THE ROLE OF EXTRAOCULAR PHOTORECEPTORS IN NEWT MAGNETIC COMPASS ORIENTATION: PARALLELS BETWEEN LIGHT-DEPENDENT MAGNETORECEPTION AND POLARIZED LIGHT DETECTION IN VERTEBRATES

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Summary

Theoretical models implicating specialized photoreceptors in the detection of the geomagnetic field have been the impetus for studying the effects of light on magnetic compass orientation. Magnetic orientation in flies, amphibians and birds has been found to be influenced by light, and in all these groups a shift of approximately 90° in the direction of magnetic compass orientation has been observed under certain wavelengths and/or intensities of light. In the eastern red-spotted newt *Notophthalmus viridescens*, wavelength-dependent effects of light on magnetic compass orientation appear to result from an antagonistic interaction between short-wavelength (≤450 nm) and long-wavelength (≥500 nm) photoreception mechanisms. We have demonstrated that at least the short-wavelength input to the newt's magnetic compass is mediated by extraocular photoreceptors located in or near the pineal organ, and here we present new findings that indicate that the putative long-wavelength mechanism is also associated with pineal photoreceptors. Interestingly, the amphibian pineal organ mediates orientation to both the e-vector of plane-polarized light and the magnetic field. Although the wavelength-dependence of the polarized light orientation in amphibians has not been studied, polarization sensitivity in fishes appears to be mediated by two antagonistic photoreception mechanisms that have similar spectral characteristics to those of the newts' magnetic compass response. These parallels, along with similarities in the types of receptors that are expected to be involved in light-dependent magnetoreception and polarized light detection, suggest that similar photoreception mechanisms may mediate the light-dependent magnetic and polarized light compasses.

Key words: compass orientation, magnetic field, polarized light, pineal, extraocular photoreceptors, newt, *Notophthalmus viridescens*.

Introduction

A magnetic compass sense has been demonstrated in a large and taxonomically diverse group of organisms. In terrestrial organisms, magnetic orientation appears to be mediated by more than one type of mechanism (for reviews, see Wiltschko and Wiltschko, 1995; Phillips and Deutschlander, 1997; Deutschlander et al., 1999a; Lohmann and Johnsen, 2000). In some cases, the underlying magnetoreception mechanism appears to be independent of light, e.g. in the subterranean mole rat (*Cryptomys* sp.; Burda et al., 1990; Marhold et al., 1997). In contrast, magnetic compass orientation has been shown to be sensitive to the wavelength and/or intensity of light in the eastern red-spotted newt (*Notophthalmus viridescens*; Phillips and Borland, 1992a; Deutschlander et al., 1999a; Deutschlander et al., 1999b), bullfrog (*Rana catesbeiana*; M. J. Freake, S. C. Borland and J. B. Phillips, manuscript in preparation and unpublished data), fruit fly (*Drosophila melanogaster*; Phillips and Sayeed, 1993),

homing pigeon (*Columba livia*; Wiltschko and Wiltschko, 1998) and several species of migratory bird (Wiltschko et al., 1993; Wiltschko et al., 2000a; Wiltschko et al., 2000b; Wiltschko and Wiltschko, 1995; Wiltschko and Wiltschko, 1999; Rappl et al., 2000). In each of these organisms, except pigeons, a shift in the direction of magnetic compass orientation of roughly 90° has been observed under one or more lighting conditions. The effects of light on magnetic compass orientation are consistent with biophysical mechanisms involving a radical pair reaction (Schulten, 1982; Ritz et al., 2000) or an array of single-domain magnetite particles (Edmonds, 1996) in a photoreceptor-based magnetoreceptor. Only in the newt, however, is there evidence for a direct effect of light on the perception of the magnetic field (Phillips and Borland, 1992a; Deutschlander et al., 1999a; Deutschlander et al., 1999b).

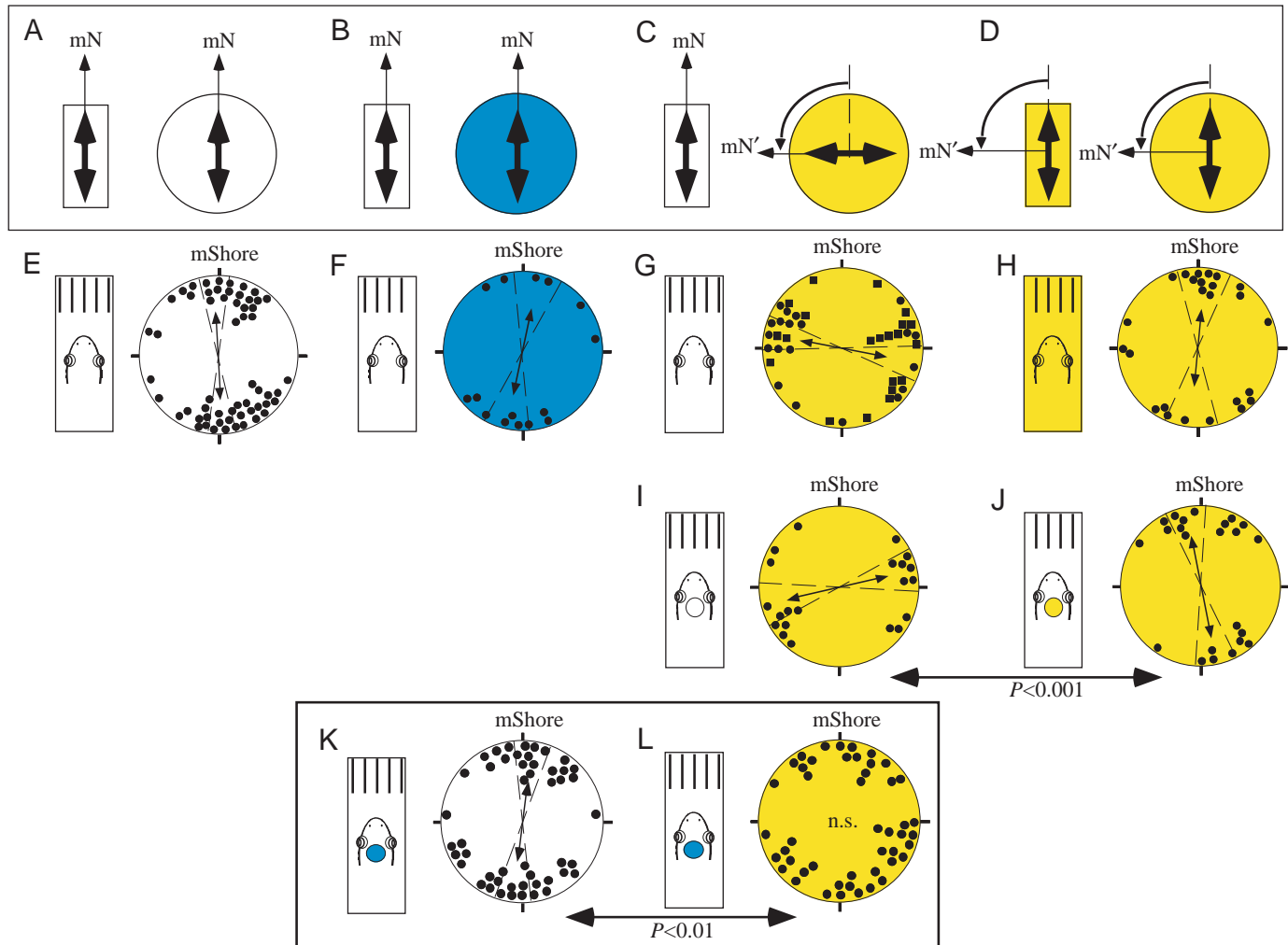Experiments investigating the light-dependence of

Fig. 1. Effects of light and head caps on bimodal magnetic compass orientation in newts. (A–D) The predicted orientation of newts with respect to the wavelength conditions during training and testing (based on the findings in Phillips and Borland, 1992a). A diagram of a training tank with the shore towards magnetic North (mN) is shown for each training condition, and a diagram of the circular test arena shows the predicted magnetic response of the newts (double-headed arrow) under full-spectrum light (no color), short-wavelength light (in blue), or long-wavelength light (in yellow). (A,B) When trained under full-spectrum light, the newts should perceive the shore to be towards magnetic North (indicated by the single-headed arrow) and exhibit bimodal magnetic orientation along the shoreward axis when tested under full-spectrum (A) or short-wavelength (B) light. (C) When trained under full-spectrum light and tested under long-wavelength (>500 nm) light, the newts' perception of magnetic North during testing (mN'), and hence their orientation in the test arena, should be rotated by 90°. (D) When trained under long-wavelength light, the newts' perception of magnetic North (mN') and, therefore, of the direction of shore, should be rotated by 90°. When subsequently tested under long-wavelength light, the newts' perception of the direction of the magnetic field in the arena would be the same as it was in the outdoor tank, and they should orient in the correct shoreward direction. Wavelength conditions during training and testing, as well as the spectral properties of the caps (circle on the diagram of the head in I–L), are indicated in E–L. Each data point represents the magnetic bearing of a single newt. All data are plotted with respect to the magnetic direction of shore in the training tank (i.e. the shore direction=360°). Double-headed arrows at the center of each plot indicate the mean axis of orientation with the mean vector length proportional to the strength of orientation, $\mathbf{r}$ (the diameter of the circle corresponding to $\mathbf{r}$=1). Dashed lines indicate the 95% confidence intervals for the mean axis. Each distribution for which a mean axis is shown is significant at $P<0.05$ (Rayleigh test). (E,F). Newts trained under natural sky light and tested under full-spectrum (E) or short-wavelength (450 nm) (F) light oriented along the shoreward magnetic axis (mShore). (G) Newts trained under natural sky light and tested under long-wavelength light exhibited orientation rotated by 90° from the shoreward magnetic direction (filled circles were tested under broadband >500 nm light; filled squares were tested under 550 nm light). (H) Newts trained and tested under long-wavelength (>500 nm) light oriented along the shoreward axis. (I) After training under natural sky light, newts with clear caps exhibited orientation rotated by 90° from the shoreward direction under long-wavelength (>500 nm) light. (J) After training under natural sky light, newts with long-wavelength-transmitting caps oriented along the shoreward axis under long-wavelength (>500 nm) light. (K) When tested under full-spectrum light, newts with caps transmitting short-wavelength light exhibited significant orientation along the shoreward axis. (L) When tested under long-wavelength light (550–650 nm, indicated in yellow), however, these newts failed to exhibit significant shoreward orientation. (Parts A–J of this figure are modified from Deutschlander et al., 1999a; Deutschlander et al., 1999b, in which all original data and statistical analyses can be found.)

shoreward magnetic compass orientation indicate that under long-wavelength (>500 nm) light the directional response of the newt's magnetic compass is rotated by 90° from that under short-wavelength (<450 nm) and full-spectrum light (Phillips and Borland, 1992a). In a recent replication of these earlier experiments, newts were 'trained' to the direction of a shore in outdoor tanks under natural skylight for 12–16 h (Deutschlander et al., 1999a). When subsequently tested in a visually symmetrical indoor arena illuminated with either full-spectrum (from a xenon arc source) or short-wavelength (450 nm) light, the newts exhibited magnetic orientation that coincided with the shoreward axis in the training tank (Fig. 1A,E and B,F, respectively). In contrast, when tested under long-wavelength (>500 nm) light, the newts' orientation was rotated by approximately 90° from the shoreward direction (Fig. 1C,G). To determine whether the 90° shift in orientation under long-wavelength light was due to a direct effect of light on the newts' perception of the magnetic field (as suggested in Fig. 1C), newts were trained under long-wavelength light by covering the tank with a long-wavelength-transmitting gel filter. Newts trained and tested under long-wavelength light oriented along the shoreward magnetic axis (Fig. 1H), indicating that the newts had learned the direction of shore with respect to rotated directional information from the magnetic compass under long-wavelength light (as indicated in Fig. 1D).

The wavelength-dependent effects of light on shoreward magnetic orientation suggest that the newt's magnetic compass is mediated by two spectral absorption mechanisms (i.e. a short-wavelength mechanism, with a peak absorption<450 nm, and a long-wavelength mechanism, with a peak absorption>500 nm), that act antagonistically on the output of the magnetoreceptor to produce complementary bimodal patterns of response (see Phillips and Borland, 1992a; Deutschlander et al., 1999a). To test this hypothesis, newts were tested for shoreward magnetic compass orientation under 475 nm light (Phillips and Borland, 1992a), intermediate to the regions of the spectrum that produced shifted (>500 nm) and unshifted (<450 nm) orientation. Phillips and Borland predicted that 475 nm light should stimulate both spectral mechanisms equally, causing the opposing effects of the magnetic field on the two mechanisms to cancel out (Phillips and Borland, 1992a). Consistent with this prediction, newts tested under 475 nm light failed to exhibit significant shoreward magnetic compass orientation (see Fig. 2A).

The antagonistic interaction that is inferred to occur between the two spectral inputs to the newt's magnetic compass could also reduce the efficiency of magnetoreception under natural (i.e. broad-band) lighting conditions. Indeed, if the two spectral mechanisms were stimulated to a similar degree under full-spectrum 'white' light (as was the case for newts tested under 475 nm light), the newt's magnetic compass response should be degraded or eliminated. However, newts tested under full spectrum light exhibited the same orientation as newts tested under short-wavelength light. Therefore, the short-wavelength

mechanism appears to be preferentially stimulated under full-spectrum light, suggesting that the short-wavelength mechanism is appreciably more sensitive than the long-wavelength mechanism (Phillips and Borland, 1992a; Deutschlander et al., 1999a).

The reason why newts (for references, see above) and other animals (Phillips and Sayeed, 1993; Wiltschko et al., 2000a; Wiltschko et al., 2000b; M. J. Freake, S. C. Borland and J. B. Phillips, manuscript in preparation and unpublished data) exhibit wavelength-dependent shifts in magnetic orientation is unclear. It may be that two spectral mechanisms are somehow required for light-dependent magnetoreception (as suggested by Phillips and Borland, 1992a; Deutschlander et al., 1999a) and/or that the wavelength-dependent 90° shift is a byproduct of the biophysical mechanism responsible for magnetoreception (Ritz et al., 2000; Edmonds, 1996). Alternatively, the low-sensitivity, long-wavelength mechanism may have evolved secondarily, and not necessarily to produce 90°-shifted orientation. For example, under natural conditions the function of the long-wavelength mechanism may be to 'cancel out' the response of the short-wavelength mechanism, and thus prevent the magnetic compass from operating. This could occur when the organism is exposed to direct sunlight, which is rich in long-wavelength light (Coemans et al., 1994), and may explain why amphibians (and many other vertebrates) rely on directional information from the sun compass, rather than the magnetic compass, when the sun disk is visible (Ferguson, 1971; Adler, 1976). If so, the 90°-shifted orientation observed in laboratory experiments may be a result of using long-wavelength stimuli that are more highly saturated than naturally occuring illumination, resulting in selective excitation of the long-wavelength mechanism rather than more equal excitation of both mechanisms as might occur when the organism is exposed to direct sunlight. Finally, it is important to emphasize that the wavelength-dependent shift in the direction of magnetic compass orientation may have different explanations in different groups of organisms (Wiltschko et al., 2000a; Wiltschko et al., 2000b).

To begin to address some of the fundamental questions surrounding light-dependent magnetoreception, localizing the photoreception mechanisms responsible for this sensory phenomenon is essential. Newts, together with many other vertebrates, possess both ocular and extraocular photoreceptors (EOPs), found mainly in the pineal gland and nearby brain areas (Adler, 1976; Foster et al., 1994; Menaker et al., 1997). The pineal gland of birds has been shown to be sensitive to magnetic stimuli (Semm et al., 1982; Semm, 1983; Demaine and Semm, 1985). The role of such magnetosensitivity, however, has not been established (see Phillips and Deutschlander, 1997), and the pineal gland does not appear to be directly involved in compass orientation in birds (Maffei et al., 1983; Schneider et al., 1994). In amphibians, however, extraocular photoreceptors in the pineal complex and associated structures have been found to mediate orientation responses to polarized light (Adler and Taylor, 1973; Taylor

Fig. 2. Comparison of the wavelength-dependence of light-dependent
magnetic compass orientation and polarized light responses.
(A) Wavelength-dependence of shoreward magnetic compass
orientation in newts (data from Phillips and Borland, 1992a). The
shoreward components (filled symbols, *y* axis on left) and 90 °-shifted
components (open symbols, *y* axis on right) of mean vector bearings
were calculated from the distributions of magnetic bearings of newts
tested under different wavelengths of light (*x* axis) and plotted relative
to the magnetic direction of shore (0 °). The shoreward components
were highest under 400 and 450 nm light, whereas the 90 °-shifted
(90–270 °) components were highest under 500, 550 and 600 nm light.
Under 475 nm light, both components were close to zero, indicating
that the newts failed to exhibit a consistent direction of magnetic
orientation. Shoreward component=cosine(mean vector bearing)×(mean
vector length). 90 °-shifted component=−sine(mean vector bearing)×
(mean vector length). (B) Wavelength-dependence of sensitivity to the
alignment of the e-vector of plane polarized light in the optic nerve of
rainbow trout *Oncorhynchus mykiss* (from Parkyn and Hawryhsyn,
1993). Parkyn and Hawryshyn determined sensitivity by extracellular
recordings from the optic nerve in which individual cone mechanisms
were isolated by spectral adaptation (Parkyn and Hawryhsyn, 1993).
Sensitivity to each e-vector alignment was calculated as $\log_{10}$ of the
reciprocal of irradiance at a criterion response of 30 μV. Data taken
from Fig. 5 in Parkyn and Hawryshyn, 1993 were used to calculate a
mean axis of response by vector addition, from which the components
of the response to vertically aligned e-vectors (0–180 ° component, *y*
axis on left, filled squares) and to horizontally aligned e-vectors
(90–270 ° component, *y* axis on right, open squares) were calculated.
The component of the response to vertically aligned e-vectors was
highest in the 'ultraviolet' mechanism stimulated by 380 nm light, while
the component of response to horizontally aligned e-vectors was
highest in the 'green' mechanism stimulated by 540 nm light and the
'red' mechanism stimulated by 660 nm light. The 'blue' mechanism
stimulated by 440 nm light was insensitive to e-vector alignment. The
mean axes of the response were calculated by the present authors using
vector addition on the relative sensitivities (the antilogarithm of the
responses measured from Fig. 5 in Parkyn and Hawryshyn, 1993) after
first doubling the e-vector angles; the mean axis of the response was
obtained by dividing the mean vector bearing of the distribution of
doubled angles by 2. 0–180 ° component=|cosine(deviation of mean axis
from vertical)×(mean axis length)|. 90–270 ° component=|sine(deviation
of mean axis from vertical)×(mean axis length)|. Absolute values were
used because there was no basis for distinguishing between clockwise
and anticlockwise deviations from vertical. So, for example, the vertical component of the response to an e-vector of 60–240 ° is the same as
that of a comparable response to an e-vector of 120–300 °. (C) Wavelength-dependence of sensitivity to the alignment of the e-vector of plane
polarized light in goldfish *Carassius auratus* (from Hawryshyn and McFarland, 1987). Hawryshyn and McFarland determined polarization
sensitivity by measuring increment thresholds obtained by heart-rate conditioning while using spectral adaptation to isolate individual cone
mechanisms (Hawryshyn and McFarland, 1987). Sensitivity to each e-vector alignment was calculated as $\log_{10}$ of the reciprocal of irradiance at
threshold. Data taken from Fig. 4 in Hawryshyn and McFarland, 1987, were used to calculate a mean axis of response by vector addition, from
which the components of response to vertically aligned e-vectors (0–180 ° component, *y* axis on left) and to horizontally aligned e-vectors
(90–270 ° component, *y* axis on right) were calculated. The component of response to vertically aligned e-vectors was highest in the
'ultraviolet' mechanism stimulated by 380 nm light, while the component of response to horizontally aligned e-vectors was highest in the
'green' mechanism stimulated by 540 nm light and the 'red' mechanism stimulated by 660 nm light. The 'blue' mechanism stimulated by
460 nm light was insensitive to e-vector alignment. Mean axes of response were calculated as in B.
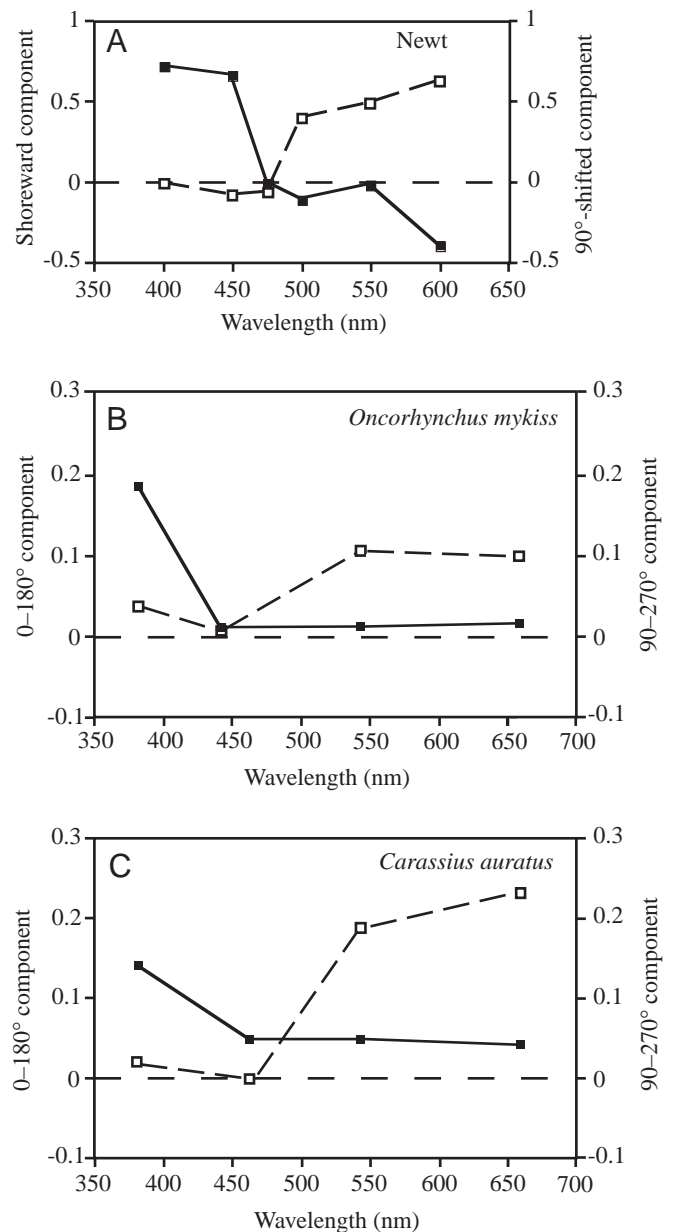
and Adler, 1973; Taylor and Adler, 1978; Taylor and Auburn,
1978). Moreover, single photoreceptors with two antagonistic
photoreception mechanisms, such as those that we propose
mediate magnetic compass orientation in the newt (Phillips and
Borland, 1992a; Deutschlander et al., 1999a), are present in the

parapineal lobe of the pineal complex of lizards and anuran
amphibians and, in anurans, exhibit spectral properties that are
consistent with the behavioral responses in the newt (Eldred
and Nolte, 1978; Solessio and Engbretson, 1993). Therefore,
these findings suggest (i) that the pineal gland of at least some

organisms is magnetically sensitive, (ii) that the pineal complex of amphibians is involved in obtaining directional information for compass orientation and (iii) that spectral mechanisms exist in the amphibian pineal complex that match the wavelength-dependence observed in the newt's magnetic compass response.

We previously tested whether extraocular photoreceptors located in, or near, the pineal gland are involved in the newt's magnetic compass response by covering the area of the head above the pineal with long-wavelength-transmitting (>500 nm) filters prior to training and testing (Deutschlander et al., 1999b). Long-wavelength-capped newts trained under full-spectrum light and tested under long-wavelength light exhibited orientation parallel to the shoreward/waterward axis of the training tank (Fig. 1J), whereas newts trained and tested under the same two lighting conditions with clear caps oriented perpendicular to the shoreward direction (Fig. 1I). The two distributions were significantly different ($P<0.001$, $U^2=0.753$, Watson U^2 test). In other words, covering the region of the head above the pineal organ with a long-wavelength-transmitting (i.e. short-wavelength-blocking) filter was sufficient to mimic the effect of exposing the whole newt to long-wavelength light during training (as in Fig. 1D,H). These findings demonstrate that the short-wavelength mechanism of the newt's magnetic compass involves extraocular photoreceptors located in the pineal complex or deeper in the brain (e.g. the hypothalamus). However, these experiments provide no information about the location of the long-wavelength input to the newt's magnetic compass. The results of the long-wavelength cap experiments are consistent with either an ocular or an extraocular location for the long-wavelength mechanism.

Here, we report findings from experiments designed to determine whether the long-wavelength input to the newt's magnetic compass response is mediated by extraocular photoreceptors located in, or near, the pineal gland. We also discuss similarities in the spectral dependence of magnetic compass orientation in newts and that of polarization vision in fish. These findings raise the possibility that similar photoreception mechanisms may be involved in light-dependent magnetoreception and polarization vision in at least some vertebrates, or that similar selection pressures have shaped the functional properties of these two sensory modalities.

Materials and methods

The general training and testing methods for these experiments have been described elsewhere (Deutschlander et al., 1999a; Deutschlander et al., 1999b; Deutschlander et al., 2000). As in the previous experiments (Deutschlander et al., 1999b), small round 'caps' (5 mm diameter) constructed from plastic spectral filters (Lee Filters) were attached to the dorsal surface of the head of each newt using cyanoacrylate glue. In the present experiments, the newts were capped with a short-wavelength-transmitting gel filter (Lee HT120; peak at 450 nm,

approximately 40 nm bandwidth at half maximum, transmission less than 0.1 % below 350 nm and from 530 to 650 nm). The cap was positioned so that light reaching the pineal organ and nearby structures would be altered by the spectral properties of the cap, while light reaching the eyes was unaffected. Newts were trained and tested with the caps in place. All newts were trained outdoors under natural skylight. As in earlier experiments using a 'one day' training protocol (Deutschlander et al., 1999a, Deutschlander et al., 1999b; Deutschlander et al., 2000), newts were placed in a training tank in mid to late afternoon under sunny to partly cloudy conditions, remained in the tank overnight, and were tested starting shortly after sunrise the following morning. During training, therefore, the newts were exposed to a wide range of natural lighting conditions from direct sunlight and light from the blue sky (e.g. at dusk) during the day to starlight and moonlight at night.

Three different training tank alignments were used, with the direction of the artificial shore to the north, west or east. After residing in one of the training tanks overnight, each newt was tested for magnetic orientation in an indoor arena under either full-spectrum or long-wavelength light. The full spectrum light used in testing was produced by means of a 150 W xenon arc lamp (emission spectrum from 320 nm to >700 nm). The long-wavelength light (550–650 nm, log intensity approximately 12.8, where intensity was measured in quanta cm^{-2} s^{-1}) was produced by passing the output of the 150 W xenon arc lamp through a Schott OG 550 long-pass filter (transmission less than 0.1 % below 530 nm) and an Oriel 58832 650 nm short-pass filter (transmission less than 0.1 % above 665 nm). The intensity of the long-wavelength light was similar to that used in earlier experiments in which we tested the newts' response under wavelengths from 400 to 600 nm adjusted to approximately equal quantal flux (i.e. log intensity=12.3–12.6; Phillips and Borland 1992a; Deutschlander et al., 1999a; Deutschlander et al., 1999b).

Newts with short-wavelength-transmitting caps tested under full-spectrum (320 nm to >700 nm) light served as controls. Under full-spectrum light, the short-wavelength-transmitting caps should have no effect on the newt's shoreward compass orientation, regardless of the location of the long-wavelength mechanism. If the long-wavelength input to the newt's compass is located in the eyes, then both the short-wavelength mechanism (located in, or near, the pineal organ; Deutschlander et al., 1999b) and the less-sensitive long-wavelength mechanism would be stimulated during both training and testing. Therefore, the newts should be able to orient along the magnetic axis coinciding with the shoreward direction (similar to newts with no caps trained and tested under full-spectrum light, Fig. 1A,E). If the long-wavelength mechanism is located in the vicinity of the pineal organ (i.e. in a region of the head covered by the caps), the effect of the short-wavelength-transmitting caps would be equivalent to that of newts trained and tested under short-wavelength light. Because newts orient in the correct shoreward magnetic direction when tested under short-wavelength light (Fig. 1F),

newts trained and tested under short-wavelength light (or short-wavelength-capped newts trained and tested under full-spectrum light) should be able to learn the magnetic axis of shore in the training tank and orient along the shoreward magnetic axis in the test arena.

The predicted orientation of short-wavelength-capped newts tested under long-wavelength (550–650 nm) light depends on the location of the long-wavelength input to the magnetic compass. Under the long-wavelength light used in these experiments (550–650 nm), the short-wavelength-transmitting caps (i.e. long-wavelength blocking) would prevent 99.99 % of the overhead light from reaching the area around the pineal complex. Previous experiments have shown that newts tested for shoreward magnetic compass orientation in the absence of visible light are disoriented (Phillips and Borland, 1992b). Therefore, if both the long-wavelength and short-wavelength inputs to the magnetic compass are located in, or near, the pineal complex, where both would have been covered by the caps, neither mechanism would have been effectively stimulated when newts with short-wavelength-transmitting caps were tested under long-wavelength light. This would be expected to cause a deterioration in the newts' magnetic compass response. In contrast, if the long-wavelength mechanism is not located in the area affected by the caps (e.g. if it is located in the retina), then newts tested under long-wavelength light should orient perpendicular to the shoreward axis (as did newts in earlier experiments that had been trained under full-spectrum light and tested under long-wavelength light; see Fig. 1C,G,I). Similarly, if long-wavelength light were to reach extraocular photoreceptors by an indirect path that bypassed the short-wavelength caps (e.g. through surrounding tissue), the newts should also orient perpendicular to the shoreward axis.

Each newt was individually tested indoors in a circular, visually symmetrical, terrestrial arena (described in Phillips and Borland, 1994; Deutschlander et al., 2000). The directional bearing of the each newt was recorded at a distance of 20 cm from the center of the arena using the same criteria as described previously (individual trials were discontinued if the newt did not move off the release device in the center of the arena within 10 min or if the newt did not cross the 20 cm criterion radius within 15 min; Deutschlander et al., 2000). Each newt was tested only once in one of four symmetrical alignments of an earth-strength magnetic field [i.e. magnetic North (mN)=geographic North (gN), mN=gE, mN=gW or mN=gS, where E is east, W is west and S is south]. The horizontal alignment of the magnetic field in the arena was altered using two orthogonally oriented, double-wrapped, Ruben's coils (Phillips and Borland, 1994). The magnetic inclination and total intensity of the rotated magnetic fields were within ±1 ° and ±1.5 %, respectively, of the ambient geomagnetic field (measured using a model 105395 3-axis magnetometer; DevelCo). In each test, at least four newts were scored, one in each of the four alignments of the magnetic field. By testing the directional response of an equal number of newts in the four different field alignments and pooling the results with respect to the magnetic field direction during testing, we could assess whether the newts were orienting with respect to the direction of the magnetic field. Data from a number of tests from each of the three shore alignments were pooled relative to the shoreward direction.

All data were normalized with respect to the magnetic direction of shore during training. The resulting distributions of magnetic bearings were analyzed using standard circular statistics (Batschelet, 1981). Because the responses of the newts after 1 day of training were bimodal (Deutschlander et al., 1999a; Deutschlander et al., 1999b; Deutschlander et al., 2000), statistical analyses were carried out after first doubling the magnetic bearings. Mean vectors were calculated by vector addition and tested for significance using the Rayleigh test. 95 % confidence intervals around the mean vector bearing were used to determine whether the distribution was oriented with respect to the shoreward direction (Batschelet, 1981). A non-parametric test for dispersion using the Mann–Whitney statistic (Batschelet, 1981; Zar, 1984) was used to determine whether the distributions from the two wavelength conditions differed significantly in angular deviation from their respective means (i.e. whether they differed in scatter). A χ^2 test was used to determine whether the proportion of newts that crossed that 20 cm criterion radius within the time criterion specified above differed in the control and experimental conditions.

Results

As predicted, newts tested under full-spectrum light oriented along the shoreward magnetic axis, indicating that the newts were able to learn the shoreward direction while wearing short-wavelength transmitting head caps. The newts' response under full-spectrum light was significant in both years (Table 1) and in the pooled distribution (9–189 °, N=49, mean vector length, $\mathbf{r}$=0.45; P<0.001, Rayleigh test; Fig. 1K). In contrast, in the data pooled from the 2 years the distribution of magnetic bearings from newts tested under long-wavelength light (550–650 nm) was indistinguishable from a random distribution (179–359 °, N=47, $\mathbf{r}$=0.10, P>0.50; Fig. 1L). In the first year, although the response of newts tested under long-wavelength light was not significant, there appeared to be some residual orientation along the shoreward magnetic axis (Table 1). When we repeated this experiment a second time, however, the distribution of magnetic bearings under long-wavelength light was again non-significant (Table 1). In addition, the pooled distribution of magnetic bearings from newts tested under long-wavelength light was significantly more scattered than that of newts tested under full-spectrum light (Z=2.577, two-tailed P<0.01, non-parametric test for dispersion). However, the proportion of newts that crossed the 20 cm scoring radius within the allotted time criterion was not significantly different between the two wavelength conditions (49 out of 68 individuals tested under full-spectrum light and 47 of 74 under long-wavelength light, χ^2=1.18, P>0.25).

Table 1. *Statistical analysis of data from short-wavelength-transmitting cap experiments*

	Testing light conditions	
	Full-spectrum light	Long wavelength (550–650 nm)
Fall 1997		
Magnetic bearings (degrees)	175–355	3–183
N	25	22
r	0.49	0.19
P	<0.005	NS
Fall 1998		
Magnetic bearings (degrees)	22–202	154–334
N	24	25
r	0.53	0.03
P	<0.01	NS
Pooled data		
Magnetic bearings (degrees)	9–189	179–359
N	49	47
r	0.45	0.10
P	<0.001	NS

For details, see text.
r, mean vector length; *N*, sample size; NS, not significant.

Discussion

In the present experiment, newts tested under long-wavelength light, which was blocked by the 'blue'-transmitting pineal caps, failed to exhibit a consistent direction of orientation relative to the magnetic field (Fig. 1L). Previous experiments have shown that the magnetic compass is eliminated when newts are tested in the absence of visible light (Phillips and Borland, 1992b). It is possible that a decrease in intensity of light stimulating the extraocular photoreceptors in, or near, the pineal organ has a non-specific effect on the newts' behavior (e.g. a decrease in overall activity or a change in the type of behavioral response exhibited by newts in the indoor test arena). While the available evidence does not rule out this explanation, there are several factors that suggest that the lack of orientation of newts tested under long-wavelength light in the present experiments resulted from an inability to obtain directional information from the magnetic field rather than from a generalized change in behavior. First, newts wearing 'blue'-transmitting caps tested under full-spectrum light exhibited a significantly bimodal orientation along the shoreward magnetic axis (Fig. 1K). Therefore, the 'blue'-transmitting pineal caps did not prevent newts from learning the direction of shore in the outdoor tanks. Second, although newts tested under long-wavelength failed to exhibit a consistent direction of orientation relative to the magnetic field (Fig. 1L), the proportion that scored within the allotted time period (see Materials and Methods) did not differ significantly from that of newts tested under full-spectrum light. Therefore,

blocking light to the pineal did not cause a decrease in overall activity, locomotor ability or 'willingness' to leave the center of the arena. Third, in previous studies of both anuran and urodele amphibians, blocking or ablating the pineal complex in animals with intact eyes did not eliminate shoreward compass orientation in tests conducted outdoors with the sun visible (i.e. when amphibians are able to use their sun compass; Taylor and Ferguson, 1970; Taylor, 1972; Justis and Taylor, 1976; Taylor and Adler, 1978). If eliminating photic input from the pineal complex had a generalized effect on behavior or caused a change in the nature of the orientation response, this effect should be independent of the source of directional information used to determine the shore direction. However, covering or ablating the photoreceptors in the pineal complex has been found to cause disorientation only when polarized light and/or an earth-strength magnetic field are the sole orientation cues available (Adler and Taylor, 1973; Taylor and Adler, 1973; Taylor and Adler, 1978; Taylor and Auburn, 1978; present experiments, see Fig. 1). These and other experiments suggest that extraocular photoreceptors in the pineal complex of amphibians mediate polarization detection and light-dependent magnetoreception in amphibians and that manipulating pineal organ disrupts these sensory functions.

Although the 'blue'-transmitting caps prevented long-wavelength overhead light from reaching the pineal organ, light to the eyes was unaffected. If the photoreceptors mediating long-wavelength input to the magnetic compass are located in the retina, or anywhere else in the body that was not covered by the caps, these photoreceptors should have been stimulated by the long-wavelength testing condition. Since the directional response of the magnetic compass differs by 90° under short-wavelength (i.e. <450 nm) and long-wavelength (i.e. >500 nm) light, stimulation of the long-wavelength mechanism during testing would be expected to produce a shift in orientation of 90° (as in Fig. 1C,G,I). Consequently, the failure of newts to orient under long-wavelength light (and, more specifically, to exhibit 90°-shifted magnetic orientation relative to the shore/water axis) is consistent with the putative long-wavelength mechanism having the same approximate location as the short-wavelength mechanism, i.e. in or near the pineal organ. The parapineal lobes of the pineal organ in both frogs and lizards contain unusual 'chromatic' photoreceptors in which there are two photoreception mechanisms that have antagonistic effects on the response of the photoreceptor to light (Eldred and Nolte, 1978; Solessio and Engbretson, 1993). In frogs, the spectral properties of this chromatic mechanism closely match those of the of the newt's shoreward magnetic compass response (i.e. antagonistic short- and long-wavelength mechanisms that have equal sensitivity at approximately 460–470 nm). Whether a similar chromatic mechanism exists in the pineal complex of the newt is unknown, but the similarities in the spectral characteristics of the newt's magnetic compass response and the physiology of the frog's pineal response are close enough to deserve further consideration. We have recently obtained evidence that bullfrog *Rana catesbeiana* tadpoles have a magnetic compass

sense that exhibits a similar wavelength-dependent 90 ° shift to that of newts (M. J. Freake, S. C. Borland and J. B. Phillips, manuscript in preparation and unpublished data), but have no information as yet concerning the identity or location of the photoreceptors that mediate this response.

The long-wavelength input to the chromatic units in the frog parapineal lobe is less sensitive (by approximately 2 log units) than the short-wavelength input (Dodt and Heerd, 1966). Since the response of newts tested under full spectrum light from the 150 W xenon arc source, which is somewhat long-wavelength biased, is indistinguishable from that of newts tested under 400 and 450 nm light, the short-wavelength input to the newt's magnetic compass also appears to be appreciably more sensitive than the long-wavelength input (Phillips and Borland, 1992a; Deutschlander et al., 1999a; Deutschlander et al., 1999b). A difference in sensitivity of the magnitude exhibited by the chromatic units could explain why the wide range of natural lighting conditions experienced in the outdoor training tanks does not prevent newts and tadpoles from learning a consistent shoreward response (Phillips and Borland, 1992a; Phillips and Borland, 1992b; Deutschlander et al., 1999a; Deutschlander et al., 1999b, Deutschlander et al., 2000; M. J. Freake, S. C. Borland and J. B. Phillips, manuscript in preparation and unpublished data). Although the spectral properties of natural illumination vary considerably at different times of day and under different weather conditions, such illumination is much less saturated than the spectral stimuli used in the laboratory experiments. Therefore, although we were able to selectively excite the long-wavelength mechanism in the laboratory experiments (e.g. Fig. 1G), this may occur rarely, if ever, under natural (i.e. broad band) lighting conditions due to the higher sensitivity of the short-wavelength mechanism.

As mentioned above, the available data suggest that photoreceptors in the pineal complex of amphibians mediate orientation to the e-vector of plane polarized light (Adler and Taylor, 1973; Taylor and Adler, 1973; Taylor and Auburn, 1978) and may also mediate orientation to the geomagnetic field (Deutschlander et al., 1999a; and see Fig. 1). Both light-dependent magnetoreception and polarized light detection are likely to involve receptors that contain an ordered array of light-absorbing molecules (Wehner and Rossel, 1985; Wehner, 1989; Edmonds, 1996; Ritz et al., 2000). In a photoreceptor-based magnetoreception mechanism involving a radical-pair reaction (Schulten, 1982, Ritz et al., 2000), the constraints on the alignment of the molecules in which the magnetic interaction occurs are likely to be more stringent than in a typical vertebrate photoreceptor. In a typical vertebrate photoreceptor, the photopigment molecules are non-randomly aligned with respect to the plane of the membrane in the outer segments, but free to rotate within this plane. The importance of the ordered array of the light-absorbing molecules in a radical-pair mechanism stems from the complex three-dimensional pattern of response generated by this type of mechanism (Ritz et al., 2000). For example, at some field intensities, this pattern would consist of large circular fields

with or without surrounding concentric rings at either end of the magnetic field lines (see Fig. 6 in Ritz et al., 2000). Deriving directional information from such a pattern would require either sequentially sampling with a single receptor or simultaneously sampling with a three-dimensional array of receptors (Ritz et al., 2000). In either case, variation in the alignment of molecules involved in the radical-pair reaction within an individual photoreceptor would degrade the three-dimensional pattern and, consequently, decrease or eliminate the dependence of the receptor's response on magnetic field alignment. Therefore, if a radical-pair-based magnetoreceptor is present in newts, or in any other organism, selection should favor a reduction of variation in the alignment of the light-absorbing molecules, ultimately resulting in a highly ordered linear array. One consequence of such a highly ordered array would be strong dichroic absorption of light, resulting in sensitivity to the e-vector of polarized light in addition to the alignment of the magnetic field.

A photoreceptor-based magnetoreceptor involving freely rotating single-domain particles of magnetite (Edmonds, 1996) may also be affected by polarized light. The mechanism proposed (Edmonds, 1996) involves 'needle-shaped' single-domain particles of magnetite suspended in a liquid crystal made up of elongate carotenoid molecules, like those found in the oil droplets in some vertebrate photoreceptors. Edmonds has shown that the alignment of the carotenoid molecules can be affected by the mechanical strain energy resulting from the rotation of the single-domain particles by an earth-strength magnetic field (Edmonds, 1996; D. T. Edmunds, personal communication). The minimum strain energy occurs when the molecules are aligned parallel to the long axes of the particles and, thus, parallel to the axis of the magnetic field. Because the absorption of light by carotenoid molecules is strongly anisotropic (Sackman, 1968), transmission of the light through such a magnetite-containing oil droplet would vary with alignment of the magnetic field. Magnetic fields aligned parallel to the long axis of the photoreceptor causing the magnetite particles and associated carotenoid molecules also to be aligned along this axis would result in a higher intensity of light reaching the outer segment, while fields aligned orthogonal to the long axis of the receptor causing the particles and carotenoid molecules to be aligned perpendicular to the photoreceptor axis would result in a lower intensity of light reaching the outer segment (Edmonds, 1996). In addition, changes in the alignment of the magnetic field (and corresponding changes in the alignment of the carotenoid molecules) in the plane orthogonal to the long axis of the photoreceptor would result in differences in the transmission of different e-vectors of polarized light. As in the case of a radical-pair-based mechanism (Schulten, 1982; Ritz et al., 2000), therefore, the mechanism proposed by Edmonds (Edmonds, 1996) would be likely to exhibit both magnetic and polarized light sensitivity.

Considering both (i) the evidence for polarization sensitivity and light-dependent magnetosensitivity in the pineal complex of amphibians and (ii) the inherent polarization sensitivity of

the mechanisms that have been proposed to explain light-dependent magnetoreception, it is interesting to consider that the photoreception mechanism for both polarization and magnetic orientation may be one in the same, or at least very closely associated, in amphibians. However, additional studies are needed to clarify how these two senses interact in the pineal organ. In fact, for both senses, we still do not know the cellular basis or biophysical transduction mechanism that leads to sensory perception. As a starting point, complete action spectra are needed for the magnetic-field and polarized-light compass responses. Similarities or differences in the wavelength-dependence of light-dependent magnetoreception and polarization vision would help to determine whether the neural substrates of these senses involve similar receptor types.

Although the spectral dependence of polarization sensitivity in amphibians is unknown, at least one vertebrate does exhibit wavelength-dependent polarization responses. In fish, both psychophysical responses (Hawryshyn and McFarland, 1987) and neurophysiological responses from the optic nerve and torus semicircularis (Parkyn and Hawryhsyn, 1993; Coughlin and Hawryshyn, 1995) provide evidence for a polarization-sensitive system that is mediated by two receptor classes with spectral properties similar to those inferred in the mediation of the newt's magnetic compass response (Fig. 1; and see Phillips and Borland, 1992a). In the retina of salmonids and goldfish, the ultraviolet cone mechanism responds maximally to vertically polarized light, and the green and red cone mechanisms (which make up the two dissimilar pairs of the double cone) respond maximally to horizontally polarized light (Hawryshyn and McFarland, 1987; Parkyn and Hawryhsyn, 1993). Single-unit recordings from biphasic cells in the torus semicircularis demonstrate that the inputs from these two orthogonally sensitive mechanisms interact antagonistically, i.e. input from the ultraviolet mechanism produces an ON response, and input from the green and red mechanisms gives an OFF response (Coughlin and Hawryshyn, 1995). Although sensitivity to polarized light in rainbow trout *Oncorhynchus mykiss* is mediated by retinal photoreceptors (Hawryshyn et al., 1990), while extraocular photoreceptors are implicated in the newt's magnetic compass, the similarity in the spectral dependence of these two responses is noteworthy. Like the shoreward magnetic compass orientation of newts, neurophysiological recordings from the optic nerve of trout and conditioned cardiac responses of goldfish *Carassius auratus* exhibit maximum responses to e-vector alignments that differed by 90° under conditions that stimulated short-wavelength and long-wavelength photoreceptors (Fig. 2). Unfortunately, the possibility of a link between photoreception and magnetoreception has not been investigated in fish. For example, magnetic compass orientation has been demonstrated in salmonids, but there is no information on whether this response is influenced by different wavelengths and intensities of light (Quinn, 1980; Quinn, et al., 1981; Quinn and Brannon, 1982; Quinn and Dittman, 1992).

In summary, although far from complete, the available evidence is sufficient to suggest a number of interesting parallels between the detection of polarized light and the light-dependent dectection of magnetic fields, at least in amphibians and fish. (i) In both cases, the underlying sensory mechanism is likely to involve an ordered array of light-absorbing molecules. (ii) In amphibians, extraocular photoreceptors located in, or near, the pineal complex appear to be involved in mediating responses to both the magnetic field and polarized light. (iii) The magnetic compass of newts and the physiological mechanisms responsible for polarized light sensitivity in rainbow trout exhibit similar wavelength-dependent 90° shifts in the axis of response. Further neurophysiological and behavioral investigations of both sensory mechanisms are needed to determine whether these similarities are merely coincidental, or instead reflect the involvement of similar receptor mechanisms and/or the influence of similar selection pressures (that have yet to be identified) on the functional properties of these two systems. At the very least, investigations of the similarities of these two sensory modalities are likely to increase our understanding of both the underlying sensory mechanisms and the orientation behaviors that they mediate.

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