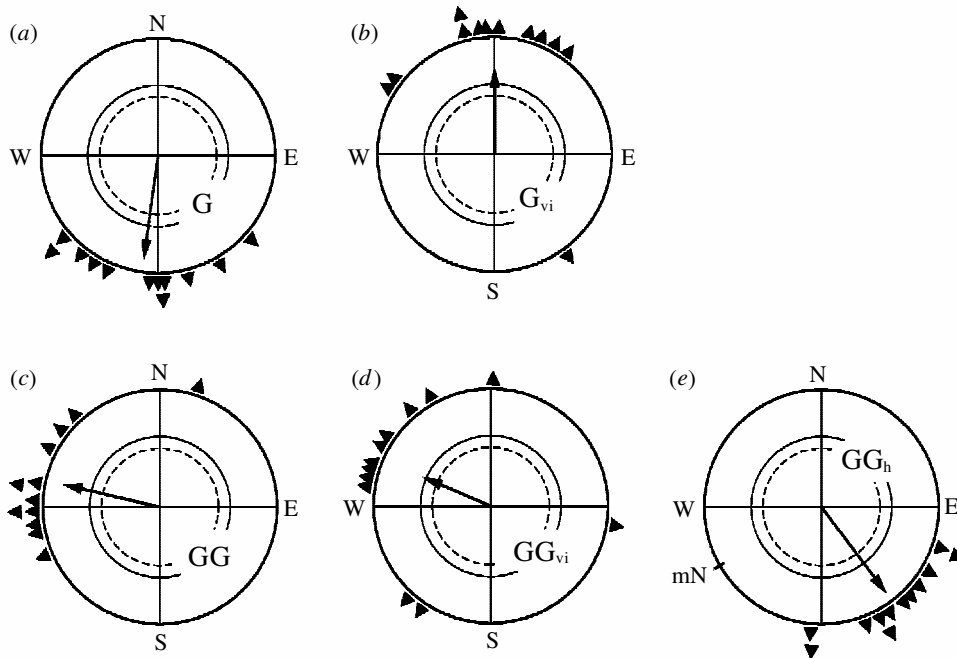
Figure 2. Orientation behaviour under 565 nm green (G) light with the magnetic field as the only cue. (*a,b*) Tests under green with an intensity of 7×10^{15} quanta $m^{-2} s^{-1}$, and (*c–e*) under bright green (GG) with an intensity of 43×10^{15} quanta $m^{-2} s^{-1}$. (*a,c*) Tests in the local geomagnetic field; (*b,d*) in a magnetic field with the vertical component inverted (vi); and (*e*) with magnetic north turned by 120° to west–southwest (h). G, green; GG, bright green; mN, magnetic north; other symbols as in figure 1.

their headings now being significantly different from those in the geomagnetic field ($p < 0.001$, Watson Williams test). In short, under bright green light, the birds' response depends on the direction of the ambient magnetic field, but it does not seem to involve the inclination compass.

In all test conditions, the birds' individual mean vectors, r_b, were rather long. Under green and blue light of 7×10^{15} quanta $m^{-2} s^{-1}$, the medians were 0.90 and above, indicating little intra-individual variation in locating the migratory direction; under the bright light with 43×10^{15} quanta $m^{-2} s^{-1}$, the medians are slightly lower, but these differences are not statistically significant ($p > 0.05$, all comparisons).

The light level also had a certain effect on activity, as the birds tended to be more active under brighter light (see also Wiltschko *et al.* 2000*a*). This difference is significant ($p < 0.05$, Wilcoxon test), except for the tests under bright green with the vertical component of the magnetic field inverted ($p > 0.05$). The concentration of the activity within the recordings is similar in all green light conditions ($p > 0.05$); under bright blue, it was lower than under low intensity blue light ($p < 0.05$).

4. DISCUSSION

Our results clearly show an intensity-dependent change in behaviour that involves not only the directions preferred, but also the mechanisms by which they are located.

(a) *Normal migratory orientation under low intensity light*

Under blue and green light of 7×10^{15} quanta $m^{-2} s^{-1}$, Australian silvereyes preferred their seasonally appropriate southerly migratory direction and reversed their headings

when the vertical component was inverted, the latter indicating normal use of the inclination compass. In an earlier study (Wiltschko *et al.* 1993), we reported northerly tendencies recorded during the southern autumn; together with the present data, they document the expected seasonal change in direction. Under low intensity blue and green light, silvereyes thus show the same responses as observed under 'white' light: their behaviour must be considered to be normal migratory orientation. This, in turn, implies normal magnetoreception under these conditions: as long as the level of monochromatic light remains low, the birds can derive the required directional information from the magnetic field in the usual way.

These findings from silvereyes correspond to recent findings from European robins tested under the same green light of low intensity during spring and autumn and in the geomagnetic field and a field with inverted vertical component (W. Wiltschko *et al.* 2001). So far, all directional responses that show the normal seasonal change were found to reverse when the vertical component is inverted, whereas preferences not showing the seasonal change also appeared to be unaffected by the inversion of the vertical component.

(b) *Why a change in behaviour at higher intensities?*

The reasons for the different behaviour at higher intensities are not entirely clear. The observed amount of activity—it is mostly somewhat higher than that under the lower light level—indicates that the motivation to migrate was not depressed. The fact that the tests under the bright lights were alternated with other tests in the same rooms argues against artefacts of the test rooms. The significant vectors or axes indicate agreement between the birds. In

addition, the preference under bright green shifts with altered magnetic north. These results make a purely non-specific response rather unlikely: the birds prefer directions in response to the direction of the ambient magnetic field.

The specific responses under the 'bright' lights thus seem to be caused by the light regime, but they cannot be attributed to the higher intensity itself, because robins and silvereyes are well oriented in migratory direction when tested under 'white' light of considerably higher intensities. Our 'bright' lights were not extremely bright: they are equivalent to light levels reached after sunset or before sunrise. Even when considering only the specific band of wavelengths involved, the respective portion of the spectrum on a sunny day is brighter by powers of 10. Birds are able to use their magnetic compass during the daytime, as has been shown by Munro & Wiltschko (1993) for a passerine day migrant. Hence the receptors must be expected to work in their normal functional range: the change in behaviour cannot be caused by stimuli being beyond the saturation level. It appears to be the intense light presented by only a narrow band of wavelengths that upsets the magnetoreception system and leads to the change in behaviour.

This leads to explanations based on possible interactions between different types of receptor, which would mean that the behavioural change does not originate in the receptors themselves, but at a higher level. Natural light is always more or less 'white', comprising wavelengths from all parts of the visual spectrum (see McFarland & Munz 1975). If two or more receptors activated by different wavelengths are involved in providing magnetic information, their interaction at a higher level might be upset because the narrow band of monochromatic light leads to an extreme difference between their inputs: larger than can be tolerated without affecting the functionality of the system. The altered output of some higher level units might lead to patterns of activation that birds are unable to interpret in the usual way and thus cannot use for locating their migratory direction.

(c) *Different behavioural patterns at higher intensities*

The significant tendencies observed under higher intensities of light, however, in particular the response to the shift in magnetic north, suggest that the birds still obtain some directional information from the magnetic field. It is unclear, however, whether they still 'believe' that they are orienting in their migratory direction, but are mistaken, or whether they changed their intention for a different heading. When first describing the fixed west-northwesterly preference, we interpreted it as a response 'similar to taxes or alignments' (W. Wiltschko *et al.* 2000*b*). Alignments in magnetic fields have been reported (see R. Wiltschko & Wiltschko 1995); they usually have two features in common, namely (i) they involve the prominent axes of the magnetic field, and (ii) the responses are usually axially bimodal, often even quadrimodal. The axial preference of the east–west axis under bright blue would thus represent a typical alignment, whereas the unimodal preference under bright green in a non-prominent magnetic direction is out of the ordinary.

The difference in behaviour of silvereyes under bright blue and bright green is interesting, because it differs from corresponding results with European robins (W. Wiltschko & Wiltschko 2001): robins also ceased to prefer their migratory direction; but they showed an axial preference of the east–west axis under both bright blue and bright green (see W. Wiltschko & Wiltschko 2001, fig. 1E,G). The difference between robins and silvereyes under bright green might be smaller than it looks, however: the mean headings of the silvereyes, with 283° and 293°, are not very far from the western end of the axis preferred by robins, and the robins had most mean headings at the western end (see W. Wiltschko & Wiltschko 2001, fig. 1G). Muheim *et al.* (2002), testing European robins under similar green light at intermediate light levels of 14 and 29×10^{15} quanta m^{-2} s^{-1}, described a third pattern: an axial preference of the migratory direction and its opposite. However, another pattern was observed in robins under 'bright' turquoise light of 43×10^{15} quanta m^{-2} s^{-1}: a northerly tendency slightly left of the north–northeasterly migratory direction and slightly more scattered (see W. Wiltschko & Wiltschko 2001, fig. 1F).

Altogether, different types of response to higher intensity monochromatic light have been observed at different wavelengths and intensities, with the list probably not complete. Also, it is unknown exactly at what light levels birds begin to change from migratory behaviour to the other types of preference. Tests under 565 nm green indicated that silvereyes were still oriented unimodally in migratory orientation at 22×10^{15} quanta m^{-2} s^{-1} (W. Wiltschko *et al.* 2000*a,b*); robins, by contrast, seem to have changed to an axial tendency along the migratory axis already at 14×10^{15} quanta m^{-2} s^{-1} (Muheim *et al.* 2002). This suggests possible differences between species not only in the preferences under certain light conditions, but also in the intensity where migratory orientation is given up.

At the same time, the different types of preference observed so far indicate that migratory orientation can be replaced by more than one alternative response. What if the different preferences represent transitional steps when the intensity of light is increasing? An increase might thus lead to a sequence of different patterns following one after the other when intensity is further increased. Our previous data (W. Wiltschko & Wiltschko 2001) together with those of Muheim *et al.* (2002) suggest that robins' preference first becomes axial along the migratory axis, and, with further increasing intensity, changes into an axial preference of the east–west axis. The intensity where a specific pattern is observed would vary with wavelength, as the different responses under different wavelengths with the same quantal flux suggest (see W. Wiltschko & Wiltschko 2001). These latter considerations are a highly speculative interpretation of the available data; future experiments will have to show whether the patterns of preference continue to change with increasing intensity as suggested.

(d) *What model can explain a polar response?*

Our finding that magnetic orientation depends on the ambient light regime is in agreement with the two models proposing light-dependent processes on magnetoreception, the Edmonds (1996) model and the radical pair

model recently detailed by Ritz *et al.* (2000). Magnetoreception in the eyes, in particular in the right eye, is supported by new findings from similar cage experiments (W. Wiltschko *et al.* 2002*b*). But, none of the models predicts the observed changes in behaviour with increasing intensity of light. As pointed out above, however, this change appears to arise from neurological interactions of two (or more) receptors with higher units, not at the level of the primary processes covered by the two models.

Interactions between possible types of magnetoreceptor in birds are largely unknown. Deutschlander *et al.* (1999) suggested an antagonistic interaction between short-wavelength and long-wavelength receptors in amphibians, based on a wavelength-dependent shift observed in salamanders (Phillips & Borland 1992, 1994). But although some findings suggest a similar interaction between two types of receptor in birds (see W. Wiltschko & Wiltschko 1999, 2001), a concept like this cannot explain the changes in behaviour observed under identical blue or green wavelengths when the intensity of light is increased without approaching the saturation level.

The most puzzling aspect of our findings, however, is that the west–northwesterly preference under bright green was not reversed when the inclination pointed downwards instead of upwards. This clearly shows that this directional tendency is not based on the magnetic inclination compass. The inclination compass provides birds with axially bimodal information on the course of the field lines without indicating their polarity; unimodal information is obtained by interpreting this axial information with the help of gravity (Wiltschko & Wiltschko 1972). The response under bright green, by contrast, suggests that here the magnetic input itself is unimodal, containing a polar element. This is incompatible with the radical-pair model suggested by Ritz *et al.* (2000) and with the Edmonds (1996) model, because both of these models postulate processes that provide axial information only. It leads to the question whether the birds have switched to another magnetic sense.

Two types of magnetic compass, an inclination compass for shoreward and a polarity compass for homeward orientation, have been described in amphibians (Phillips 1986). Birds, however, seem to use their inclination compass in migration and homing (e.g. Walcott & Green 1974; Visalberghi & Alleva 1979); there are no indications for more than one magnetic compass in birds so far. Looking for an alternative explanation for the behaviour under bright green, magnetoreception based on magnetite is an obvious choice, because magnetite-based mechanisms could, in principle, provide birds with polar information. Phillips *et al.* (2002) recently described an unexplained preference of a northeast–southwest axis in salamanders that appeared to be largely independent of the ambient light regime; in part of the sample, the preference seemed to be related to the orientation of the natural remanent magnetism of the test animals, suggesting that magnetite may be involved in this reponse. Magnetite has also been identified in birds (see, for example, Williams & Wild 2001; Fleissner *et al.* 2003); pulse experiments with migrants suggest that magnetite-based receptors may also play a role in migratory orientation (see, for example, W. Wiltschko *et al.* 1994, 2002*a*; Beason *et al.* 1995). However, inexperienced migrants remained unaffected by the

pulse and continued in the correct migratory direction (Munro *et al.* 1997), and so did experienced birds whose ophthalmic nerve (the nerve innervating the area where magnetite is found) was blocked (Beason & Semm 1996). These observations showed that the magnetic compass was unaffected by the pulse and led to the conclusion that a magnetite-based receptor provides birds with information on position used by experienced migrants for navigation. This is in agreement with electrophysiological findings that units in the ophthalmic nerve respond to small changes in magnetic intensity (Semm & Beason 1990).

An additional function of a magnetite-based receptor such as providing a reference for alignments cannot be excluded. In this case, one would have to postulate that the polar mechanism controlled behaviour only if the inclination compass was not working. Such an assumption meets certain problems, however. Robins tested in the geomagnetic field with their right eye covered were disoriented (Wiltschko *et al.* 2002*b*), suggesting that their only means of orientation was disrupted. The different types of preference observed at higher intensities are likewise difficult to interpret as a magnetite-based alignment, because it is hard to see how a magnetite-based mechanism could be affected by the ambient light regime to produce different patterns. Magnetite thus does not appear to provide a plausible explanation for the birds' polar response under bright green.

5. CONCLUSION

Our test series thus answers the initial questions by revealing a novel kind of response to the magnetic field: these responses are polar and thus fundamentally different from the normal orientation process used for locating the migratory direction. They are incompatible with the light-dependent models of magnetoreception currently in discussion and also with what is known about magnetite-based receptors in birds so far. At the same time, the general phenomenon of changing preferences with increasing intensity of light requires further analysis; the results, whatever the outcome, will have a marked impact on considerations about possible interactions between receptors at higher levels. In summary, the findings presented here urge us to think along new lines, for primary processes as well as for neural interactions.

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