

'Fixed-axis' magnetic orientation by an amphibian: non-shoreward-directed compass orientation, misdirected homing or positioning a magnetite-based map detector in a consistent alignment relative to the magnetic field?

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Summary

Experiments were carried out to investigate the earlier prediction that prolonged exposure to long-wavelength (>500 nm) light would eliminate homing orientation by male Eastern red-spotted newts *Notophthalmus viridescens*. As in previous experiments, controls held in outdoor tanks under natural lighting conditions and tested in a visually uniform indoor arena under full-spectrum light were homeward oriented. As predicted, however, newts held under long-wavelength light and tested under either full-spectrum or long-wavelength light (>500 nm) failed to show consistent homeward orientation. The newts also did not orient with respect to the shore directions in the outdoor tanks in which they were held prior to testing. Unexpectedly, however, the newts exhibited bimodal orientation along a more-or-less 'fixed' north-northeast–south-southwest magnetic axis. The orientation exhibited by newts tested under full-spectrum light was indistinguishable from that of newts tested under long-wavelength light, although these two wavelength conditions have previously been shown to differentially affect both shoreward compass orientation and homing orientation. To investigate the possibility that the 'fixed-axis' response of the newts was mediated by a magnetoreception mechanism involving single-domain particles of magnetite, natural remanent magnetism (NRM) was measured from a subset of the newts. The distribution of NRM alignments with respect to the

head–body axis of the newts was indistinguishable from random. Furthermore, there was no consistent relationship between the NRM of individual newts and their directional response in the overall sample. However, under full-spectrum, but not long-wavelength, light, the alignment of the NRM when the newts reached the 20 cm radius criterion circle in the indoor testing arena (estimated by adding the NRM alignment measured from each newt to its magnetic bearing) was non-randomly distributed. These findings are consistent with the earlier suggestion that homing newts use the light-dependent magnetic compass to align a magnetite-based 'map detector' when obtaining the precise measurements necessary to derive map information from the magnetic field. However, aligning the putative map detector does not explain the fixed-axis response of newts tested under long-wavelength light. Preliminary evidence suggests that, in the absence of reliable directional information from the magnetic compass (caused by the 90° rotation of the response of the magnetic compass under long-wavelength light), newts may resort to a systematic sampling strategy to identify alignment(s) of the map detector that yields reliable magnetic field measurements.

Key words: navigation, homing, magnetic field, newt, *Notophthalmus viridescens*, map detector, natural remanent magnetism, orientation.

Introduction

The Eastern red-spotted newt *Notophthalmus viridescens* uses the geomagnetic field for two forms of spatial orientation: (1) shoreward orientation, which utilizes only directional ('compass') information (Phillips, 1986a,b; Phillips and Borland, 1992a,b; Deutschlander et al., 1999a,b, 2000; Phillips et al., 2001) and (2) map-based homing orientation ('true

navigation'), which utilizes both compass and geographic position ('map') information (Phillips, 1987; Phillips and Borland, 1994; Phillips et al., 1995, 2002; Fischer et al., 2001). The magnetic field provides a source of compass information that is used both in shoreward compass orientation and the compass component of homing (Phillips, 1986a,b, 1987; Phillips

and Borland, 1992a,b, 1994; Phillips et al., 1995; Deutschlander et al., 1999a,b). Findings from recent experiments suggest that newts may also use the geomagnetic field to derive map information (Fischer et al., 2001; Phillips et al., 2002).

Newts displaced from their home ponds while being deprived of access to directional visual, olfactory, magnetic and inertial compass cues have been shown to exhibit accurate homing orientation from distances well beyond their normal range of movement, indicating that they are capable of map-based homing (Phillips et al., 1995). Recent experiments investigating the effects of small changes in magnetic inclination on the newt's homing response suggest that this component of the magnetic field may be used to derive one coordinate of a uniconordinate or biconordinate map (Fischer et al., 2001; Phillips et al., 2002). If so, newts must be able to detect the natural spatial variation in magnetic inclination, which is extremely weak, averaging approximately $0.01^\circ \text{ km}^{-1}$. Moreover, spatial irregularities and temporal variation make detection of spatial variation exceedingly difficult. Even at localities where a consistent magnetic gradient is present, averaging measurements over extended periods of time and/or at night, when the magnetic field is least variable, would be necessary to factor out temporal variation (Rodda, 1984; Phillips, 1996; Phillips and Deutschlander, 1997).

A magnetic map would require an animal like the newt, with a range of movement of at most a few km, to detect differences in inclination of $0.01\text{--}0.001^\circ$ (or changes in total intensity of approximately $0.01\text{--}0.001\%$ of the ambient field), depending on the steepness of the local gradient(s) and the accuracy of geographic position fixing. A light-dependent magnetoreception mechanism, like that implicated in the shoreward magnetic compass response of the newt (Phillips and Borland, 1992a,b; Deutschlander et al., 1999a,b; Phillips et al., 2001), is unlikely to exhibit such a high level of sensitivity (Schulten and Windemuth, 1986; Edmonds, 1996; Ritz et al., 2000). Consequently, if newts use magnetic map information, they are likely to use a specialized 'map detector' that is distinct from the magnetic compass and may involve particles of magnetite or a similar magnetic material (Yorke, 1979; Walcott, 1980; Kirschvink and Walker, 1985; Phillips and Borland, 1994; Kobayashi and Kirschvink, 1996; Phillips and Deutschlander, 1997).

Previous studies carried out by our laboratory indicate that the magnetoreception systems used by newts for shoreward compass orientation and for homing exhibit different functional properties. Newts using the magnetic compass for shoreward orientation are sensitive to the axis, but not the polarity, of the magnetic field ('axial' sensitivity; Phillips, 1986b). To distinguish between the two ends of the magnetic field axis, shoreward-orienting newts use the inclination or dip angle of the magnetic field, as shown previously in migratory birds (Wiltschko and Wiltschko, 1972). Magnetic compass orientation by newts has also been shown to depend on the presence (Phillips and Borland, 1992b) and wavelength (Phillips and Borland, 1992a; Deutschlander et al., 1999a) of light. Under wavelengths of light of $>500\text{ nm}$, the newt's

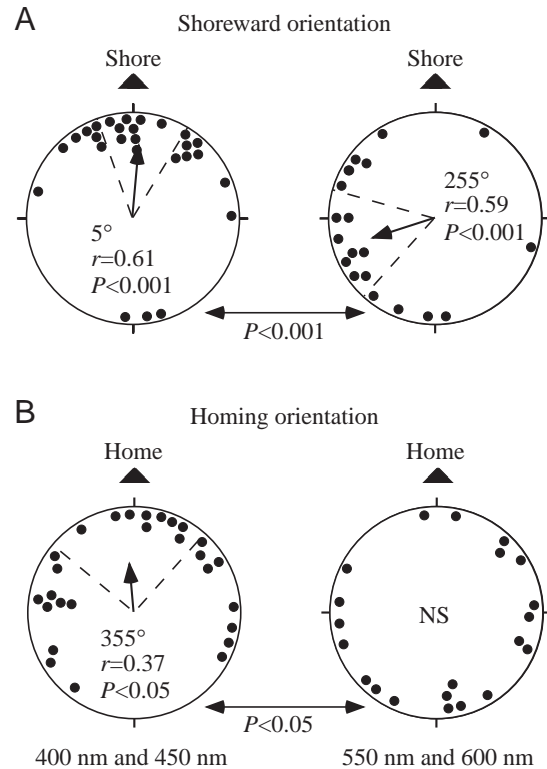


Fig. 1. Wavelength-dependence of shoreward compass orientation (A,B) and homing orientation (C,D) by newts housed in outdoor tanks under full-spectrum light prior to testing (data from Phillips and Borland, 1994). In shoreward orientation tests, (A) newts tested under 400 nm and 450 nm light oriented in the correct shoreward direction and were indistinguishable from controls tested under full-spectrum light (not shown), while (B) newts tested under 550 nm and 600 nm light exhibited significant magnetic orientation that was rotated approximately 90° counterclockwise of the shore direction. In homing tests, (C) newts tested under 400 nm and 450 nm light exhibited homeward orientation, while (D) newts tested under 550 nm and 600 nm light failed to show a consistent direction of orientation relative to home (NS, not significant). In the homing tests, newts tested under 550 nm and 600 nm light were also randomly distributed with respect to the direction of shore in the outdoor training tanks and with respect to magnetic north (not shown). Data points are magnetic bearings of individual newts tested in one of four symmetrical magnetic field alignments (see Materials and methods) plotted relative to the magnetic bearing of the artificial shore in the outdoor training tank (A,B) or relative to the magnetic direction of the newts' home ponds (C,D). In both the shoreward and homing tests, data are pooled from newts collected from ponds that differed in home direction by approximately 90° , and held prior to testing in tanks with three different shore directions; see Phillips and Borland (1994).

shoreward magnetic compass response undergoes a 90° counter-clockwise rotation relative to that exhibited under full-spectrum or short-wavelength light (Fig. 1A). This wavelength-dependent 90° shift appears to result from a direct effect of light on the underlying magnetoreception mechanism (Phillips and Borland, 1992a) and is mediated by extraoptic photoreceptors located in or near the pineal organ (Deutschlander et al., 1999b;

Phillips et al., 2001). These properties are consistent with a photoreceptor-based magnetoreception mechanism like that proposed by Ritz et al. (2000).

Use of the magnetic field by newts for map-based homing (i.e. true navigation) exhibits a number of functional properties that are distinct from shoreward compass orientation. Newts that are homing are sensitive to the polarity of the magnetic field ('polar' sensitivity; Phillips, 1986a). Polar sensitivity is compatible with a magnetoreception mechanism involving single-domain (SD) or interacting superparamagnetic (SPM) particles of the mineral magnetite that are at least partially fixed (i.e. not free to rotate) with respect to the surrounding tissue. Measurements of natural remanent magnetism (NRM) and induced remanent magnetism (IRM) from a subsample of newts used in the present study have demonstrated the presence of SD magnetite (Brassart et al., 1999). Magnetite-based receptors have been implicated in the navigational map of birds (e.g. Wiltschko et al., 1994; Beason and Semm, 1996; Munro et al., 1997a,b; Beason et al., 1997) and have been suggested to play a similar role in a salmonid fish, *Oncorhynchus mykiss* (Walker et al., 1997; Diebel et al., 2000). Although the polarity sensitivity of the newt's homing response is consistent with a magnetite-based receptor, this response is also affected by the wavelength of light. In contrast to the 90°-shifted orientation exhibited by shoreward-orienting newts (Fig. 1A), however, newts attempting to home were disoriented under long-wavelength (>500 nm) light (Fig. 1B; Phillips and Borland, 1994).

Phillips and Borland (1994) proposed that the properties of the newt's homing response result from an interaction between the light-dependent magnetic compass and a non-light-dependent 'map detector'. According to this hypothesis, sensitivity to the wavelength of light (Fig. 1B) is a consequence of input from the light-dependent magnetic compass, while polar sensitivity (Phillips, 1986a) results from an input from a map detector involving magnetite or a similar magnetic material. Properties that are not characteristic of either type of system (e.g. random orientation under long-wavelength light) arise from an interaction between the two systems (see below). Specifically, newts were proposed to use the magnetic compass to position the putative map detector in a fixed alignment relative to the magnetic field to increase the accuracy of magnetic-field measurements (Fig. 2A). The model proposed by Phillips and Borland (1994) could explain the failure of newts to orient under long-wavelength light in the homing experiments (Fig. 1B), because a 90° rotation of the directional response of the magnetic compass under long-wavelength light would cause the map detector to be aligned at right angles to its normal alignment relative to the magnetic field and, therefore, should interfere with measurements of the magnetic field component(s) used to derive map information (Fig. 2C). Disorientation would also be expected if this hybrid system was used to determine the polarity of the magnetic field for the compass component of homing, because the polarity of the magnetic field would be specified along an axis perpendicular to the axis indicated by the rotated magnetic compass and, thus, would be ambiguous with respect to the

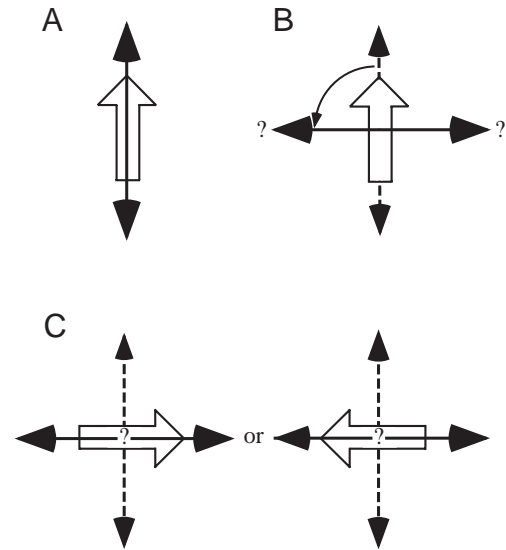


Fig. 2. Hypothesized response on the hybrid magnetoreception mechanism under full-spectrum and long-wavelength light (Phillips and Borland, 1994). (A) In the proposed hybrid magnetoreception system, the magnetic compass (double-headed solid arrow) is used to align the map detector (single-headed open arrow) with respect to the axis of the magnetic field (north at top of figure) and, thus, to obtain more accurate measurements of one or more magnetic field components used for the map component of homing. In turn, the map detector, which is sensitive to the polarity of the magnetic field, is used to distinguish between the two ends of the magnetic axis when the newt is carrying out the compass component of homing, replacing the inclination ('dip angle'), which newts use when exhibiting shoreward magnetic compass orientation (Phillips, 1986a). (B,C) Under long-wavelength light, the directional response of the magnetic compass is rotated by 90° (Phillips and Borland, 1992a). (B) When newts are carrying out the compass component of homing, the 90° rotation of the magnetic compass' response would cause the axis indicated by the magnetic compass to be perpendicular to the polarity of the magnetic field indicated by the map detector, preventing newts from using the hybrid system to determine compass direction. [Previous homing studies have shown that newts held in the outdoor tanks under full-spectrum light and tested under long-wavelength light are disoriented, suggesting that they do not fall back on the inclination compass for the compass component of homing when polarity information is ambiguous (Fig. 1B; and see Phillips and Borland, 1994)]. (C) When newts are carrying out the map component of homing, the 90° rotation of the magnetic compass' response under long-wavelength light would cause newts to position the map detector perpendicular to the alignment in which it is normally positioned to take map readings, and, therefore, prevent them from obtaining map information.

two ends of the magnetic axis (Fig. 2B). Only when exposed to wavelengths that allow the magnetic compass to operate normally would it be possible to use the proposed hybrid system to derive map or compass information. If newts use the hybrid system to derive map information, therefore, we predicted that newts held in the outdoor tanks under long-wavelength (>500 nm) light should be unable to obtain map information and, as a consequence, should fail to exhibit

consistent orientation in the home direction when subsequently tested in the indoor arena under either full-spectrum or long-wavelength light (Phillips and Borland, 1994).

Materials and methods

Experimental subjects

Adult male Eastern red-spotted newts *Notophthalmus viridescens* Rafinesque were used in these experiments. Newts were seined from ponds 20–25 km east-southeast (ESE; home direction = 103–115°) and 40–45 km south-southwest (SSW; home direction = 207°) of the testing facility, which was located adjacent to the main Indiana University campus in Bloomington, IN, USA. Newts were held prior to training in 120 l water-filled, all-glass aquaria in the laboratory building and were fed salmon pellets (Rangen Inc., Buhl, ID, USA) three times per week. Immediately prior to being placed in outdoor tanks, they were held for several days in an aquarium with only moist gravel or shallow (i.e. <1 cm) water in the bottom until they began to transform into the terrestrial form (i.e. cornified skin, reduced tail fin).

Behavioral experiments

Training tanks

Outdoor tanks consisted of water-filled 120 l all-glass aquaria (90 cm×30 cm×45 cm) located outdoors 13–15 m from the laboratory building. The tanks contained an artificial shore consisting of a sheet of opaque Plexiglass that sloped upwards at one end of the tank. Shelter was provided at the shallow end of the tank. Water was circulated up from beneath the Plexiglass floor of the training tank at the shallow end by means of a pair of bubblers. The water flowed towards the deep end of the tank through a Plexiglass grill, which prevented the newts from leaving the water, and returned beneath the floor through a grid of small holes at the deep end. The sides of the tanks were enclosed in clear 'bubble plastic' (Consolidated Plastics, Twinsburg, OH, USA) to provide insulation for year-round testing. The tops of the tanks were covered with borosilicate glass, which is transparent to both visible and near-UV light. The glass covering the deep end of the tank was frosted to diffuse the incoming light and to help to eliminate shadows. Finally, the outermost layer on the top and sides of the training tank consisted of 2–4 layers of aluminum window screening to decrease the intensity of sun light, which otherwise caused overheating during the summer months (for additional details of the design of outdoor tanks, see Deutschlander et al., 2000).

Three outdoor tanks were used in these experiments. The tanks were located to the east, south and west of the laboratory building, with the shore end of each tank towards the building (i.e. the shore directions were west, north and east, respectively). Groups of newts were placed in tanks in which the shoreward direction differed from the home direction to distinguish shoreward orientation from homing (see Phillips, 1987). Newts were held in the water-filled outdoor tanks for 4–7 days prior to testing.

Water temperature plays an important role in eliciting different types of orientation behavior by newts (Phillips, 1986b, 1987). Training tank water temperature was controlled by circulating water from a 6000 l underground cistern, which was located 6–9 m from each training tank. Water from the cistern was circulated through a glass heat exchanger located beneath the Plexiglass shore of the tank. The water was pumped from the cistern to the training tank by means of a pneumatic pump located in a small wooden pump house above each cistern.

Testing facility

The Animal Orientation Research Facility at Indiana University was designed specifically for studies of magnetoreception and magnetotactic orientation (Phillips and Borland, 1992a,b; 1994). Experiments were carried out in a 6.5 m×6.5 m testing room in which the humidity was elevated to nearly 100% of saturation and the temperature was maintained at 24–27°C. The orientation of the newts was observed in an enclosed, visually symmetrical, terrestrial arena (72 cm diameter). The floor of the arena consisted of a circular, polished glass surface that sloped upwards from the center towards the outer edge at an angle of approximately 4°. Beneath the glass was a layer of Plexiglass marked with a circular grid that was used to record the directional responses of the newts. At the center of the arena floor was a release device consisting of a vertical Plexiglass cylinder (7.5 cm inner diameter) that protruded approximately 10 cm above the arena floor. The release cylinder could be lowered until the top was flush with the arena floor by means of a hydraulic mechanism controlled by an observer in an adjacent room. The floor of the release device consisted of the top end of a stationary, vertically aligned cylindrical chamber (7.5 cm outer diameter × 20 cm height) that was level with the arena floor. Water from a temperature-controlled water bath was circulated through the chamber to maintain a temperature of 30–36°C. The water bath was turned off during each trial to eliminate any vibration that might bias the newts' orientation.

A newt's movements were monitored by means of its silhouette, which was visible through the floor of the arena and reflected in a 45° mirror located underneath. A video camera (MTI, SC-65X, Michigan City, IN, USA), pointed at the mirror from a location 3 m from the center of the arena, allowed an observer in the adjacent room to observe the newt's movements on a video monitor. The arena was illuminated from above by means of a 150 W xenon arc lamp (Opti Quip, Inc., New York, USA). The arc lamp was located in the adjacent room 6 m from the center of the test arena to minimize electromagnetic disturbance. The arc lamp remained on at all times; a shutter located in front of the arc lamp was closed when necessary to block light from reaching the arena. When the shutter was open, light from the arc lamp was projected through a 10 cm-diameter PVC pipe and reflected down into the arena by a front surface mirror. The light passed through two 75 cm-diameter frosted Pyrex glass diffusers centered above the arena.

In the present experiments, long-wavelength light was produced by enclosing the outdoor tank, or inserting in the light path to the testing arena, two layers of long-wavelength-transmitting (wavelengths >500 nm) gel filter (Lee Filters #101, Lee Filters, Inc., Andover, UK) and 1–2 layers of 0.7 cm acrylic plastic. Transmission of light was $<1\%$ of light at wavelengths of <490 nm and $<0.1\%$ at wavelengths of <470 nm. A large hood of the same filter material was erected over an outdoor tank on the day of testing so that newts could be removed from the tank without admitting short-wavelength light.

Newts were tested in four horizontal magnetic field alignments (see below), i.e. the ambient magnetic field (magnetic north at north) and three artificial magnetic fields (magnetic north rotated to east, south or west). The rotated fields closely resembled the ambient field in inclination ($\pm 1^\circ$) and total intensity ($\pm 1\text{--}2\%$). Rotation of the magnetic field was accomplished using a double cube-surface-coil system described by Phillips (1986b). In the present experiments, each of the cube coils was wrapped with two strands of wire. When current was flowing in the same direction in the two strands, the coil produced an artificial magnetic field. However, when the connections to one of the strands were reversed, so that current in the two strands flowed in the opposite direction, there was no net effect on the magnetic field (Phillips, 1986a). The output of the power supplies (Lambda Electronics LQ-533) controlling the two coils remained the same in all four horizontal alignments of the magnetic field.

Testing procedures

Groups of newts were placed in an outdoor tank at least 4 days prior to testing. Prior to the day of testing, the water temperature of the training tank was maintained between 14°C and 18°C and generally varied $<2^\circ\text{C}$ within a 24 h period. Homing orientation was studied in newts collected during the fall/winter (end of November–January) and early summer (May–June) migratory periods. For the homing experiments, the water temperature of the training tank was lowered to $1\text{--}4^\circ\text{C}$ on the night prior to testing (Phillips, 1987)[†]. To accomplish this, the water circulation system was disconnected from the underground cistern, and antifreeze was added to a small reservoir in the pump house that was connected to the heat-exchange coils in the training tank. Remote cooling coils from two or three refrigeration units (Grant CZ2, Lauda IC-6) were placed in the small reservoir and controlled by a remote temperature controller connected to a small non-magnetic temperature sensor in the tank. The temperature controller was set to approximately $1\text{--}2^\circ\text{C}$. A single 500 W or 1000 W heater regulated by the temperature controller prevented the training tank water from freezing when the air temperature was $<0^\circ\text{C}$. The time required to lower the training tank water temperature was 6–10 h, depending on outside air temperature. On the following morning, beginning at or before dawn, the coolers were replaced with two 1000–1100 W heaters, and the training

tank water temperature rapidly increased to $30.5\pm 1^\circ\text{C}$, where it remained for the duration of the test. After testing, each group of newts was placed in cool water and then returned to their home pond, usually within 1–2 weeks.

For testing, a newt was removed from the shallow end of the training tank by grasping it gently by the base of the tail. It was then placed in a small plastic transport box, freshly rinsed with water from the training tank. The plastic box was placed inside a light-tight cloth bag and carried into the testing room. Upon entering the testing room, the newt was removed from the transport box in total darkness and gently placed in the release device from a constant direction. Newts that struggled violently or received rough handling at any stage of transportation to the test arena were not tested. After the observer exited the room, the arena was illuminated by opening a shutter in front of the light source in the adjacent room. The newt was then released after a 60 s delay. The newt's directional response was measured at the point at which it first made contact with a 20 cm-radius circle centered on the release device. Bearings obtained from newts that were startled by the release device (i.e. newts that exited immediately after the release device was lowered and/or scored at the 20 cm-radius circle in <1 min) were not used. Previous work has shown that such animals exhibit a randomly oriented escape response (see Phillips, 1986b). Furthermore, a trial was discontinued if the newt did not leave the center of the arena within 8–10 min or did not reach the 20 cm-radius circle within 15 min (Phillips, 1986b, 1987).

Each newt was tested only once. Roughly equal numbers of newts were tested in each of the four field alignments. This testing protocol made it possible to factor out any consistent non-magnetic bias from the data when the magnetic bearings were pooled from newts tested in the four field alignments (Phillips, 1986b). A test, which lasted 3–5 h, generally yielded 4–10 bearings (i.e. 2–5 experimental animals and 2–5 controls). Typically, an equal number of newts in each test failed to meet the time criterion described previously. To achieve the balanced design necessary to factor out any non-magnetic bias, data were pooled from a series of tests, each involving a new group of newts.

For data analysis, magnetic bearings were pooled. Data were analyzed according to the procedures in Batschelet (1981). The Rayleigh test was used to test for a significant clustering of bearings; the 95% confidence interval around the mean vector direction was used to test for orientation with respect to a predicted direction. The Watson U^2 -test was used to test for differences between distributions.

Measurements of natural remanent magnetism

NRM measurements were carried out by Joe Kirschvink and Jacques Brassart at the California Institute of Technology. The results of these measurements have been published previously (Brassart et al., 1999). There was an interval of at least two days after behavioral observations before newts were anesthetized, frozen with liquid nitrogen, and shipped on dry ice to the California Institute of Technology for measurements. During

[†]Phillips (1987) discusses the possible biological significance of the response of Eastern newts to variation in water temperature.

the interval prior to freezing, the newts were maintained under normal housing conditions (see above). Analysis of the distribution of NRM alignments ('declinations') relative to the newts' heads was carried out using standard circular statistics. To determine whether the fixed-axis response of newts was an attempt to align a single-axis magnetoreceptor involving permanent magnetic material relative to the magnetic field[‡], we estimated the NRM alignment relative to the magnetic field when the newts reached the 20 cm criterion circle ('NRM20') by adding each newt's NRM declination to its 20 cm magnetic bearing.

Results

The experiments reported here were carried out during the seasonal migratory periods when newts held in outdoor tanks under natural lighting and tested indoors under full-spectrum (near-ultraviolet and visible) light exhibit map-based homing (Phillips, 1987; Phillips and Borland, 1994; Phillips et al., 1995, 2002; Fischer et al., 2001). As expected, a small sample of controls held and tested under full-spectrum light exhibited significant homeward orientation (352° , $r=0.47$, $N=20$, $P<0.02$, Rayleigh test; data from SSW and ESE ponds combined). By contrast, newts held in the outdoor tanks under long-wavelength light (>500 nm) failed to show a consistent direction or axis of orientation relative to the homeward direction (Fig. 3) or relative to the shoreward direction (Fig. 4) when tested under either lighting condition (Table 1). Instead, the newts were bimodally distributed along a roughly NNE–SSW magnetic axis under both full-spectrum (38 – 218° , $r=0.40$, $N=26$, $P<0.02$; Fig. 5A) and long-wavelength (26 – 206° , $r=0.56$, $N=24$, $P<0.001$; Fig. 5B) light. The greater scatter in the distribution of magnetic bearings under full-spectrum light was due, in part, to a difference in the response of the two pond groups. Under full-spectrum light, the distribution of magnetic bearings of newts from the ESE ponds approached significance along an axis of 8 – 188° ($r=0.46$, $P<0.10$; represented by diamonds in Fig. 5A), while newts from the SSW ponds were significantly oriented along an axis of 53 – 233° ($r=0.59$, $P<0.005$; represented by circles in Fig. 5A). The difference between the two distributions was significant ($P<0.05$, Watson U^2 -test on doubled angles). There was no difference in the distributions of bearings obtained from the two pond groups under long-wavelength light (Fig. 5B; $P>0.10$). Furthermore, there was no evidence of a 90° shift in the direction of magnetic orientation under long-wavelength light like that observed when newts are exhibiting shoreward compass orientation (Phillips and Borland, 1992b;

[‡]Although much of the single-domain magnetite found in animals is non-sensory, such particles tend to be randomly aligned and, thus, are unlikely to exhibit an appreciable net magnetic moment (Kobayashi and Kirschvink, 1996; J. L. Kirschvink, unpublished observation). Consequently, a moderately large population of non-randomly aligned single-domain particles involved in a magnetoreception mechanism (i.e. 10^6 – 10^8 particles suggested to be necessary for a map detector; Yorke, 1979; Kirschvink and Walker, 1985) might make a detectable contribution to the newts' NRM.

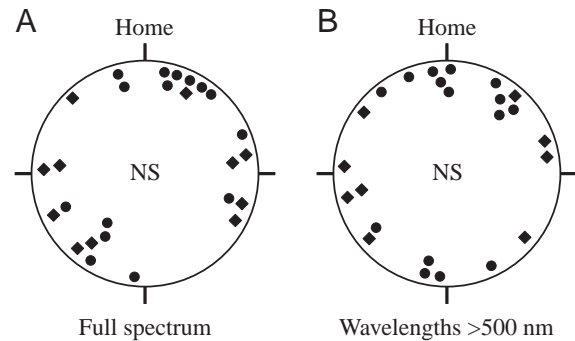


Fig. 3. Magnetic bearings plotted relative to home direction after housing in outdoor tanks under long-wavelength light (data from Table 1). (A) Magnetic bearings of newts housed under long-wavelength light and tested under full-spectrum light failed to show a significant direction of orientation relative to home (13° , $r=0.11$, $P>0.10$; Rayleigh test). (B) The same was true of newts housed and tested under long-wavelength light (351° , $r=0.19$, $P>0.10$). Diamonds represent newts collected in ponds to the east-southeast (ESE) of the testing site, and circles represent newts collected from ponds to the south-southwest (SSW) of the testing site. NS, not significant.

Deutschlander et al., 1999a,b). For the ESE group (diamonds in Fig. 5A,B), the difference in the axes of magnetic orientation under full-spectrum and long-wavelength light was 0° , and, for the SSW group (circles in Fig. 5A,B), the difference was 17° . In neither case was the difference significant ($P>0.10$; Watson U^2 -test).

The distributions of magnetic compass bearings obtained from the sample of newts from which NRM measurements were obtained ($N=18$; Fig. 5A,B, open symbols) was indistinguishable from that of the remaining newts both in the overall sample and in the samples tested under the two lighting

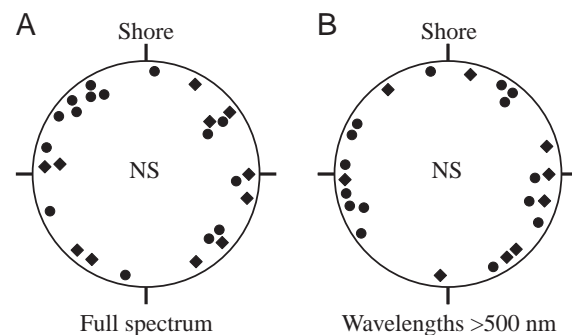


Fig. 4. Magnetic bearings plotted relative to shore direction after housing in outdoor tanks under long-wavelength light (data from Table 1). (A) Magnetic bearings of newts housed under long-wavelength light and tested under full-spectrum light failed to show a significant direction of orientation relative to shore (8° , $r=0.11$, $P>0.10$). (B) The same was true of newts housed and tested under long-wavelength light (76° , $r=0.04$, $P>0.10$). Diamonds represent newts collected in ponds to the east-southeast (ESE) of the testing site, and circles represent newts collected from ponds to the south-southwest (SSW) of the testing site. NS, not significant.

Table 1. Directional responses of newts after housing in outdoor tanks under long-wavelength light

Test wavelength (nm)	Test field; mN= (°)	10 cm actual bearing (°)	10 cm magnetic bearing (°)	20 cm actual bearing (°)	20 cm magnetic bearing (°)	Shore direction (°)	20 cm magnetic bearing rel. to shore (°)	Home direction (°)	20 cm magnetic bearing rel. to home (°)	Time to score at 20 cm (min:s)
ESE ponds										
Full	360	39	39	60	60	270	150	103	317	3:23
>500	360	155	155	176	176	270	266	103	73	7:16
>500	180	36	216	180	360	270	90	103	257	12:48
>500	270	283	13	287	17	270	107	103	274	10:01
Full	270	50	140	234	324	270	54	103	221	10:24
Full	180	199	19	194	14	270	104	103	271	2:40
Full	90	49	319	273	183	270	273	103	80	1:24
>500	90	315	225	323	233	270	323	103	130	2:29
Full	360	175	175	186	186	270	276	103	83	7:35
Full	90	100	10	51	321	270	51	103	218	5:37
>500	360	254	254	49	49	270	139	103	306	10:33
Full*	90	352	262	90	360	360	90	115	245	14:41
>500*	90	90	360	75	345	360	75	115	230	11:11
>500*	180	175	355	193	13	360	13	115	258	10:32
Full*	180	75	255	210	30	360	30	115	275	3:58
Full*	270	131	221	131	221	360	221	103	118	3:55
>500*	270	312	42	94	184	360	184	103	81	12:01
>500*	180	189	9	325	145	360	145	103	42	6:45
Full*	180	29	209	32	212	360	212	103	109	7:16
Full*	90	245	155	222	132	360	132	103	29	1:25
SSW ponds										
>500	360	81	81	31	31	360	31	207	184	1:40
Full	360	125	125	192	192	360	192	207	345	1:09
Full	90	182	92	184	94	360	94	207	247	4:41
>500	90	325	235	129	39	360	39	207	192	13:10
>500	180	221	41	219	39	360	39	207	192	2:27
Full	180	32	212	68	248	360	248	207	41	1:29
>500	270	100	190	146	236	360	236	207	29	1:55
Full	270	351	81	225	315	360	315	207	108	1:52
Full	90	165	75	148	58	90	328	207	211	2:05
Full	270	89	179	303	33	90	303	207	186	1:25
>500	90	299	209	289	199	90	109	207	352	1:05
>500	270	148	238	154	244	90	154	207	37	3:50
Full	180	85	265	38	218	90	128	207	11	3:26
Full	360	232	232	225	225	90	135	207	18	1:58
>500	180	266	86	260	80	90	350	207	233	3:04
>500	360	120	120	209	209	90	119	207	2	1:30
>500	270	139	229	112	202	270	292	207	355	3:57
>500	360	49	49	185	185	270	275	207	338	5:08
Full	360	315	315	275	275	270	5	207	68	3:46
Full	270	331	61	132	222	270	312	207	15	11:14
>500*	90	198	108	342	252	360	252	207	45	6:57
Full*	90	125	35	148	58	360	58	207	211	3:05
Full	180	235	55	241	61	360	61	207	214	10:01
>500*	180	105	285	69	249	360	249	207	42	1:06
>500*	90	149	59	298	208	270	298	207	1	2:40
Full*	90	325	235	331	241	270	331	207	34	1:02
Full*	180	75	255	14	194	270	284	207	347	2:49
>500*	180	61	241	182	2	270	92	207	155	10:57
>500*	360	281	281	169	169	270	259	207	322	5:01
Full*	360	271	271	234	234	270	324	207	27	1:42

*Newts from which natural remanent magnetism (NRM) measurements were obtained; see Table 2.
Full, full-spectrum light; >500, wavelengths >500 nm; mN, magnetic north.

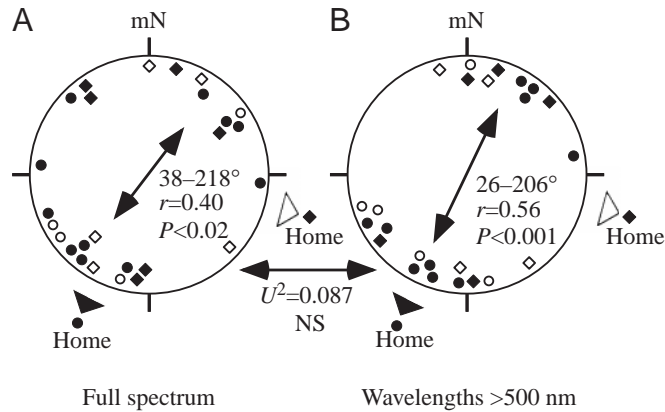


Fig. 5. Magnetic bearings plotted relative to magnetic north (mN) after housing in outdoor tanks under long-wavelength light (data from Table 1). (A) Magnetic bearings of newts housed under long-wavelength light and tested under full-spectrum light exhibited significant bimodal orientation (black double-headed arrow) along a northeast–southwest magnetic axis (38–218°, $r=0.40$, $P<0.02$; Rayleigh test). (B) Newts housed and tested under long-wavelength light exhibited similar bimodal orientation (26–206°, $r=0.56$, $P<0.001$). The two distributions were not significantly (NS) different ($U^2=0.087$, $P>0.10$; Watson U^2 -test). Triangles at the edges of the two distributions show the home directions for the south-southwest (SSW; circles, filled triangles) and east-southeast (ESE; diamonds, open triangles) groups. Open circles and diamonds represent the magnetic bearings of newts from which natural remanent magnetism (NRM) measurements were later obtained (Brassart et al., 1999).

conditions (Fig. 5A,B, filled symbols). The distribution of NRM declinations (i.e. horizontal alignment of the NRM relative to the front of the head) for the sample of 18 newts was indistinguishable from random (38°, $r=0.24$, $N=18$, $P>0.10$; Fig. 6), suggesting that the permanent magnetic material responsible for the NRM was not aligned in a consistent direction with respect to the newts' heads or bodies. Moreover, there were no differences in the distributions of NRM declinations obtained from newts collected from the ESE and SSW ponds, from newts tested under full-spectrum and long-wavelength light, or from newts that scored at opposite ends of the 'fixed' magnetic axis ($P>0.10$, Watson U^2 -test; Table 2).

To investigate whether the fixed-axis response resulted from the newts positioning the NRM in a consistent alignment relative to the magnetic field, we examined the distribution of NRM20 bearings, obtained by adding each newt's NRM declination to its 20 cm magnetic bearing (see Materials and methods). The distribution of NRM20 bearings for the entire sample was indistinguishable from random ($P>0.10$, Rayleigh test). When data from newts tested under full-spectrum and long-wavelength light were analyzed separately, however, there was significant clustering of the NRM20 bearings under full-spectrum light (Fig. 7A) but not under long-wavelength light (Fig. 7B).

Newts tested under long-wavelength light did not exhibit a consistent distribution of NRM20 bearings. Nevertheless, they

Fig. 6. Distribution of natural remanent magnetism (NRM) declinations (data from Brassart et al., 1999). Horizontal alignment of the NRM relative to the front of the newt's head (NRM declination) for 18 newts used in behavioral studies (see Tables 1,2). Diamonds represent newts from the east-southeast (ESE) group, and circles represent newts from the south-southwest (SSW) group. NS, not significant.

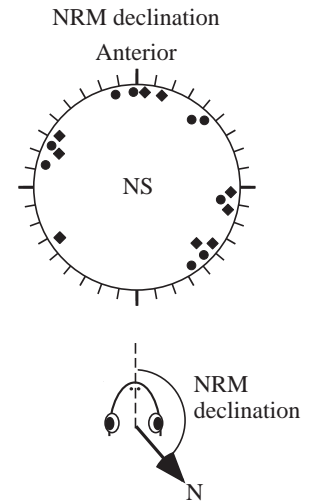


Table 2. Comparison of behavioral responses and natural remanent magnetism (NRM) declinations of individual newts

Test wavelength (nm)	20 cm magnetic bearing (°)	NRM declination* (°)	NRM20 bearing (°)	Time to score (min s ⁻¹)
ESE ponds				
Full	360	305	305	14:41
>500	345	128	113	11:11
>500	13	93	106	10:32
Full	30	290	320	3:58
Full	221	15	236	3:55
>500	184	247	71	12:01
>500	145	134	279	6:45
Full	212	3	215	7:16
Full	132	104	236	1:25
SSW ponds				
>500	252	348	240	6:57
Full	58	137	195	3:05
>500	249	284	173	1:06
>500	208	298	146	2:40
Full	241	47	288	1:02
Full	194	147	341	2:49
>500	2	41	43	10:57
>500	169	97	266	5:01
Full	234	358	232	1:42

*Data from Brassart et al., 1999.

exhibited bimodal (fixed axis) orientation that was as least as strong as, if not stronger than, that of newts tested under full-spectrum light (Fig. 5). We investigated the possibility that the fixed-axis response reflected an alternative method of aligning the map detector that was used when the magnetic compass was inoperable (see below). The distribution of scoring times for newts tested under long-wavelength light formed three discrete clusters, i.e. 1–4 min, 5–8 min and 10–14 min (Fig. 8; and see Table 3). The magnetic bearings of newts scoring in

the shortest time interval were bimodally distributed along an axis of $44\text{--}224^\circ$ ($r=0.78$, $N=11$, $P<0.001$), in the intermediate

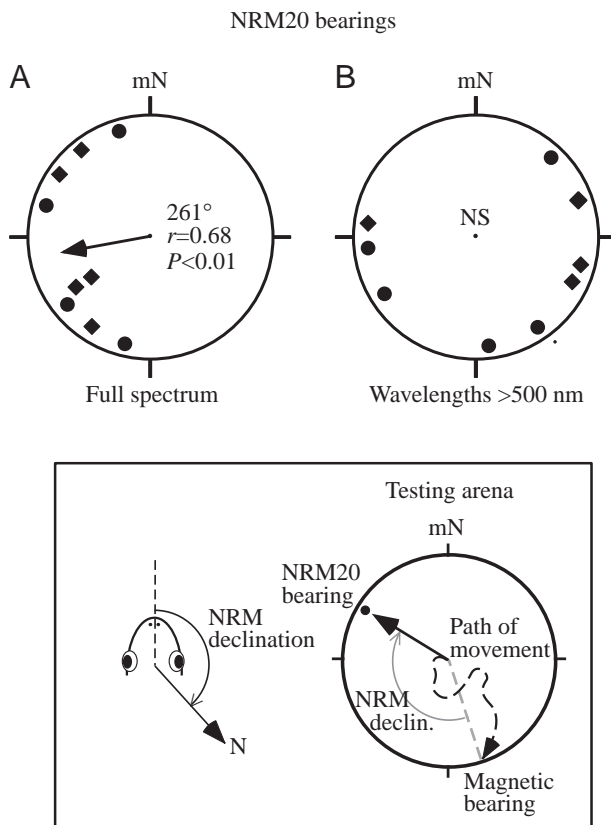


Fig. 7. Distribution of NRM20 bearings. (A) Distribution of NRM20 bearing for newts tested under full-spectrum light. (B) Distribution of NRM20 bearings for newts tested under long-wavelength light. Each NRM20 bearing provides an estimate of the alignment of a newt's natural remanent magnetism (NRM) when it contacted the 20 cm criterion circle. NRM20 bearings were calculated by adding a newt's NRM declination (Fig. 6) to its magnetic bearing at the 20 cm criterion circle (Fig. 5); see text. NS, not significant; mN, magnetic north.

time interval were unimodally distributed with a mean bearing of 183° ($r=0.82$, $N=5$, $P<0.03$) and in the longest time interval were unimodally distributed with a mean bearing of 17° ($r=0.70$, $N=8$, $P<0.02$). After correcting for testing each distribution for both unimodal and bimodal orientation, the distributions of newts scoring in the shortest and longest time intervals were significant ($P<0.025$), while that of newts scoring in the intermediate time interval approached significance. The sample size of newts tested under long-wavelength light from which NRM measurements were obtained ($N=9$) was too small to determine whether newts scoring in the different time intervals were positioning the NRM in different alignments relative to the magnetic field, although the data are suggestive (Table 2). In contrast to newts tested under long-wavelength light, only newts that scored in the shortest time interval under full-spectrum light exhibited significant orientation ($41\text{--}221^\circ$, $r=0.51$, $N=18$, $P<0.01$; Table 3).

Discussion

Newts from the populations used in these experiments are capable of map-based homing (Phillips et al., 1995). At the times of year and under the conditions used in these experiments, newts held and tested under full-spectrum light use the magnetic field to orient in the direction of their home pond (Phillips, 1987; Phillips and Borland, 1994; Phillips et al., 1995, 2002; Fischer et al., 2001). However, in the present experiments, when newts were held under wavelengths of >500 nm in the outdoor tanks under otherwise similar conditions, they oriented along a more-or-less fixed magnetic axis under both full-spectrum and long-wavelength (i.e. >500 nm) light (Fig. 5). Three possible explanations for this 'fixed-axis' magnetic orientation are considered below.

1. Non-shoreward-directed magnetic compass orientation

One explanation for the fixed-axis orientation (Fig. 5) is

Table 3. Responses of newts tested under full-spectrum and long-wavelength light scoring in different time intervals

Test wavelength	Mean vector or axis ($^\circ$)	Mean vector length (r)	Sample size (N)	Rayleigh test	U^2	Watson U^2 -test
1.0–4.5 min						
Full	41–221	0.51	18	$P<0.01$		
>500	44–224	0.78	11	$P<0.001$	0.0769	$P>0.10$
Combined	43–223	0.61	29	$P<0.001$		
4.5–8 min						
Full	193	0.29	4	$P>0.10$		
>500	183	0.82	5	$P<0.05$	0.1148	$P>0.10$
Combined	185	0.58	9	$P<0.05$		
>10 min						
Full	346	0.40	4	$P>0.10$		
>500	17	0.70	8	$P<0.01$	0.1143	$P>0.10$
Combined	10	0.58	12	$P<0.02$		

that the newts were exhibiting a compass (i.e. non-homing) response that was not oriented with respect to the shore direction. Phillips and Borland (1992a) showed that training under full-spectrum light and testing under long-wavelength light, as well as training under long-wavelength light and testing under full-spectrum light, cause a 90° shift in the direction of shoreward magnetic compass orientation (Fig. 1). Moreover, this wavelength-dependent 90° shift results from a direct effect of light on the underlying magnetoreception mechanism (see also Deutschlander et al., 1999a,b). The absence of an effect of long-wavelength light on the fixed-axis response (Fig. 5) suggests that the newt's magnetic compass does not mediate this response.

An effect on homing orientation?

Newts in the present experiments were tested at times of year and exposed to conditions (with the exception of exposure to long-wavelength light) that have been shown to reliably elicit homing orientation (Phillips, 1987; Phillips and Borland, 1994; Phillips et al., 1995, 2002; Fischer et al., 2001). Despite the absence of consistent homeward orientation (Fig. 3), therefore, the newts may have been attempting to home. The difference in the orientation of newts from the ESE and SSW ponds under full-spectrum light (Fig. 5A), but not under long-wavelength light (Fig. 5B), is consistent with an effect on homing and, more specifically, an effect on the map. This difference in orientation is unlikely to result from an effect on the compass, as there is no reason to expect that the two pond groups would exhibit different compass preferences (whether learned or innate) under full-spectrum, but not long-wavelength, light (Phillips and Borland, 1992a; Deutschlander et al., 1999a,b; Phillips et al., 2001). By contrast, the hybrid detector hypothesis predicts that newts should be able to derive map information from the magnetic field under full-spectrum, but not under long-wavelength, light (Phillips and Borland, 1994). If the brief exposure to full-spectrum light in the indoor arena was sufficient for newts to derive at least rudimentary map information, this could explain why the difference in the orientation between the two pond groups was only observed under this lighting condition. Although our earlier work suggested that newts normally obtain the map information necessary for homing in the outdoor tanks prior to testing (Phillips, 1987; Phillips and Borland, 1994), this conclusion was based on the results of experiments in which newts were held in outdoor tanks under full-spectrum light. In the present experiments, exposure to long-wavelength light may have prevented the newts from obtaining map information in the outdoor tanks and, thus, predisposed them to begin gathering map information as soon as more favorable conditions permitted, i.e. when exposed to full-spectrum light in the test arena. In order to obtain accurate map information, however, newts would have to average over extended periods of time

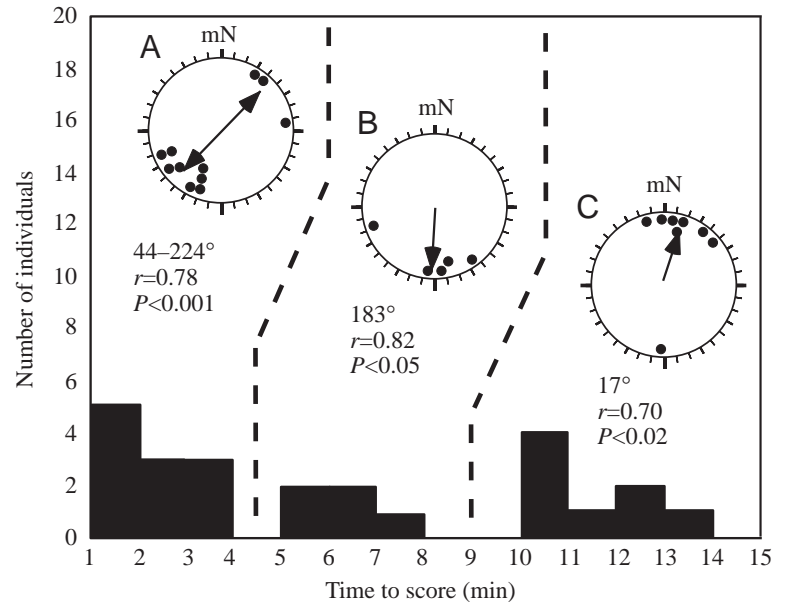


Fig. 8. Possible relationship between orientation and scoring time of newts tested under long-wavelength light. Histogram shows the number of newts scoring in different time intervals. Three clusters of scoring times are evident. Circular diagrams are the distributions of magnetic bearings of newts from each of the three clusters (separated by dashed lines). mN, magnetic north.

(possibly hours, rather than seconds or minutes) and/or take measurements at night when temporal variation in the magnetic field is reduced (Rodda, 1984; Phillips, 1996; Phillips and Deutschlander, 1997). A brief exposure to full-spectrum light during the middle of the day would not be sufficient for an accurate determination of the home direction. Therefore, the tendency for the orientation of the two pond groups to diverge when tested under full-spectrum light without showing accurate homeward orientation (Fig. 5A) is consistent with the earlier suggestions: (1) that exposure to full-spectrum light is necessary for newts to obtain magnetic map information but (2) that they must have access to this information for extended periods of time and/or at specific times of day in order to accurately determine the home direction (Phillips and Borland, 1994; Phillips, 1996). If so, what accounts for the overall similarity in the distribution of bearings under full-spectrum and long-wavelength light (Fig. 5)?

2. Misdirected homing

If newts held under long-wavelength light prior to testing were attempting to home, could the fixed-axis (i.e. NNE–SSW) component of the newts' orientation observed under both lighting conditions also represent homing based on incomplete or inaccurate information. Such misdirected homing is unlikely to result from an effect on the compass, as this would produce either a consistent error in the direction of orientation relative to the true home direction or disorientation, neither of which was observed (Figs 3, 5). It is also unlikely that homing using

incorrect map information[§] can account for the fixed-axis response (Fig. 5), because the map-based homing orientation of newts is wavelength dependent (see earlier discussion); in neither pond group was the orientation observed under full-spectrum light significantly different from that observed under long-wavelength light (Fig. 5). [As discussed previously, however, the difference in the orientation of the two pond groups under full-spectrum light (Fig. 5A), but not under long-wavelength light (Fig. 5B), is consistent with newts having access to rudimentary map information only under this lighting condition.] The available evidence, therefore, does not support the conclusion that the 'fixed' NNE–SSW component of the newts' orientation (Fig. 5A,B) resulted from an incorrect determination of map position.

3. Aligning a 'map detector' relative to the magnetic field

According to the hybrid detector hypothesis, the 90° rotation of the directional response of the magnetic compass under long-wavelength light should cause the map detector to be positioned at right angles to its normal alignment relative to the magnetic field (Fig. 2) and should, therefore, interfere with the newt's ability to obtain map information from the geomagnetic field (Phillips and Borland, 1994). Under long-wavelength light, therefore, the only way that newts could obtain map information would be by adopting an alternate strategy that does not require directional input from the magnetic compass. For example, they could use trial and error, or a more systematic sampling strategy, to determine detector alignment(s) that provide reproducible measurements of the magnetic field.[¶]

The polar sensitivity of the newt's homing response (Phillips, 1986a) suggests that the putative map detector involves permanent material that is at least partially fixed (i.e. unable to rotate freely) with respect to the surrounding tissue (Phillips and Deutschlander, 1997). As a consequence, positioning the map detector relative to the magnetic field should produce a corresponding alignment of the head and/or body when newts are obtaining map measurements. A

consistent alignment of the magnetic material in the map detector across individuals could, therefore, cause newts to exhibit a non-random distribution of head/body alignments relative to the magnetic field and, thus, a non-random distribution of magnetic headings. Analysis of NRM declinations, however, yielded a distribution that was indistinguishable from random (Fig. 6), indicating that the alignment of the magnetic material was not consistent across individuals. Despite the absence of a consistent alignment of magnetic material in different individuals, however, there was a non-random distribution of NRM20 bearings under full-spectrum (Fig. 7A), but not long-wavelength (Fig. 7B), light. This finding suggests that under full-spectrum light each newt was selecting a magnetic heading that would align an ordered array of magnetic material (i.e. the putative map detector) in a consistent direction relative to the magnetic field. The absence of significant clustering of NRM20 bearings under long-wavelength light (Fig. 7B) indicates that alignment of the putative map detector may require a normally functioning magnetic compass.

We should emphasize that the clustering of NRM20 bearings under full-spectrum light was not anticipated. In an earlier paper (Phillips and Borland, 1994), we predicted that newts housed in the outdoor tanks under long-wavelength light would be deprived of map information and, therefore, should fail to orient in the correct home direction (Fig. 3). However, we failed to consider the possibility that, when exposed to full-spectrum light in the test arena, the newts might immediately use the (now properly functioning) magnetic compass to align the map detector (Fig. 7A). Nevertheless, this finding provides additional support for the hybrid detector hypothesis. Moreover, the difference in the orientation of newts from the SSW and ESE ponds under full-spectrum light (Fig. 5A), but not long-wavelength light (Fig. 5B), suggests that aligning the putative map detector under full-spectrum light enabled the newts to derive at least rudimentary map information. The newts' behavior under full-spectrum light, therefore, may have included elements of at least two different behaviors: (1) aligning the map detector to obtain map information and (2) using map information obtained in this way in an attempt to orient in the home direction. It is likely, therefore, that both the distribution of magnetic bearings (Fig. 5A) and the distribution of NRM20 bearings (Fig. 7A) underestimate the accuracy of the putative homing and aligning responses, respectively.

Although these findings lend support to the hybrid detector hypothesis, they do not explain the newt's fixed-axis response. This is because the fixed-axis orientation of newts tested under long-wavelength light (Fig. 5B) was at least as strong, if not stronger, than that of newts tested under full-spectrum light (Fig. 5A), despite the absence of significant clustering in the distribution of NRM20 bearings (Fig. 7B). If newts tested under long-wavelength light were not using the magnetic compass to position the magnetic material in a putative map detector in a consistent alignment relative to the magnetic field, were they doing something else? One possibility suggested by differences in the orientation of newts scoring in different time

[§]One possibility, consistent with the results of earlier studies of newts from the SSW ponds (Fischer et al., 2001; Phillips et al., 2002), is that newts held under long-wavelength light were prevented from using one coordinate of a bicoordinate map to determine approximate north–south geographic position (e.g. magnetic inclination) but were still able to use a second (as yet unidentified) map coordinate to determine approximate east–west position. In other words, newts held and tested under long-wavelength light may have been forced to rely on a uniconordinate, rather than a bicoordinate, map. By contrast, newts tested under full-spectrum light would have had access to at least rudimentary bicoordinate map information in the testing arena, which could account for the difference in orientation of the two pond groups under this lighting condition.

[¶]For example, the torque experienced by horizontally aligned single-domain particles of magnetite would be greatest when their magnetic moments were aligned perpendicular to the magnetic field, i.e. 90° clockwise and 90° counterclockwise of magnetic north. In theory, therefore, these alignments of the magnetite particles could be determined without reference to the magnetic compass by sampling different particle alignments. During the normal ontogeny of the newt's magnetic navigation system, a trial and error strategy might be used to determine alignment(s) of the map detector that yields reproducible magnetic field measurements and, thus, could be part of the newt's normal behavioral repertoire.

intervals (Fig. 8) is that newts tested under long-wavelength light were systematically sampling different alignments of the putative map detector relative to the magnetic field (Fig. 8)^{||}. Similar changes in orientation were not evident under full-spectrum light, although the bimodal orientation of newts scoring in the shortest time interval was similar to that observed under long-wavelength light (Table 3).

Clearly, many questions remain to be answered. In particular, future experiments with newts housed under long-wavelength light are needed to determine: (1) whether individual newts tested under long-wavelength light exhibit reproducible changes in orientation over time, as would be expected if they are systematically sampling different compass headings relative to the magnetic field (Fig. 8), (2) whether these changes in orientation result in different alignments of the NRM relative to the magnetic field (NRM20 bearings) and (3) whether newts tested under full-spectrum light increase the accuracy of homing orientation if they are allowed to sample over longer time periods and/or at different times of day.

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^{||}The differences in orientation of newts that scored in the three time intervals (Fig. 8) are consistent with individual newts reaching the 20cm criterion circle by chance during different phases of a systematic sampling sequence. However, these findings do not rule out the alternative possibility that there were three distinct subpopulations of newts that differed in both scoring time and orientation behavior.