The Journal of Experimental Biology 214, 3096-3101

doi:10.1242/jeb.059212

RESEARCH ARTICLE

Magnetic orientation of migratory robins, *Erithacus rubecula*, under long-wavelength light

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Accepted 24 June 2011

SUMMARY

The avian magnetic compass is an inclination compass that appears to be based on radical pair processes. It requires light from the short-wavelength range of the spectrum up to 565 nm green light; under longer wavelengths, birds are disoriented. When pre-exposed to longer wavelengths for 1 h, however, they show oriented behavior. This orientation is analyzed under 582 nm yellow light and 645 nm red light in the present study: while the birds in spring prefer northerly directions, they do not show southerly tendencies in autumn. Inversion of the vertical component does not have an effect whereas reversal of the horizontal component leads to a corresponding shift, indicating that a polar response to the magnetic field is involved. Oscillating magnetic fields in the MHz range do not affect the behavior but anesthesia of the upper beak causes disorientation. This indicates that the magnetic information is no longer provided by the radical pair mechanism in the eye but by the magnetite-based receptors in the skin of the beak. Exposure to long-wavelength light thus does not expand the spectral range in which the magnetic compass operates but instead causes a different mechanism to take over and control orientation.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/214/18/3096/DC1

Key words: magnetic compass, magnetoreception, magnetite-based receptors, oscillating fields, radical pair processes, wavelength dependency.

INTRODUCTION

The avian magnetic compass is an inclination compass: the birds do not use the polarity of the magnetic field but instead rely on the axial course of the field lines and their inclination in space (Wiltschko and Wiltschko, 1972). This seemingly odd functional mode arises from the underlying physical mechanism mediating magnetic directions: the magnetic compass of birds is based on radical pair processes (Ritz et al., 2000; Ritz et al., 2004; Thalau et al., 2005). The initial step of magnetoreception, the formation of radical pairs, involves the absorption of photons by specialized photopigments, which makes the avian magnetic compass light dependent. A wavelength dependency has been demonstrated in numerous behavioral experiments with migratory birds under low monochromatic lights; magnetic compass orientation was observed only under light from the short-wavelength end of the spectrum, from below 370 nm ultraviolet to about 567 nm green light (Muheim et al., 2002). From 580 nm yellow light onward, birds were no longer oriented (for a review, see Wiltschko, R. et al., 2010a). Interestingly, when migratory birds had been pre-exposed to red light for 1 h prior to testing, they were oriented also under red light – the exposure to red light seemed to have conferred the ability to detect magnetic directions under longer wavelengths (Wiltschko, W. et al., 2004).

Aside from compass information, a second type of directional response to the magnetic field has been observed under extreme light conditions, such as bright monochromatic light, bichromatic lights combining short-wavelength and yellow light or in total darkness, namely so-called ‘fixed direction responses’. They differ from normal migratory orientation, being fixed in the sense that they do not show the seasonal change between spring and autumn. Their manifestation differs in that the direction depends on the ambient light regime (Wiltschko et al., 2010a). The analysis of the underlying processes revealed that they are indeed fundamentally different from normal compass orientation: they are polar responses to the magnetic field. Oscillating fields in the MHz range that interfere with the radical pair processes, and were found to disrupt the magnetic compass, do not affect ‘fixed direction’ responses. Instead ‘fixed directions’ break down into disorientation when the magnetite-based receptors in the upper beak (see Fleissner et al., 2003; Fleissner et al., 2007; Falkenberg et al., 2010) are temporarily disabled with the help of a local anesthetic, indicating that the magnetic information on which they are based originates in these receptors (see Wiltschko, R. et al., 2010a).

The occurrence of this second type of directional response raised the question about the nature of the orientation under long-wavelength light. The directions preferred under red light after pre-exposure seemed to coincide with the migratory direction, suggesting that the observed behavior was compass orientation (Wiltschko, W. et al., 2004). However, to make sure, we decided to analyze the responses under red light after pre-exposure more thoroughly: (1) by inverting the vertical component of the local magnetic field in order to test whether they were controlled by the inclination compass; and (2) by applying oscillating fields and a local anesthetic to the upper beak in order to identify the underlying mechanism. And, while the former tests with pre-exposure (Wiltschko, W. et al., 2004) were performed under red light only, we now included corresponding tests under yellow light at a wavelength just beyond those that still allowed magnetic orientation.

MATERIALS AND METHODS

The experiments were performed in Frankfurt, Germany (50°08′N, 8°40′E), during spring migration in 2006, 2007 and 2010 and autumn migration in 2007, 2008 and 2010.

Test birds

The test birds were European robins, *Erithacus rubecula* (L.) (Turdidae). This species breeds all over Europe; the northern and eastern populations are nocturnal migrants and winter in the Mediterranean countries. Robins were mist-netted during September each year in the Botanical Garden at the Zoological Institute in 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, when it was decreased to 8 h:16 h light:dark. Around New Year, the photoperiod was increased in two steps to 13 h:11 h light:dark. 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.

At the end of March when the natural photoperiod outside had reached 13 h light, the test birds were released at the site of capture.

Test performance

The test protocol followed the procedures of the previous study (Wiltschko et al., 2004). On a testing day, the birds to be tested were moved in cages in a pre-exposure room about 3 h before the beginning of the tests. Here they stayed under normal 'white' light until about 1 h before testing, when the red or yellow light-emitting diodes (LEDs) were additionally switched on. At the time when their normal photoperiod ended, the 'white' light was switched off, and the birds remained under monochromatic red or yellow light of an intensity of about 15 mW m^{-2} and 6.5 mW m^{-2}, respectively, for another hour, before they were placed in the test cages.

The birds were tested one at a time, and their activity was recorded in funnel-shaped cages (Emlen and Emlen, 1966) whose inclined walls were lined with coated paper (BIC, Germany, formerly Tipp-EX) or, in the 2010 experiments, lined with thermo-paper (Blumberg Systempapiere, Ratinger-Lintorf, Germany) (see Mouritsen et al., 2009), where they left marks as they moved. Each cage was placed in an aluminum or plastic cylinder whose top consisted of the disk carrying the LEDs (see below).

Testing lasted approximately 75 min or, when thermo-paper was used, approximately 60 min. After this the birds were returned to their housing cages. Each bird was tested three times in each condition. Between the tests described here, the birds were tested under additional conditions with different light regimes that were part of other test series.

Testing conditions

The monochromatic test lights were produced by LEDs that were mounted in three circles of eight diodes each on a plastic disk, which 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 1.9 mW m^{-2}, a light condition where robins had always shown excellent orientation in their natural migratory direction using their inclination compass (see Wiltschko, R. et al., 2010a). The LEDs producing the red test lights had peak wavelengths of 645 nm (half bandwidth 625–666 nm); those producing the yellow test light of 582 nm (half bandwidth 443–601 nm). Their intensity was set to 1.7 mW m^{-2} and 1.8 mW m^{-2}, respectively, to be of equal quantal flux with the green control light. The light level was controlled before each test using a radiometer, Optometer P-9710-1 with the probe 'Visible' RW-3703-2, a silicon photo-element for the wavelength range 400–800 nm (Gigahertz Optik, Puchheim, Germany), with specific calibrations for the wavelengths of the LEDs.

The robins were tested in the local geomagnetic field of Frankfurt of 47 μT, +66 deg inclination and in two experimental magnetic fields: (1) a field with the vertical component inverted but unchanged intensity and magnetic North (mN=360 deg, 47 μT, –66 deg inclination); and (2) under yellow light only, in a field with the horizontal component reversed, but with unchanged intensity and inclination (mN=180 deg, 47 μT, +66 deg inclination). These experimental fields were produced by Helmholtz coils (2 m diameter, 1 m clearance), with the coil axis positioned vertically to invert the vertical component and horizontally along the North–South axis to reverse the horizontal component. The direction of the magnetic fields was controlled by a free-swinging dip needle (51402, Leybold-Heraeus, Hanau, Germany), and the intensity was controlled by a Fluxgate Magnetometer MAG-01H (Bartington Instruments, Oxford, UK).

To identify the receptor mechanism providing the magnetic directions, we also tested the robins: (1) with an oscillating field of 1.315 MHz, the local Larmor frequency, added vertically, i.e. at 24 deg with respect to the magnetic vector (see Thalau et al., 2005); and (2) with their upper beak locally anesthetized by Xylocaine 2% [(AstraZeneca, Wedel, Germany) active substance: lidocaine hydrochloride] to temporarily deactivate the iron-containing structures in the upper beak (see Fleissner et al., 2003; Fleissner et al., 2007; Falkenberg et al., 2010). These tests were performed under red as well as under yellow light.

The experiments were conducted according the rules and regulations for animal protection in Germany.

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 due to insufficient migratory activity.

From the distribution of activity, we calculated the heading of each recording. However, in many cases, the activity was axially distributed; here, we calculated the axial vector and used the end of this axis with more activity for further analysis. The three headings of each bird in each condition were pooled for the mean vector of that bird with the heading α_b and the length $\mathbf{r}_b$. We also calculated the corresponding axial vector. The mean headings α_b of the 16 or 12 birds or, if the axial vector was longer, the end of the axis closest to the unimodal direction were comprised in the grand mean vector of that test condition with the direction α_N and the length $\mathbf{r}_N$ or in the grand mean axis α_{N2}–α_{N2} with the length $\mathbf{r}_{N2}$, giving each mean equal weight. These second-order mean vectors or axes were tested for directional preference using the Rayleigh test (Batschelet, 1981), with N being the number of birds tested. From the unimodal or axial vector lengths $\mathbf{r}_b$ of the test birds, we determined the median value characterizing the intra-individual variance.

The orientation behavior of the birds in the various test conditions was compared with that under the green control light, with that in the other test conditions under the same light and the behavior in corresponding test conditions under different wavelengths using the Mardia–Watson–Wheeler test indicating differences in distribution (see Batschelet, 1981).

Table 1. Data of the autumn experiments in the geomagnetic field

Light	Year	*N*	$\mathbf{r}_b$	ax	α_N (deg)	$\mathbf{r}_N$
G	2007	16	0.95	6	178	0.80***
G	2008	16	0.85	6	189	0.73***
G	2010	16	0.68	8	220	0.54**
RpeR	2007	16	0.89	10	11– 191	0.85***
RpeR	2008	16	0.76	9	30–210	0.60**
YpeY	2010	16	0.70	8	1	0.53**

Light: G, under green (control); RpeR, under red light after 1 h pre-exposure to red light; YpeY, under yellow light after 1 h pre-exposure to yellow light. *N*, number of birds tested; $\mathbf{r}_b$, median vector length per bird (based on three recordings); ax, number of birds showing axial behavior; α_N and $\mathbf{r}_N$, direction and lengths of grand mean vector, respectively. Asterisks at $\mathbf{r}_N$ indicate significance by the Rayleigh test: ***P*<0.01; ****P*<0.001.

RESULTS

Table 1 gives the data obtained in autumn under 565 nm green light and, after pre-exposure, under 582 nm yellow light and 645 nm red light. Table 2 gives the data obtained in spring in the various test conditions. The data for the individual birds are given in supplementary material Tables S1 and S2.

In autumn, the birds were tested in the geomagnetic field only. They were oriented in all three light conditions but in different ways (Fig. 1). In the control condition under green light, they preferred their seasonally appropriate southerly migratory direction. Under yellow light, they showed a weak northerly preference, with two birds heading South, and under red light, they showed a pronounced axial preference of a NNE–SSW axis, where it is not possible to decide whether it corresponds to the North–South axis or to the migratory axis. Both distributions under long-wavelength light are significantly different from that in the control condition (yellow: *P*<0.001; red: *P*<0.05). The number of birds with an axial preference was rather high, even in the control condition (see Table 1).

In spring we analyzed the behavior under yellow and red light after pre-exposure in more detail (Fig. 2). In the geomagnetic field, the birds headed slightly east of North, and their behavior does not differ from the orientation in the northern migratory direction observed in the control condition under green light (*P*>0.05, both samples). When the vertical component of the magnetic field was inverted, the birds tested under yellow light showed an axis tendency with the majority of birds continuing to head North; the birds tested under red light also headed North. Both these distributions do not differ statistically from those observed under the same light in the geomagnetic field (*P*>0.05). When the horizontal component is reversed, however, the birds showed a corresponding shift in heading, so that this distribution is different from the control and from that obtained under yellow light in the geomagnetic field (*P*<0.001, both samples). Together this indicates that the robins used the magnetic field for orientation, but their response was polar, indicating that it was not controlled by the inclination compass.

The following tests were designed to determine the origin of the directional information used. When an oscillating field of 1.315 MHz, 480 nT was added, the birds under yellow light as well as under red light showed oriented behavior, which was not significantly different from that observed under the green control light and from the tests under yellow or red light in the geomagnetic field (*P*>0.05, all samples). Under red light, we also tested the robins in a much stronger oscillating field with an intensity of 4800 nT, i.e. more than 1/10 of the geomagnetic field but without affecting their behavior (comparison with orientation under red light in the geomagnetic field: *P*>0.05; see Table 2). This indicates that the radical pair mechanism in the eye was not involved. When the beak was locally anesthetized to temporally deactivate the magnetite-based receptors, however, the birds became disoriented under yellow light as well as under red light (Fig. 3). Both distributions are significantly different from control (*P*<0.001, both samples) and from the corresponding samples without this treatment (yellow light, *P*<0.05; red light, *P*<0.01), identifying the magnetite-based receptors as the source of magnetic information.

Comparing the behavior under 582 nm yellow light and under 645 nm red light under the corresponding test conditions, we never found a significant difference between distributions of headings under the two wavelengths (*P*>0.05, all four comparisons).

Table 2. Data of the spring experiments

Light	Magnetic field	Other treatment	Year	*N*	$\mathbf{r}_b$	ax	α_N (deg)	$\mathbf{r}_N$
G	Geomagnetic field	None	2006	12	0.90	3	14	0.90***
G	Geomagnetic field	None	2007	23	0.97	3	28	0.95***
G	Geomagnetic field	None	2010	12	0.94	1	7	0.96***
RpeR	Geomagnetic field	None	2006	12	0.95	1	2	0.88***
RpeR	Geomagnetic field	None	2007	12	0.95	5	9	0.80***
RpeR	Vertical component inverted	None	2007	12	0.86	3	352	0.72***
RpeR	Geomagnetic field	1.3 MHz, 480 nT	2006	12	0.82	1	8	0.86***
RpeR	Geomagnetic field	1.3 MHz, 4800 nT	2007	12	0.78	3	10	0.80***
RpeR	Geomagnetic field	Beak anesthetized	2007	12	0.72	4	16	$0.19^{\text{n.s.}}$
YpeY	Geomagnetic field	None	2010	12	0.90	0	10	0.74***
YpeY	Vertical component inverted	None	2010	12	0.80	5	1–181	0.60*
YpeY	Horizontal component reversed	None	2010	12	0.92	3	172	0.83***
YpeY	Geomagnetic field	1.3 MHz, 480 nT	2010	12	0.84	4	7–187	0.57*
YpeY	Geomagnetic field	Beak anesthetized	2010	12	0.78	7	252	$0.12^{\text{n.s.}}$

For light conditions and abbreviations, see Table 1. 1.3 MHz and 480 nT (or 4800 nT) indicate the frequency and intensity, respectively, of the added oscillating field. Asterisks at $\mathbf{r}_N$ indicate significance by the Rayleigh test: **P*<0.05; ***P*<0.01; ****P*<0.001. n.s., not significant.

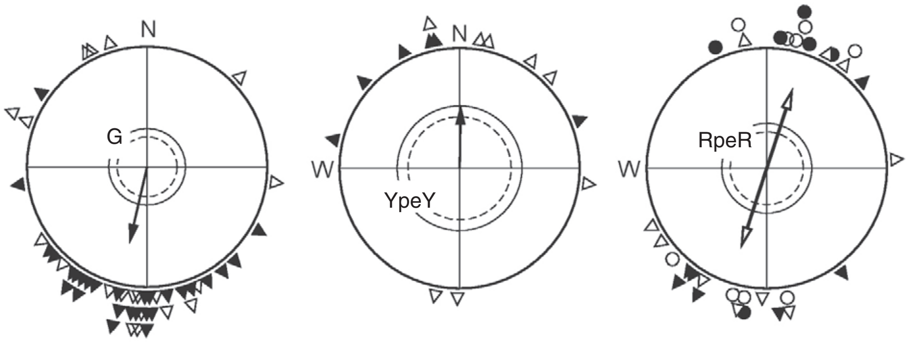

Fig. 1. Autumn experiment in the geomagnetic field. G, under 565 nm green light (control); YpeY, under 582 nm yellow light after 1 h pre-exposure to yellow light; RpeR, under 645 nm red light after 1 h pre-exposure to red light, with triangles marking data from autumn 2007 and circles data from autumn 2008. The symbols at the periphery mark the mean headings of individual birds (based on three recordings): solid symbols, unimodal preferences; open symbols, preferred ends of axes. The arrows indicate the grand mean vectors (solid arrow tips) or the grand mean axis (open arrow tips), with the two inner circles representing the 5% (dotted) and the 1% significance border of the Rayleigh test.

DISCUSSION

Normal migratory orientation, as observed under 'white' light and under monochromatic green, turquoise and blue light, shows seasonal changes, with birds heading southward in autumn and northward in spring. It is controlled by the inclination compass, indicated by the reversal of headings when the vertical component of the magnetic field is inverted (see Wiltschko, R. et al., 2010a). Oscillating fields in the MHz range lead to disorientation (Ritz et al., 2004; Thalau et al., 2005), while anesthesia of the upper beak have no effects (for a review, see Wiltschko, R. et al., 2010a). The orientation observed here under monochromatic 582 nm yellow light and 645 nm red light after pre-exposure to these lights proved to be fundamentally different: there was no clear reversal between autumn and spring, and an inversion of the vertical component did not lead to a significant change in behavior. Oscillating fields failed to have an effect whereas anesthesia of the receptors in the beak caused a breakdown in orientation. Altogether, the behavior under yellow and red light after pre-exposure showed conspicuous similarities with the so-called 'fixed direction responses' observed under extreme light conditions, in particular because the directional information likewise does not originate in radical pair processes in the eye but is mediated by the magnetite-based receptors (see Wiltschko, R. et al., 2010a).

When we did our earlier experiments under red light after pre-exposure to red light (Wiltschko, W. et al., 2004), we had interpreted the observed behavior as migratory orientation, because the birds had been heading South in autumn. Our present autumn data look different, with scattered headings towards North and axial North–South preferences. Yet a more detailed analysis of the earlier data also revealed considerable axial tendencies; many recordings were axial rather than unimodal, and nine of the 16 birds tested had axial vectors that exceeded the unimodal ones, indicating that two

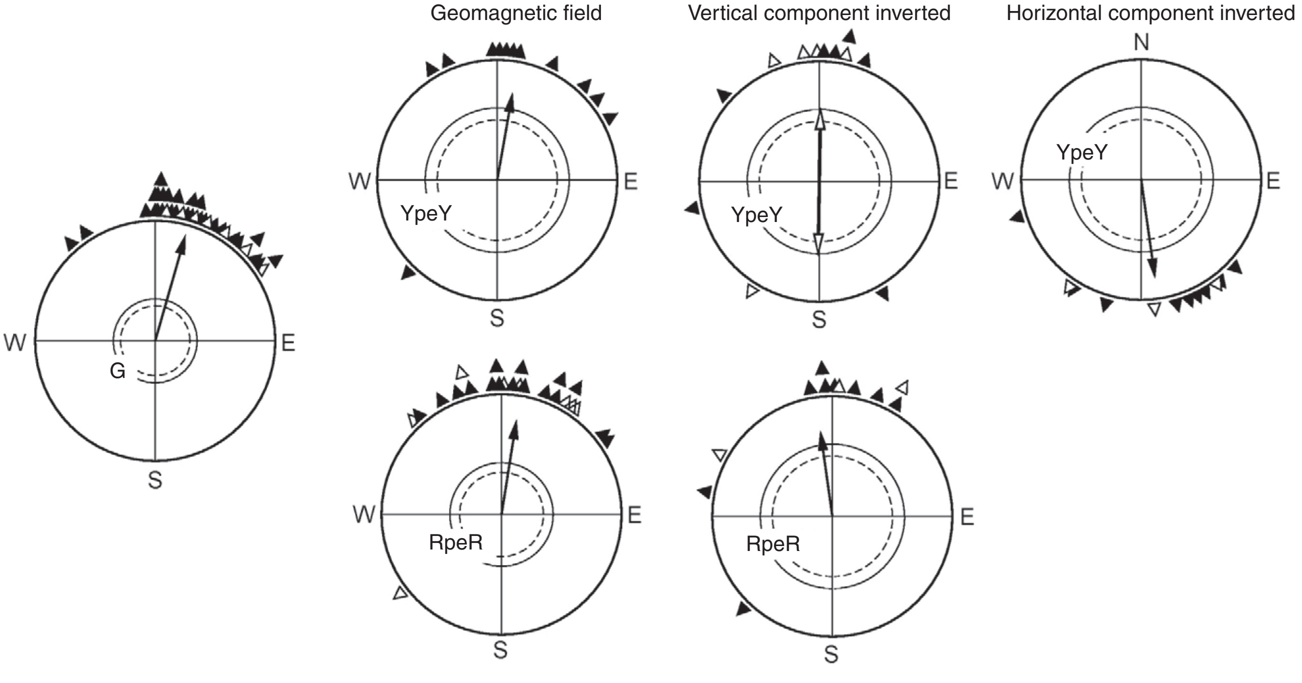

Fig. 2. Spring experiments in different magnetic fields analyzing the nature of the directional response. Abbreviations and symbols as in Fig. 1.

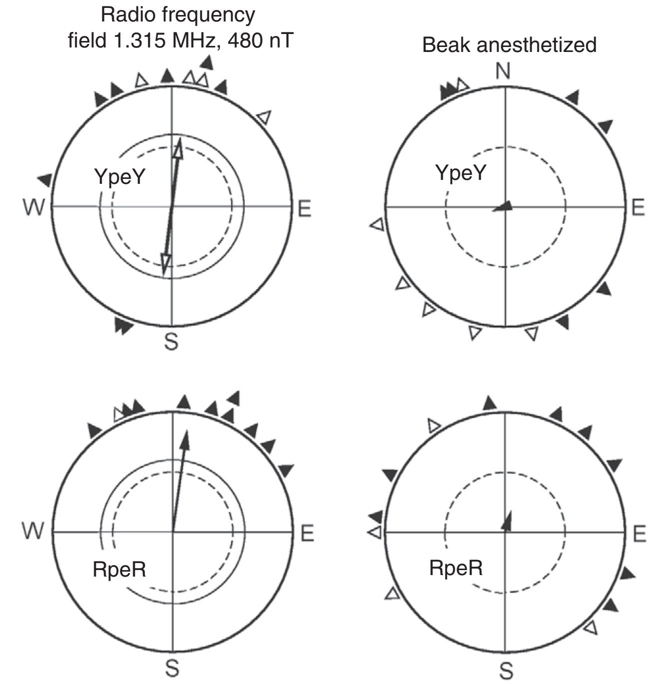

Fig. 3. Spring experiments in the geomagnetic field with a radio frequency field added or with the beak anesthetized to identify the underlying mechanism of magnetoreception. Abbreviations and symbols as in Fig. 1.

of their headings lay on one side and the third on the other. This is in many ways similar to the axial preferences observed in the present study, only that the vast majority of birds in 2000 headed South or had the preferred end of the axis in the South whereas in 2007 and 2008, half lay North, half lay South.

When the corresponding test conditions under yellow and red light are compared, they occasionally look a bit different, with a longer unimodal grand mean vector under the one wavelength and a longer axial vector under the other. However, these differences never reached statistical significance, indicating that the corresponding distributions were not truly different. This suggests largely uniform responses with a certain tendency towards axiality in the entire long-wavelength range where the inclination compass no longer works.

Muheim and colleagues, also testing robins, observed a westerly tendency under dim red light of 1.0 $\mathrm{mW\,m^{-2}}$, which they interpreted as a wavelength-dependent shift in heading, involving two antagonistic spectral mechanisms (Muheim et al., 2002). This interpretation was inspired by a similar wavelength-dependent shift beyond 500 nm described in salamanders by Phillips and Borland (Phillips and Borland, 1992a; Phillips and Borland, 1992b). Based on these data, the authors speculated about two antagonistic spectral mechanisms, with the short-wavelength one indicating the correct directions and the long-wavelength one indicating directions shifted by 90 deg. In birds, the existence of two antagonistic spectral mechanisms does not seem unlikely, because only such an antagonism can explain the remarkably rapid transition from oriented behavior under 565 nm green light to disoriented behavior under 582 nm yellow light (see Wiltschko, W. and Wiltschko, 1999; Muheim et al., 2002) and the effect of adding yellow light to monochromatic short-wavelength light (see Wiltschko, R. et al., 2010a). However, while a long-wavelength mechanism appears to inhibit the normal reception of magnetic directional information presumably based on radical pair processes, it does not contribute any magnetic information of its own. The westerly orientation under dim red light of 1.0 $\mathrm{mW\,m^{-2}}$ described by Muheim and colleagues was no shift but proved to be a ‘fixed direction response’ (Muheim et al., 2002). It seems identical to that observed in total darkness (Stapput et al., 2008; Wiltschko, R. et al., 2008); possibly, the light level was so low that it was already ‘dark’ for the birds. Likewise, the northerly orientation under yellow and red light after pre-exposure reported here does not involve a spectral mechanism but also originates in the magnetite-based receptors in the skin of the upper beak, a mechanism that appears to take over when the radical pair mechanism is disrupted.

Without pre-exposure to long wavelengths, birds are disoriented in light beyond 565 nm. This is not only true for European robins, where the transition could be narrowed down to 567–568 nm using interference filters (Muheim et al., 2002), but also for other passerine migrants (Wiltschko, W. et al., 1993; Rappl et al., 2000), homing pigeons, *Columba livia* f. *domestica* (Wiltschko and Wiltschko, 1998) and domestic chickens, *Gallus gallus* (Wiltschko, W. et al., 2007), three only distantly related lineages of birds (see Ericsen et al., 2006). The magnetic compass based on radical pair processes requires light from the short-wavelength part of the spectrum – this appears to be a common feature in all birds. How does pre-exposure change the response from disorientation to oriented behavior and how is the observed oriented behavior after pre-exposure to long-wavelength light to be interpreted? Our present data clearly show that the induced orientation does not represent an adaptation of the normal magnetic compass to long-wavelength light. Instead pre-exposure elicits a different type of response that is no longer mediated by the radical pair processes in the eyes but by the magnetite-based receptors in the upper beak. This switch to the other mechanism in the control of orientation does not occur at once but appears to require a certain amount of time – this is why birds tested under yellow or red light without pre-exposure are disoriented. But the magnetite-based mechanism does not provide the birds with true compass information. In spring, the northerly directions mediated by this mechanism largely coincide with the migratory direction; however, this is not the case in autumn. The direction remains northerly and an axial tendency emerges, which makes this type of response slightly different from the other ‘fixed direction responses’ observed so far (see Wiltschko, R. et al., 2010a).

The receptors in the upper beak provide the magnetic directions but it is not clear whether this information alone controls the behavior. The input from the magnetite-based receptors should solely depend on the magnetic field and cannot be influenced by the ambient light conditions. Nevertheless, in the case of ‘fixed direction responses’, although relevant magnetic input originates in these receptors, we observed headings in different directions under different light regimes. This indicates interactions between the magnetite-based receptors in the beak and parts of the visual system, where the visual input modifies the magnetic input, leading to different manifestations of directions under different light conditions (for a review, see Wiltschko et al., 2010a). We do not know whether this is also the case with the northerly tendencies found under monochromatic 582 nm yellow light and 645 nm red light – northerly directions seem to be typical for the entire long-wavelength range. Normally, it appears to be the radical pair mechanism that mediates compass information but, under unusual light conditions, the magnetite-based receptors also provide directions and control the behavior. In previous papers (e.g. Wiltschko, R. et al., 2010a), we speculated that this might be a remnant of a former magnetite-based compass that has been replaced by the radical pair mechanism in birds. It appears to be silent under normal conditions, but when the radical pair mechanism is disrupted by extreme light conditions, it takes over. It appears possible that with the orientation under long-wavelength light, we observe a relic of an ancient mechanism.

The natural role of the magnetite-based receptors in the skin of the upper beak is not entirely clear. Normally, they seem to provide information on magnetic intensity as a component of the navigational 'map', as indicated by electrophysiological recordings from the trigeminal system (Semm and Beason, 1990; Heyers et al., 2010). This is in agreement with the observation that their deactivation or disconnection prevents birds from sensing changes in magnetic intensity in natural (Wiltschko, R. et al., 2009; Wiltschko, R. et al., 2010b) and artificial anomalies (Mora et al., 2004). They also mediate the effect of a strong magnetic pulse (e.g. Wiltschko, W. et al., 1994; Wiltschko, W. et al., 2009; Holland, 2010), which has been interpreted as an effect on the 'map', setting the compass course to be pursued (Wiltschko, W. et al., 2006). Some authors like, e.g. Kirschvink and colleagues, propose that they also provide the directional information for the avian magnetic compass, with radical pair processes in the eye playing only an indirect role in mediating this information (Kirschvink et al., 2010). This idea, however, is at variance with experimental data showing that the magnetic compass remains unaffected when the magnetite-based receptors are deactivated by a local anesthetic (e.g. Wiltschko, R. et al., 2007; Wiltschko, R. et al., 2008; Wiltschko, W. et al., 2009) or disconnected by cutting the ophthalmic nerve (Beason and Semm, 1996; Zapka et al., 2009). The magnetite-based receptors thus do not seem to be involved in the magnetic compass; they normally provide information on magnetic intensity, and only under very unusual light conditions not occurring in nature, do they appear to make birds head into specific directions.

The interactions of magnetoreception by the magnetite-based receptors with the visual system, the conditions under which they occur and which parts of the brain are involved are open questions that need to be answered before we achieve a full understanding of the mechanisms by which birds obtain magnetic information.

ACKNOWLEDGEMENTS

Our work was supported by the Human Frontier Science Programme (grant to R.W.) and the Deutsche Forschungsgemeinschaft (grants to W.W. and R.W.). We thank H. J. Bischof, Universität Bielefeld, P. Galland, Universität Marburg, J. Phillips, Virginia Tech, and K. Stapput for inspiring discussions and helpful suggestions, and L. Dehe, M. Drewing, T. Drick, E. Dylda, T. Jarosz, E. Lange, L. Psotta, M. Temesvary and A. Wagner for their valuable help with the experiments.

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