

Light-dependent magnetoreception: orientation behaviour of migratory birds under dim red light

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SUMMARY

Magnetic compass orientation in migratory birds has been shown to be based on radical pair processes and to require light from the short wavelength part of the spectrum up to 565 nm Green. Under dim red light of 645 nm wavelength and 1 mW m⁻² intensity, Australian silvereyes and European robins showed a westerly tendency that did not change between spring and autumn, identifying it as a ‘fixed direction’ response. A thorough analysis revealed that this orientation did not involve the inclination compass, but was a response based on the polarity of the magnetic field. Furthermore, in contrast to the orientation under short-wavelength light, it could be disrupted by local anaesthesia of the upper beak where iron-containing receptors are located, indicating that it is controlled by these receptors. The similarity of the response under dim red light to the response in total darkness suggests that the two responses may be identical. These findings indicate that the observed ‘fixed direction’ response under dim red light is fundamentally different from the normal compass orientation, which is based on radical pair processes.

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Key words: migratory orientation, magnetic compass, ‘fixed direction’ response, magnetoreception, iron-based receptors, radical pair mechanism.

INTRODUCTION

When the light-dependency of the avian magnetic compass was studied in the 1990s, it soon became evident that orientation was possible under ‘white’ and monochromatic blue, turquoise and green light up to about 565 nm, whereas birds were disoriented under 590 nm Yellow and longer wavelengths. This has been shown for migratory birds such as Australian silvereyes *Zosterops l. lateralis* (Wiltschko, W. et al., 1993), European robins *Erithacus rubecula* (Wiltschko, W. and Wiltschko, 1995; Wiltschko, W. and Wiltschko, 1999; Wiltschko, W. and Wiltschko, 2001) and garden warblers *Sylvia borin* (Rappl et al., 2000), with a similar light-dependency indicated in homing pigeons *Columba livia domestica* (Wiltschko, R. and Wiltschko, 1998) and, recently, in domestic chickens *Gallus gallus* (Wiltschko, W. et al., 2007a). In short, the magnetic compass of birds appeared to require light from the short-wavelength part of the spectrum for operation.

In apparent contradiction to these results are the findings from Muheim and colleagues (Muheim et al., 2002), who described oriented behaviour in robins under 617 nm Red. On closer inspection of their data, there are, however, difficulties in interpreting their findings. First, their birds showed westerly headings, a preference that was significantly different from the southerly migratory direction indicated by ringing recoveries. Second, in the control condition under ‘white’ light, their robins also did not show a preference for their migratory direction: they first headed westwards (as under red light) and later ceased to orient altogether. Our birds, by contrast, had always been significantly oriented in migratory direction under ‘white’ light (e.g. Wiltschko, W. et al., 1993; Wiltschko, W. et al., 2004a; Wiltschko, W. et al., 2007b; Wiltschko, W. and Wiltschko

1995; Rappl et al., 2000). Another difference from our studies was the very low light level used by Muheim et al.: they had observed the westerly headings under red light of only 1 mW m⁻², corresponding to 3.2 × 10¹⁵ quanta s⁻¹ m⁻² (Muheim et al., 2002), whereas we had tested our birds under red light of an irradiance between 2.0 and 2.7 mW m⁻², about 6–8 × 10¹⁵ quanta s⁻¹ m⁻².

In view of this unclear situation, we decided to repeat the orientation tests under monochromatic dim red light. First tests in spring 2003 showed that the robins indeed preferred westerly headings under this light regime. That is, we could replicate the findings of Muheim and colleagues (Muheim et al., 2002). However, although these authors had observed the westerly preference during autumn migration, we observed it in spring (see Wiltschko et al., 2004a). Autumn tests under the same dim red light produced corresponding results: the robins continued to head westwards. These observations – the same directional tendencies in spring and in autumn regardless of the migratory direction – clearly show that the behaviour under dim red is not a modification of migratory orientation, but represents a different type of response. Hence we analysed the nature of the observed response with regard to its functional mode and the underlying reception mechanism. This analysis was performed mainly with Australian silvereyes, another bird species that also shows a marked preference of a westerly direction under the dim red light.

MATERIALS AND METHODS

The experiments described in this paper were performed in southern spring 2003 and 2006 in Armidale, NSW, Australia, (30 deg. 30’ S, 151 deg. 40’ E) with Australian silvereyes of the migratory Tasmanian

race; and in autumn 2005 and spring 2006 in Frankfurt (50 deg.08'N, 8 deg.40'E) with European robins.

Test birds

Australian silvereyes of the Tasmanian population are partial migrants, with many of these birds spending their winter on the Australian continent up to northern New South Wales and southern Queensland. They migrate in flocks, predominantly during the twilight hours at dawn and dusk (Lane and Battam, 1971). Twelve test birds each were captured within their wintering range in Armidale on 8 and 9 September 2003 and 14 September 2006. They were housed indoors in groups of four in large cages, with the light regime synchronised with the local photoperiod. Tests began during the last week of September and lasted until mid-October.

European robins breed all over Europe; the northern and eastern populations are nocturnal migrants and winter in the Mediterranean countries. Sixteen robins were mist-netted during September each year in the Botanical Garden near the Zoological Institute at Frankfurt, and identified as trans migrants of probably Scandinavian origin by their wing length. They were kept individually in housing cages in the bird room over the winter. The photoperiod simulated the natural one during the autumn experiments from mid-September to mid-October until the beginning of December; then it was decreased to L:D 8:16; that is, 8 h light and 16 h darkness. Around New Year, the photoperiod was increased in two steps to L:D 13:11. This induced premature readiness for spring migration in early January and allowed us to test the robins for spring experiments from early January to the second half of February.

The silvereyes were released immediately after the end of the tests; the robins at the end of March when the natural photoperiod outside had reached 13 h light.

Test performance

The test protocol was identical in all tests and followed the standard procedures of previous studies (e.g. Wiltschko, W. et al., 1993; Wiltschko, W. and Wiltschko, 1999). The birds were tested one at a time, and their activity was recorded in funnel-shaped cages (Emlen and Emlen, 1966), the inclined walls of which were lined with coated paper (BIC, Germany, formerly Tipp-EX). The birds left scratches on the coating as they moved. Each cage was placed in an aluminium or plastic cylinder, the top of which consisted of the disk carrying the diodes (see below).

For the silvereyes, the daily testing period began about 30 min before sunset; for the robins, testing started about the time when the lights went off in the housing room. For both species, the tests lasted ~75 min, after which the birds were returned to their housing cages. Each bird was tested three times under the same test condition, except when the local anaesthetic Xylocain was applied (see below).

Testing conditions

The tests took place in wooden buildings where the local geomagnetic field was close to normal. All tests with robins were performed in the local geomagnetic field of Frankfurt of 46 μ T, +66 deg. inclination. The silvereyes were tested in the local field of Armidale of 56 μ T, -62 deg. inclination and, in 2003, in two experimental magnetic fields: (1) a field with the vertical component inverted, but unchanged intensity and magnetic North (mN=360 deg., 56 μ T, +62 deg. inclination); and (2) a field with the horizontal component shifted 90 deg. counter-clockwise, but unchanged intensity and inclination (mN=270 deg., 56 μ T, -62 deg. inclination). The experimental fields were produced by Helmholtz coils (2 m

diameter, 1 m clearance), with the coil axis aligned 225 deg.-45 deg. for shifting the horizontal component and vertically for inverting the vertical one. The direction of the magnetic fields was controlled by a free-swinging dip needle (51402, Leybold-Heraeus, Hanau, Germany) the intensity by a Fluxgate Magnetometer MAG-01H (Bartington Instruments, Oxford, UK).

The monochromatic test lights were produced by light-emitting diodes (LEDs) mounted on a plastic disk that was suspended above the test cage. For control, we used green light with a peak wavelength of 565 nm (half bandwidth 553–583 nm) and an intensity of 2 mW m⁻², a light condition under which the silvereyes and the robins have always shown excellent orientation in their natural migratory direction using their inclination compass (Wiltschko, W. et al., 1993; Wiltschko, W. et al., 2001; Wiltschko, W. et al., 2003a). The LEDs producing the dim red test lights had peak wavelengths of 645 nm (half bandwidth 625–666 nm); their intensity was regulated down to 1 mW m⁻² to correspond to that used in the Muheim et al. study (Muheim et al., 2002). This is equivalent to the light level of a largely clear sky about 45 min after sunset or before sunrise. Only in Southern spring in 2003, we also used the red LEDs to produce twice that intensity, 2 mW m⁻². The light level was controlled before each test using a radiometer, Optometer P-9710-1 (Gigahertz Optik, Puchheim, Germany), and the probe 'Visible' RW-3703-2, a silicon photoelement for the wavelength range 400–800 nm, with specific calibrations for the wavelengths of the LEDs used. Owing to the similarity of the behaviour observed under dim red light and in total darkness (see Stapput et al., 2008), we also tested the birds in total darkness in the same test arrangement with the LEDs switched off.

To identify the receptor providing magnetic directions, we also tested silvereyes in 2006 with their upper beak locally anaesthetised using Xylocain 2% (Astra Zeneca, Wedel, Germany: active substance Lidocaine Hydrochloride) to temporarily deactivate the iron-containing structures described by Fleissner et al. (Fleissner et al., 2003; Fleissner et al., 2007) as putative magnetoreceptors (see Wiltschko, R. et al., 2007a). Two tests each were performed per bird under dim red and, as a control, also under green light.

Data analysis

For evaluation, the coated paper was removed from the test cage, divided into 24 sectors of 15 deg., and the number of scratches in each sector was counted. Recordings with fewer than 35 scratches were excluded owing to insufficient migratory activity.

From the distribution of activity, we calculated the heading of each recording. The three (or two) headings of each bird in each condition were pooled for a mean vector of that bird with the heading α_b and the length r_b . The mean headings α_b of the 16 or 12 birds were comprised in the grand mean vector of that test condition with the direction α_N and the length r_N ; these second-order mean vectors were tested for directional preference using the Rayleigh test (Batschelet, 1981), with N being the number of birds tested. From the vector lengths, r_b , of the test birds, we determined the median value characterising the intra-individual variance.

The orientation behaviour of the birds in the various test conditions was compared with their behaviour under the green control light and with their behaviour in the other magnetic conditions or light intensities using the Watson Williams test, which indicates differences in direction, and the Mardia Watson Wheeler test, which indicates differences in distribution (see Batschelet, 1981).

Table 1. Orientation of Australian silvereyes under different light conditions and magnetic conditions

Season	Light condition and local anaesthetic	Magnetic condition	N	Median r_b	Grand mean vector		Angular differences	
					α_N	r_N	ΔC	ΔR
Southern spring 2003	Green	Geomagnetic field	12	0.95	175 deg.	0.86***	C	
	Dim Red	Geomagnetic field	12	0.97	276 deg.	0.89***	+101 deg.***	R
	Dim Red	Vert. comp. inverted	12	0.95	284 deg.	0.92***	+109 deg.***	+8 deg. ^{n.s.}
	Dim Red	mN=270 deg.W	12	0.83	197 deg.	0.92***	+22 deg. ^{n.s.}	-79 deg.***
	Red 2 mW m ⁻²	Geomagnetic field	12	0.76	303 deg.	0.48 ^{n.s.}	(+128 deg.)***	(+27 deg.) ^{n.s.}
Southern spring 2006	Green	Geomagnetic field	12	0.81	194 deg.	0.84***	C	
	Green Xy	Geomagnetic field	12	0.92	190 deg.	0.73**	-4 deg. ^{n.s.}	
	Dim Red	Geomagnetic field	12	0.94	280 deg.	0.61***	+86 deg.***	R
	Dim Red Xy	Geomagnetic field	12	0.63	(98 deg.)	0.06 ^{n.s.}	(-96 deg.)**	(+178 deg.)*
	Total darkness	Geomagnetic field	11	0.86	245 deg.	0.77**	+51 deg.**	-35 deg. ^{n.s.}

Test conditions: Green, 565 nm, 2 mW m⁻²; Dim Red, 645 nm, 1 mW m⁻²; Green Xy and Dim Red Xy, birds tested under these light conditions with their upper beak locally anaesthetised with Xylorin.

Magnetic conditions: Vert. comp. inverted, vertical component inverted; mN=270 deg.W, horizontal component deflected so that magnetic North was shifted to 270 deg. geographic west.

N, number of birds tested; median r_b , median vector length of three (or two) recordings per bird; α_N and r_N , direction and length of the grand mean vector.

The last two columns give the difference from the green control sample (ΔC) and from the sample under dim red (ΔR), set in parentheses if the difference is not based on two significant samples, with asterisks indicating significance by the Watson Williams test, or, if one of the vector lengths was below 0.65, by the Mardia Watson Wheeler test (Batschelet, 1981). Significance levels: *** $P<0.001$; ** $P<0.01$; * $P<0.05$; n.s., not significant.

RESULTS AND DISCUSSION

The behaviour of the Australian silvereyes in the various test conditions is summarised in Table 1, that of European robins in Table 2. For the behaviour of the individual birds, see Tables S1–S4 in the supplementary material.

Changes in behaviour with increasing intensity

Tested under green light in Southern spring, silvereyes headed in their southerly migratory direction, whereas they showed a westerly directional preference under dim red light (Fig. 1, top diagram). Their response under 645 nm Red changed as the ambient light intensity increased: as in robins, it was a clear westerly tendency at 1 mW m⁻²; under 2 mW m⁻², however, the silvereyes were no longer significantly oriented, but still had a considerable vector towards WNW, suggesting a transient state (Fig. 1). At the still higher intensity of 2.7 mW m⁻², they are clearly disoriented with a very short vector (see Wiltschko, W. et al., 1993).

A mechanism based on polarity

The type of mechanism that controlled the westerly preferences observed under dim red light was analysed in silvereyes. The birds were tested in a magnetic field with the vertical component inverted – if they were using an inclination compass, they should reverse their headings. The silvereyes, however, continued to head westwards, showing that their behaviour was a response based on the polarity of the magnetic field, in contrast to the inclination compass that ignores polarity. To control against possible artefacts, we also tested the birds in a field with the horizontal component shifted by 90 deg. to geographic west. Here, the birds altered their headings accordingly (see Fig. 2; for the respective control data, see Fig. 1, upper left diagram), indicating that their directional preferences depended on the ambient magnetic field.

Together, these data clearly show that the westerly tendency observed under dim red light is not controlled by the inclination compass that birds normally employ to locate their migratory direction; instead it involves a different mechanism of polar nature.

Table 2. Orientation of European robins in the local geomagnetic field under different light conditions

Season	Test condition	N	Median r_b	Grand mean vector		Angular differences	
				α_N	r_N	ΔC	ΔR
Autumn 2005	Green	16	0.79	190 deg.	0.73***	C	
	Dim Red	15	0.65	289 deg.	0.72**	+99 deg.***	R
	Total darkness	16	0.77	303 deg.	0.74***	+113 deg.***	+14 deg. ^{n.s.}
Spring 2006	Green	12	0.91	14 deg.	0.88***	C	
	Dim Red	12	0.86	273 deg.	0.85***	-101 deg.***	R
	Total darkness	12	0.83	278 deg.	0.88***	-96 deg.***	+5 deg. ^{n.s.}

Test conditions: Green, 565 nm, 2 mW m⁻²; Dim Red, 645 nm, 1 mW m⁻².

N, number of birds tested; Median r_b , median vector length of three (or two) recordings per bird; α_N and r_N , direction and length of the grand mean vector.

The last two columns give the difference from the green control sample (ΔC) and from the sample under dim red (ΔR), with asterisks indicating significance by the Watson Williams test, or, if one of the vector lengths was below 0.65, by the Mardia Watson Wheeler test (Batschelet, 1981). Significance levels: *** $P<0.001$; ** $P<0.01$; n.s., not significant.

The origin of the directional information

These findings raise the issue of the origin of the directional information that underlies the tendencies observed under dim red light. The inclination compass is located in the right eye (Wiltschko, W. et al., 2002; Wiltschko, W. et al., 2003b), with the respective directional information mediated by radical pair processes (Ritz et al., 2004; Thalau et al., 2005). A second magnetoreceptor has been described in birds in the skin of the upper beak: it consists of iron-rich particles containing magnetite and maghemite embedded in fibres of the ophthalmic nerve (Fleissner et al., 2003; Fleissner et al., 2007). Electrophysiological recordings (Semm and Beason, 1990) and behavioural experiments (Wiltschko, W. et

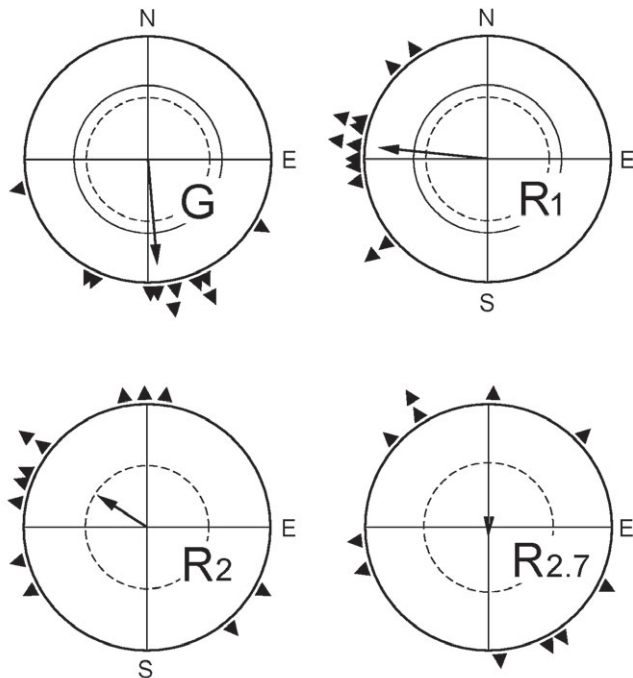


Fig. 1. Orientation of Australian silveryeyes in the geomagnetic field under green and red light. Under 565 nm Green (G), which served as control condition, the birds preferred their seasonally appropriate southerly migratory direction; under dim 645 nm Red, their response depended on the intensity of light: at 1 mW m^{-2} (R_1), they preferred westerly headings, but when the light intensity was increased to 2 mW m^{-2} (R_2) and 2.7 mW m^{-2} ($R_{2.7}$), the headings became increasingly diffuse up to random [data at 2.7 mW m^{-2} redrawn, with permission, from Wiltchko, W. et al. (Wiltchko, W. et al., 1993) and included for comparison]. The triangles at the periphery of the circle mark the mean headings of the individual test birds; the arrows represent the grand mean vector, and the two inner circles are the 5% (broken) and the 1% (unbroken) significance border of the Rayleigh test.

al., 1994; Wiltchko, W. et al., 1998; Wiltchko, W. et al., 2006; Munro et al., 1997) seem to indicate that it mediates information on magnetic intensity for use in the navigational 'map'.

We tested the silveryeyes for an involvement of the receptors in the upper beak by applying the local anaesthetic Xylocain to the skin of the respective region. This temporarily deactivates the

receptors (see Wiltchko, R. et al., 2007a) and, if they are involved, should lead to disorientation. Under green light, the treatment had no effect (Fig. 3, upper diagrams): the birds continued to be significantly oriented in their southerly migratory direction, indicating that these receptors are not involved in normal compass orientation when the birds head in their migratory direction. Under dim red light, by contrast, the birds became disoriented when their upper beak was anaesthetised (Fig. 3, lower right and centre diagram). This clearly shows that the directional information underlying the tendency towards west originates in the iron-based receptors in the upper beak

Responses in total darkness

The westerly tendencies of robins and silveryeyes under dim red light showed a striking similarity with the westerly headings of robins in total darkness (Stapput et al., 2008). It seemed possible that they reflected identical responses. To test this hypothesis, we compared the directional preferences of silveryeyes and robins under dim red light and in total darkness, with green light serving as control condition.

The tests with silveryeyes suffered from the fact that these birds are twilight migrants: there was very little activity in the dark. One bird refused to show any activity under this test condition, three birds produced only one recording and four birds only two. The available recordings resulted in a significant mean heading south of west, with the orientation not statistically different from that of the same birds under dim red light (Table 1; Fig. 3, lower right diagram).

We also compared the behaviour of robins under the same two conditions. This night-migrating species, by contrast, regularly shows activity also in total darkness (see Stapput et al., 2008). The data from the corresponding tests are presented in Fig. 4. Under green light, the birds preferred their seasonally appropriate migratory direction in autumn as well as in spring; under dim red light and in darkness, they headed westwards in both seasons and their orientation under these two conditions did not differ significantly (see Table 2).

These findings support the interpretation that the westerly headings observed under dim red light are identical to the responses in darkness.

GENERAL DISCUSSION

Our results revealed the nature of the responses of the birds under dim red light, which is basically different from normal compass

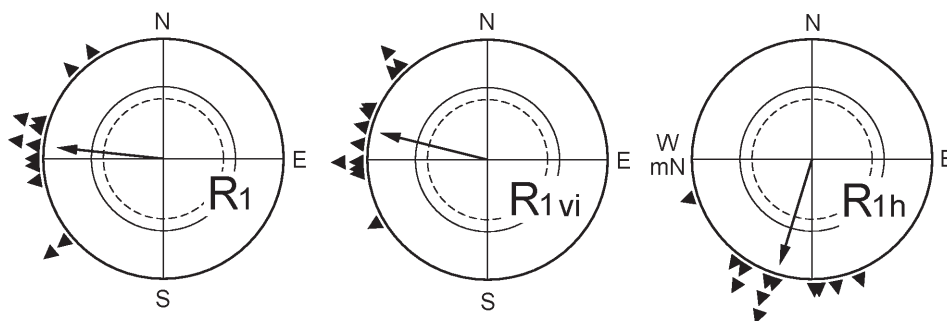


Fig. 2. Orientation of Australian silveryeyes under dim red light and various magnetic conditions, indicating a polar response to the magnetic field: left, tests in the local geomagnetic field (R_1); centre, test in a field with the vertical component inverted (R_{1vi}); right, tests in a field with the horizontal component shifted 90 deg. counter-clockwise to 270 deg. W (R_{1h}). The corresponding control data under green light are given in Fig. 1, upper left diagram. The triangles at the periphery of the circle mark the mean headings of the individual test birds; the arrows represent the grand mean vector, and the two inner circles are the 5% (broken) and the 1% (unbroken) significance border of the Rayleigh test.

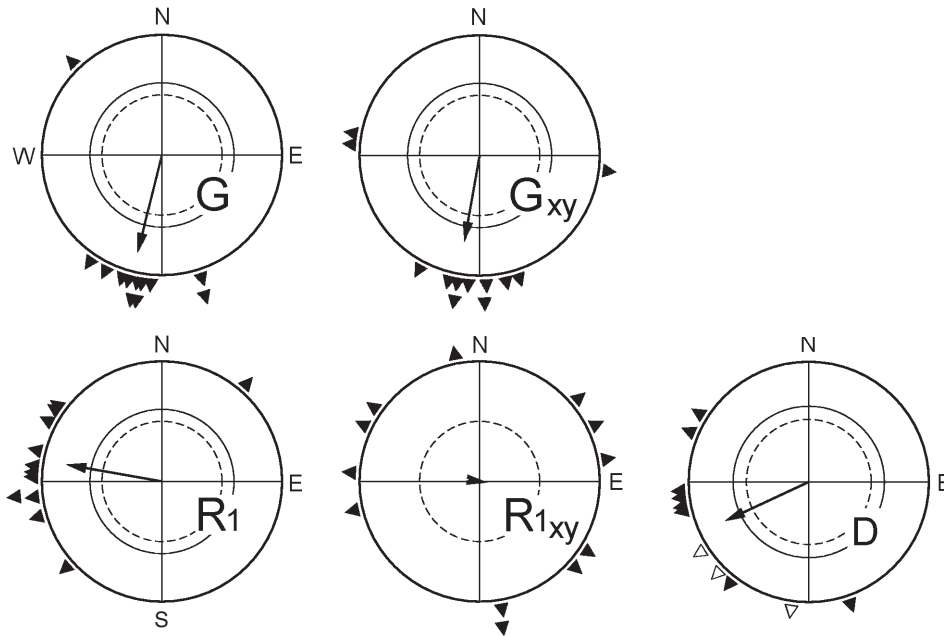


Fig. 3. Orientation of Australian silvereyes under Green (G) and dim red light (R₁) in the local geomagnetic field untreated and with their upper beak locally anaesthetised with Xylocain (G_{xy} and R_{1xy}). The data show that the compass response in migratory direction under green is not affected by Xylocain, whereas the westerly tendency under dim red light is disrupted. Lower right diagram: orientation in total darkness (D); the open arrowheads indicate data points based on one recording only. The triangles at the periphery of the circle mark the mean headings of the individual test birds; the arrows represent the grand mean vector, and the two inner circles are the 5% (broken) and the 1% (unbroken) significance border of the Rayleigh test.

orientation: the fact that orientation does not change between spring and autumn identifies the behaviour as a 'fixed direction' response.

'Fixed direction' responses

Such 'fixed direction' responses have been observed before under specific light regimes. They were first described in Australian silvereyes under monochromatic green of a higher intensity (Wiltschko, W. et al., 2000) and were subsequently also found in European robins under bright monochromatic light, under bichromatic lights combining yellow light with shorter wavelengths (Wiltschko, W. et al., 2004b; Wiltschko, R. et al., 2005; Wiltschko, R. et al., 2007a; Wiltschko, R. et al., 2007b) and recently also in total darkness (Stapput et al., 2008). The behaviour under dim red light appears to be another of these 'fixed direction' responses.

Our analysis of the response under dim red lights revealed two important differences from normal compass orientation: (1) the response does not involve the inclination compass; and (2) the respective directional information originates in the iron-containing receptors in the upper beak. The behaviour under dim red light observed here shares these properties with the other 'fixed direction' responses analysed so far (Wiltschko, R. et al., 2005; Wiltschko, R. et al., 2007b; Stapput et al., 2008) – they seem to be typical for 'fixed direction' responses.

The underlying mechanisms

When Muheim et al. (Muheim et al., 2002) observed a westerly tendency under dim red light, they interpreted it as a shift in direction, inspired by similar findings from Phillips and Borland

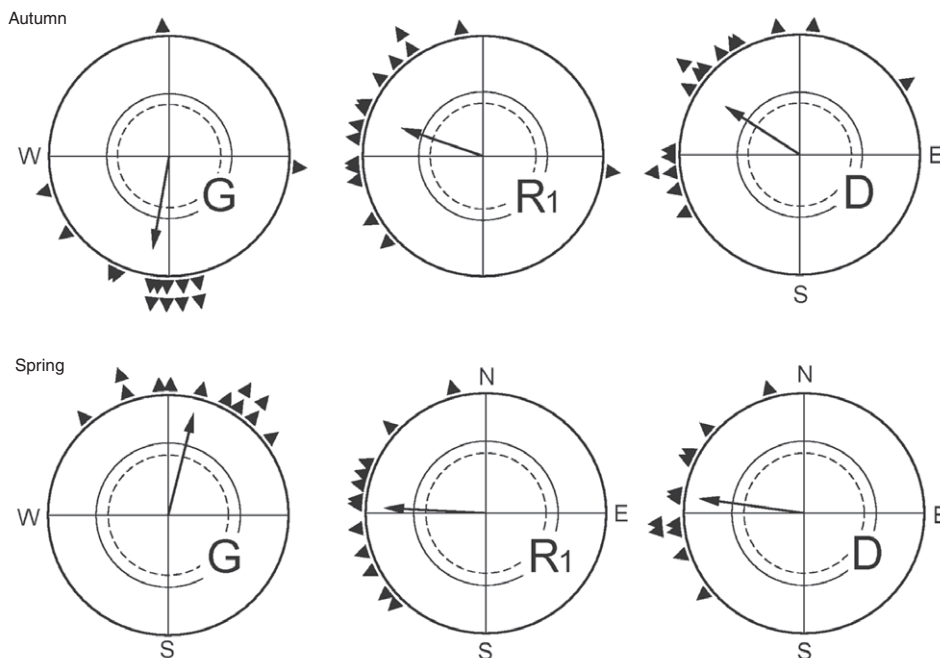


Fig. 4. Orientation of European robins in the local geomagnetic field under green (G, control) light, dim red light (R₁) and in total darkness (D). The triangles at the periphery of the circle mark the mean headings of the individual test birds; the arrows represent the grand mean vector, and the two inner circles are the 5% (broken) and the 1% (unbroken) significance border of the Rayleigh test.

(Phillips and Borland, 1992a; Phillips and Borland, 1992b) (see also Deutschlander et al., 1999a; Deutschlander et al., 1999b). These authors had described a directional shift under long-wavelength light in the newt *Notophthalmus viridescens* (Salamandridae) and attributed this to an antagonistic interaction of two different spectral mechanisms. Muheim et al. (Muheim et al., 2002) adopted that model for their data with birds: they also proposed an antagonistic interaction of two types of photoreceptors, one (activated by short-wavelength light) indicating the directions correctly, the other (activated by long-wavelength light) pointing out directions about 90 deg. shifted with respect to the natural ones. Our analysis, however, identified the behaviour under dim red light as a 'fixed direction' response, a possibility that Muheim et al. (Muheim et al., 2002) did not consider.

This raises the issue of the test conditions that lead to the westerly headings. Those of Muheim et al. (Muheim et al., 2002) and our present ones are not identical, as the peak wavelengths differ by 28 nm: it was 617 nm in the Muheim study and 645 nm in ours, that is, our test lights were farther into the long-wavelength range. Additionally, in the Muheim study, the band of red light was narrower, with a half bandwidth of only 11 nm, compared with 41 nm in our tests. Yet the behaviour of the birds was identical under the two light conditions: it was always a preference slightly north of west. The robins tested by Muheim et al. (Muheim et al., 2002) headed towards 277 deg. in autumn, and our robins headed towards 289 deg. in autumn and towards 271 deg. and 273 deg. in spring (Wiltchko, W. et al., 2004a; and present study), with the silvereyes preferring 276 deg. and 280 deg. in southern spring (present study). This suggests an identical basis for the behaviour under the long-wavelength part of the spectrum.

Two more observations support the homogeneity of behaviour in the range from 580 to 645 nm: (1) when tested at 590 nm Yellow, 635 nm Red and 645 nm Red of a quantal flux of $6\text{--}7 \times 10^{15}$ quanta $\text{s}^{-1} \text{m}^{-2}$, robins were first disoriented, but regained their ability to orient using their magnetic compass after 1 h of pre-exposure to light of the respective wavelength (Wiltchko, W. et al., 2004b; and unpublished data). (2) Electrophysiological recordings by Semm and Demaine (Semm and Demaine, 1986) from the nucleus of the basal optic root (nBOR) of pigeons under light of various wavelength showed single neurons with a high level of activation from 582 to 674 nm. Hence, different mechanisms within this wavelength range appear highly unlikely, and for that reason we assume that behaviour within the entire range from 580 to 650 nm is controlled by the same mechanism.

This means, however, that our present findings also apply to the experiments by Muheim and colleagues (Muheim et al., 2002), which should no longer be cited as evidence for a wavelength-dependent shift in the compass response. Instead of being caused by an interaction between two antagonistic spectral mechanisms, the response under dim red light can be explained by the use of the light-independent iron-containing receptors in the upper beak (Fleissner et al., 2003; Fleissner et al., 2007) – it does not seem to involve any spectral mechanism. The similarity between the responses of the birds in total darkness and under dim red light further supports this view, and suggests that both responses are due to the same underlying mechanism (see below).

The apparently similar behaviour of amphibians under red light (Phillips and Borland, 1992a; Phillips and Borland, 1992b) has yet to be analysed in detail, in particular with respect to the inclination compass. As an iron-based mechanism is also indicated in salamanders (Brassart et al., 1999; Phillips et al., 2002), further experiments need to investigate whether or not the directional

information underlying their behaviour under red light involves light-dependent or magnetite-based receptors.

Similarity between dim red light and darkness

Another aspect of our findings concerns the great similarity between the behaviour under dim red light and that in total darkness. The robins prefer the same westerly headings in both conditions, and the two responses show the same characteristics, involving a polar mechanism based on magnetic information from the receptors in the upper beak (see Stapput et al., 2008). This suggests that the westerly headings under dim red light may have nothing to do with the wavelength of that light, but simply represent the response of the birds in darkness. The light level of the dim red light was rather low, and the sensitivity of the rods decreases at wavelengths beyond 600 nm. At the same time, the long wavelengths receptor that may have been activated by this wavelength is the least sensitive of the four avian colour cones (Maier, 1992). In view of this, it seems possible that the dim red light appeared virtually 'dark' to the birds, and they showed the corresponding response.

It is not surprising that the normal inclination compass does not work under the dim red test lights: these light conditions do not support the underlying radical pair processes. It is unclear, however, why birds – robins, silvereyes and garden warblers as well as pigeons and chickens – show disorientation under red light of higher intensities (e.g. Wiltchko, W. et al., 1993; Wiltchko, W. et al., 2004a; Wiltchko, W. et al., 2007a; Wiltchko, W. and Wiltchko, 1995; Munro et al., 1997; Wiltchko, R. and Wiltchko, 1998; Rappal et al., 2000). It seems as though the behaviour changes once the red light becomes visible to the birds. This disorientation appears to reflect a lack of directional information – the birds are no longer able to find their way. One would expect that if the inclination compass by the radical pair mechanism was not available because of the long wavelengths, they might fall back on the directional information that originates in the receptors in the upper beak. But apparently this is normally not the case. This suggests complex interactions between the photoreceptors, the receptors providing magnetic information by radical pair processes and the iron-based magnetic receptor system in the upper beak that require further analysis to be fully understood.

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