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.

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 orientation under dim red light.
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 transmigrants 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 Tip-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 $46 \mu T$, +66 deg. inclination. The silvereyes were tested in the local field of Armidale of $56 \mu T$, −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., $56 \mu T$, +62 deg. inclination); and (2) a field with the horizontal component shifted 90 deg. counter-clockwise, but unchanged intensity and inclination (mN=270 deg., $56 \mu T$, −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 under 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 $\alpha_b$ and the length $r_b$. The mean headings $\alpha_b$ of the 16 or 12 birds were comprised in the grand mean vector of that test condition with the direction $\alpha_{MN}$ and the length $r_{MN}$; 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).
Magnetic conditions: Vert. comp. inverted, vertical component inverted; mN 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).

Changes in behaviour with increasing intensity

Tested under green light in Southern spring, silvereyes headed in a westerly direction; instead it involves a different mechanism of polar nature.

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

<table>
<thead>
<tr>
<th>Season</th>
<th>Light condition and local anaesthetic</th>
<th>Magnetic condition</th>
<th>N</th>
<th>Median $r_b$</th>
<th>$\alpha_N$</th>
<th>$\alpha_R$</th>
<th>$\Delta \alpha$</th>
<th>$\Delta r$</th>
<th>$\Delta C$</th>
<th>$\Delta R$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Southern spring 2003</td>
<td>Green</td>
<td>Geomagnetic field</td>
<td>12</td>
<td>0.95</td>
<td>175 deg.</td>
<td>0.86***</td>
<td>C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dim Red</td>
<td>Geomagnetic field</td>
<td>12</td>
<td>0.97</td>
<td>276 deg.</td>
<td>0.89***</td>
<td>+101 deg.</td>
<td>R</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dim Red</td>
<td>Vert. comp. inverted</td>
<td>12</td>
<td>0.95</td>
<td>284 deg.</td>
<td>0.92***</td>
<td>+109 deg.</td>
<td>+8 deg. n.s.</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dim Red</td>
<td>mN=270 deg.W</td>
<td>12</td>
<td>0.83</td>
<td>197 deg.</td>
<td>0.92***</td>
<td>+22 deg. n.s.</td>
<td>–79 deg.***</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Red 2 mW m–2</td>
<td>Geomagnetic field</td>
<td>12</td>
<td>0.76</td>
<td>303 deg.</td>
<td>0.48 n.s.</td>
<td>(+128 deg.)**(+)27 deg.) n.s.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Southern spring 2006</td>
<td>Green</td>
<td>Geomagnetic field</td>
<td>12</td>
<td>0.81</td>
<td>194 deg.</td>
<td>0.84***</td>
<td>C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Green Xy</td>
<td>Geomagnetic field</td>
<td>12</td>
<td>0.92</td>
<td>190 deg.</td>
<td>0.73**</td>
<td>–4 deg. n.s.</td>
<td>C</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dim Red</td>
<td>Geomagnetic field</td>
<td>12</td>
<td>0.94</td>
<td>280 deg.</td>
<td>0.61***</td>
<td>+86 deg.***</td>
<td>R</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dim Red Xy</td>
<td>Geomagnetic field</td>
<td>12</td>
<td>0.63</td>
<td>(98 deg.)</td>
<td>0.06 n.s.</td>
<td>(–96 deg.)**</td>
<td>(+178 deg.)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total darkness</td>
<td>Geomagnetic field</td>
<td>11</td>
<td>0.86</td>
<td>245 deg.</td>
<td>0.77**</td>
<td>+51 deg.**</td>
<td>–35 deg. n.s.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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.

The last two columns give the difference from the green control sample ($\Delta C$) and from the sample under dim red ($\Delta R$), 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.

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 Xylocain.

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.

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

<table>
<thead>
<tr>
<th>Season</th>
<th>Test condition</th>
<th>N</th>
<th>Median $r_b$</th>
<th>$\alpha_N$</th>
<th>$\alpha_R$</th>
<th>$\Delta \alpha$</th>
<th>$\Delta r$</th>
<th>$\Delta C$</th>
<th>$\Delta R$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Autumn 2005</td>
<td>Green</td>
<td>16</td>
<td>0.79</td>
<td>190 deg.</td>
<td>0.73***</td>
<td>C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dim Red</td>
<td>15</td>
<td>0.65</td>
<td>288 deg.</td>
<td>0.72***</td>
<td>+99 deg.***</td>
<td>R</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total darkness</td>
<td>16</td>
<td>0.77</td>
<td>303 deg.</td>
<td>0.74***</td>
<td>+113 deg.***</td>
<td>+14 deg. n.s.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring 2006</td>
<td>Green</td>
<td>12</td>
<td>0.91</td>
<td>14 deg.</td>
<td>0.88***</td>
<td>C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dim Red</td>
<td>12</td>
<td>0.86</td>
<td>273 deg.</td>
<td>0.85***</td>
<td>–101 deg.***</td>
<td>R</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Total darkness</td>
<td>12</td>
<td>0.83</td>
<td>278 deg.</td>
<td>0.88***</td>
<td>–96 deg.***</td>
<td>+5 deg. n.s.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

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.

A mechanism based on polarity

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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.

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 (Semml and Beason, 1990) and behavioural experiments (Wiltschko, W. et
Bird orientation under dim red light

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

The tests with silvereyes 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 Stappput 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
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 dichromatic 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; Stapput et al., 2008) 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...
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 Stapp 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. Wiltschko, W. et al., 1993; Wiltschko, W. et al., 2004a; Wiltschko, W. et al., 2007a; Wiltschko, W. and Wiltschko, 1995; Munro et al., 1997; Wiltschko, R. and Wiltschko, 1998; Rapp 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.

Our work was supported by the Human Frontier Science Program (grant to R.W.) and the Deutsche Forschungsgemeinschaft (grant to W.W.). We sincerely thank S. Debou and G. Lollback for catching the silvereyes; F. Geiser for logistic support and the Deutsche Forschungsgemeinschaft (grant to W.W.). We sincerely thank S. Münzner and A. Wagner for their help with the robin experiments; and J. Phillips and an anonymous referee for helpful comments. The experiments with silvereyes were performed in accordance with the rules and regulations of animal welfare in Australia, those with robins with the rules and regulations of animal welfare in Germany.

**REFERENCES**


