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Mechanisms of Magnetic Orientation in Birds¹

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SYNOPSIS. Behavior and electrophysiological studies have demonstrated a sensitivity to characteristics of the Geomagnetic field that can be used for navigation, both for direction finding (compass) and position finding (map). The avian magnetic compass receptor appears to be a light-dependent, wavelength-sensitive system that functions as a polarity compass (*i.e.*, it distinguishes poleward from equatorward rather than north from south) and is relatively insensitive to changes in magnetic field intensity. The receptor is within the retina and is based on one or more photopigments, perhaps cryptochromes. A second receptor system appears to be based on magnetite and might serve to transduce location information independent of the compass system. This receptor is associated with the ophthalmic branch of the trigeminal nerve and is sensitive to very small (<50 nanotesla) changes in the intensity of the magnetic field. In neither case has a neuron that responded to changes in the magnetic field been traced to a structure that can be identified to be a receptor. Almost nothing is known about how magnetic information is processed within the brain or how it is combined with other sensory information and used for navigation. These remain areas of future research.

INTRODUCTION

Precise navigational abilities have been illustrated for birds and other animals many times. The precise navigation of birds has been studied most extensively in migratory songbirds and the homing pigeon (*Columba livia*). Students of bird migration have fastened metal bands or rings to birds' legs for decades to deduce where locally breeding birds travel during their migrations. As a consequence of such activities, researchers discovered that many birds faithfully returned to the same breeding locations year after year. Subsequent studies produced information showing that migrants also use the same enroute stopover locations and non-breeding locations on successive trips. This ability is remarkable because their migratory trips are hundreds to thousands of kilometers each way; yet, somehow they know where they are going and the path they must follow to get there.

Domestication of the homing pigeon has provided researchers with a powerful tool to investigate avian navigation. Because their rearing conditions can be more or less controlled, the importance of learning various sources of sensory information can be investigated. A distinct benefit of using pigeons to study navigation is that the goals of individuals are known as well as their starting locations. With the implementation of technology, such as radiotelemetry (Michener and Walcott, 1967; Walcott, 1978) and GPS tracking (von Huenerbein *et al.*, 2000, 2001), the exact paths of individual birds can be monitored and the effects of experimental manipulations determined.

Birds use multiple sources of directional informa-

tion for their navigation. Experimenters have established the use of a time-compensated sun-compass by homing pigeons (Schmidt-Koenig, 1958) and diurnally migrating songbirds (Kramer, 1951). Manipulation of the bird's internal clock or the apparent location of the sun (using mirrors) produces a shift in heading by the bird that is predicted based on the manipulation. Nocturnally migrating birds do not have access to the sun during their migration but have been shown to use the patterns of the stars for orientation (Sauer, 1957; Emlen, 1967). Other factors, including the glow in the western sky after sunset caused by the setting sun and the N-S band of polarized light through the zenith can be used shortly after sunset in conjunction with the stellar patterns (Moore, 1986; Moore and Phillips, 1988). Use of these physical cues requires that at least part of the sky be visible to the birds.

There are many experiments in which the sky was not visible to the birds but they were able to select and maintain an appropriate direction for their flight; for example, within or between cloud layers (Griffin, 1973). Obviously, such ability requires access to non-visual sources of physical information, which could be used by themselves or in conjunction with visual cues. The Earth's magnetic field is available everywhere on the planet. It penetrates almost everything: air, water, ground, and the bodies of animals; and it is available day and night. These characteristics make the Geomagnetic field appealing as a source of directional information and has been used as such by humans for centuries.

Many behavioral studies have established that birds are sensitive to the Earth's magnetic field and its variations (reviewed by Wiltschko and Wiltschko, 1995). Not only can pigeons and other avian species use the geomagnetic field as a compass, but they also are sensitive to slight variations of the magnetic field that occur through time and space. These variations are potentially useful for navigation to determine location or as a synchronizing agent for biological clocks.

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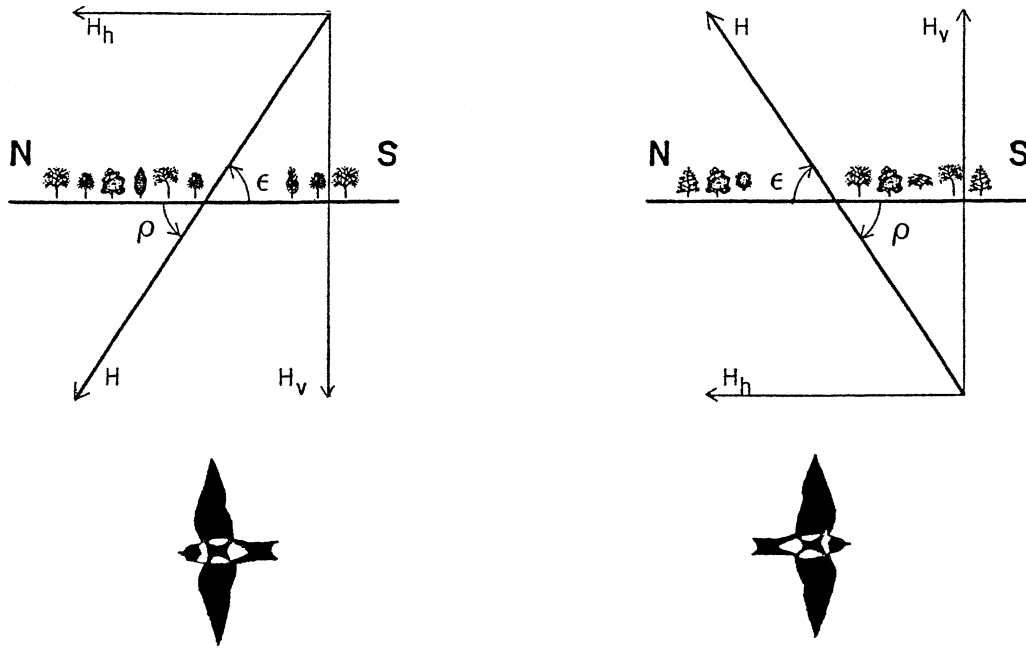


FIG. 1. Responses of birds to the inclination compass. The behavioral responses indicate that they respond to the magnetic field as equatorward versus poleward. The direction the total magnetic field dips below the horizontal is poleward; north and south are not distinguished. The left figure would correspond to the northern hemisphere and the right figure to the southern hemisphere magnetic field. H_h = horizontal component of the magnetic field vector, H_v = vertical component of the magnetic field vector, ϵ = angle of the magnetic field above the horizon, ρ = angle of the magnetic field below the horizon. (Modified from Wiltschko and Wiltschko, 1972.)

MAGNETIC COMPASS

Magnetic compass reception in birds appears to be a light dependent process based on antagonistically interacting spectral mechanisms with at least one short-wavelength and one long-wavelength mechanism (Deutschlander *et al.*, 1999b) or multiple states of a short-wavelength sensitive mechanism (Ritz *et al.*, 2000, 2004). The avian magnetic compass differs from the technical compass used by humans in that the avian compass is an inclination compass (Wiltschko and Wiltschko, 1972). Rather than distinguishing North and South, the compass distinguishes the direction of the pole from the direction of the equator; the North Pole and the South Pole are not distinguishable (Fig. 1). Thus, for a migratory songbird, fall migration is typically equatorward and spring migration is typically poleward. The system works equally well for the northern and southern hemispheres. Birds that transit the equator must somehow switch from an equatorward strategy to a poleward strategy. Experience with the horizontal magnetic field appears to trigger this response (Beason, 1992; Wiltschko and Wiltschko, 1992).

Evidence for the use of a compass that responds to changes in the ambient magnetic field comes from experiments with homing pigeons, migratory songbirds, and from radar studies of migrating birds (reviewed by Wiltschko and Wiltschko, 1995). Although the biophysical mechanism of the receptor for the magnetic compass has not been identified conclusively in any species, the most convincing evidence indicates that

the magnetic compass receptor involves photopigments.

Electrophysiological recordings from the optic tectum of the pigeon (Semm and Demaine, 1986) and the Bobolink (*Dolichonyx oryzivorus*; Beason and Semm, 1987) revealed the presence of neurons that respond to changes in the direction of the ambient magnetic field, but only in the presence of light. These data could be interpreted to mean either that there is a light-dependent magnetic receptor associated with the visual system or that there is magnetic input to the visual system that is mediated by stimulation of the retinal photoreceptors. Because most of the input to the optic tectum is from the retinal ganglion cells, it is unlikely that the magnetic responses are only gated by input from the visual system; a more parsimonious explanation is that the responses are from magnetic receptors. The responses of the visual system to magnetic stimulation resemble its responses to light. Some units responded only to specific orientations of the magnetic field. Unfortunately, there was no analysis of wavelength sensitivity in these experiments, only the presence or absence of light. The responses were extinguished in total darkness.

The avian magnetic compass must integrate information from the magnetic receptors and the vestibular system in order to determine the direction in which the magnetic field dips below the horizon. The Nucleus of the Basal Optic Root (nBOR) of the pigeon appears to be involved in this process (Semm *et al.*, 1984; Semm and Demaine, 1986); it receives input from the

vestibular system and the visual system. Its responses to changes in the magnetic field depend on both the orientation of the magnetic field and the orientation of the bird's head to the horizon. Single neurons responded to changes in orientation of the magnetic field but did not respond to changes in the intensity of the magnetic field. The neurons that responded to the magnetic field also responded to directional movements of light, especially those cells that responded to axial movements of light. Cells that did not respond to the movement of light did not respond to changes in the magnetic field. The coupling of these specific responses might be an indication of how the magnetic sensitivity of the avian visual system is mediated.

Leask (1977) proposed an optical pumping resonance model to account for light sensitivity of the avian magnetic receptor system, based on the triplet state of a visual pigment such as rhodopsin. Schulten (1982), Phillips (Phillips and Borland, 1994), and Ritz (Ritz *et al.*, 2000, 2002) subsequently modified Leask's (1977) original model so that it involves two pigments or one pigment in two states. These models postulate a wavelength (color) sensitivity in which orientation would be accurate when the animal is illuminated by one category of light and disoriented or reoriented with other categories.

Behavioral experiments also support the concept of a light-dependent, wavelength-sensitive magnetic compass system in birds. Homing pigeons transported in total darkness were more poorly oriented at the release site than pigeons transported with illumination inside their boxes (Wiltschko and Wiltschko, 1981). Neither group of pigeons could not see outside the boxes and, thus, did not have access to visual cues that might be provided by the landscape or sky. Bobolinks tested in orientation funnels in a dark planetarium were inactive. Playback of nocturnal call notes did not stimulate them to show migratory hopping (R.C.B., unpublished data). Likewise, pigeons released with their eyes covered by opaque lens flapped to the ground (C. Walcott, personal communication). One explanation is that the birds lacked a functional frame of reference and chose not to attempt to migrate or fly home.

There appears to be some species-specific responses of migratory orientation by songbirds under narrow-band illumination. All species tested under short wavelengths of light (blue to humans: 425–450 nm) at low-intensity showed normal orientation. Species differences appeared under intermediate wavelengths (green-yellow: 500–575 nm). European Robins (*Erithacus rubecula*; Wiltschko and Wiltschko, 1999, 2001, 2002; Wiltschko *et al.*, 2001) and Australian Silvereyes (*Zosterops lateralis*; Wiltschko *et al.*, 1993; Munro *et al.*, 1997) showed normal orientation but Bobolinks were disoriented (Beason and Swali, 2001; Beason, unpublished data). At longer wavelengths there were also species-specific responses. Under yellow-orange light (550–585 nm) Bobolinks showed significant rotation in their headings and became axially bimodal in their responses. European Robins were dis-

oriented under orange (590 nm) and red (635 nm) light. Bobolinks were also disoriented under red (600 nm) illumination. Homing pigeons illuminated with colored lights showed responses similar to the European Robin. They were normally oriented at the release site when transported with white or green light and disoriented when transported under red illumination (Wiltschko and Wiltschko, 1998). If robins were pre-exposed to low intensity red light, they were not disoriented but were able to orient normally under red illumination (Wiltschko *et al.*, 2004a). These results indicate that some type of adaptation is taking place within the magnetic receptors. These observations do not fit any of the current models, which all predict disorientation under long wavelength illumination, and merit further research. Juvenile robins showed appropriate orientation under 560.6 nm illumination but not with 567.5 nm; they were significantly oriented under 617 nm light but not in the migratory direction (Mueheim *et al.*, 2002). Under brighter light intensities robins sometimes exhibited bimodal fixed orientation unrelated to the migratory direction (Wiltschko and Wiltschko, 2001, 2002).

When the yellow (590 nm) was simultaneously presented with blue (424 nm) or green (565 nm), robins were oriented but not necessarily in a migratory direction. Regardless of season, the combination of yellow and blue resulted in birds orienting in a southerly direction while the combination of yellow and green produced northerly orientation (Wiltachko *et al.*, 2004b). In all cases adding yellow light resulted in a fixed direction response, as did brighter light intensities. Although illuminating a bird with monochromatic or dichromatic light is artificial, behavioral responses to these situations provide some insight into how the receptor system operates. What is unknown is whether there is a single wavelength sensitive receptor or an interaction of multiple receptors.

In the European Robin (*Erithacus rubecula*), the Silvereye (*Zosterops lateralis*), and, perhaps the pigeon, the ability to utilize the Geomagnetic field for migratory orientation is strongly lateralized, with a marked dominance of the right eye for magnetoreception (Wiltschko *et al.*, 2002, 2004a).

From these physiological and behavioral responses of birds, we can conclude that photopigments are involved with the avian magnetic compass system. The wavelength specific effects indicate the effect is on the receptor rather than a generalized motivational response. The differences among species to similar wavelengths of light might be due to differences in the visual pigments used to transduce the magnetic field. The location and structure of the wavelength-sensitive magnetoreceptor remains unresolved. It could involve retinal photoreceptors, extraretinal photoreceptors in the pineal or elsewhere (Semm *et al.*, 1980), photopigments such as cryptochromes (Cashmore *et al.*, 1999) within the retina (Möller *et al.*, 2004; Mouritsen *et al.*, 2004) or brain (Wilson, 1991), or it might be mediated through a non-visual pathway. Mechanisms

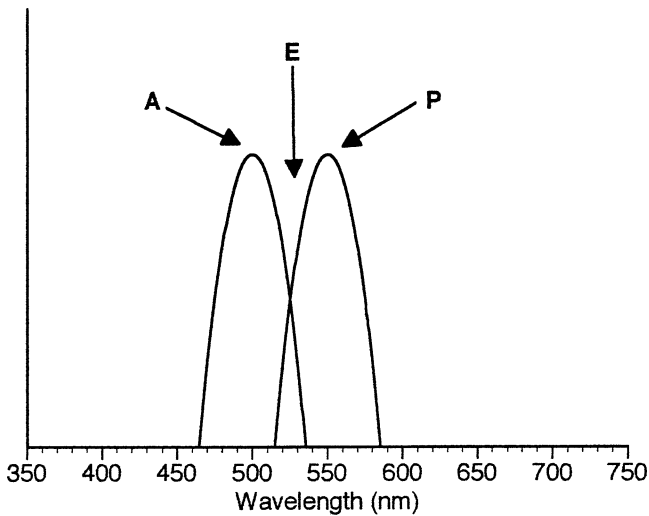


FIG. 2. Effects of the wavelength (color) of light on a magnetic receptor based on two visual pigments. When the antennal pigment (A) is illuminated at its optimum wavelength, the orientation is in the preferred direction. When the primary pigment (P) is illuminated, the result is a 90° change in orientation. When the two pigments are illuminated equally (E), the result is disorientation. (Based on Deutschlander *et al.*, 1999b.)

have been put forth for each of these ideas. Phillips and coworkers (see Deutschlander *et al.*, 1999b for review) proposed that detection of the magnetic field is through energy transfer between two dissimilar visual pigments. For this system to work most effectively the pigments must be contained within the same cell. The wavelength-sensitive magnetic receptor in the eastern red-spotted newt (*Notophthalmus viridescens*) is located in the pineal organ, which contains functioning photoreceptors (Deutschlander *et al.*, 1999a). Pineal photoreceptors of the newt contain two visual pigments or one pigment in two states, each sensitive to different wavelengths of light (Fig. 2). The avian pineal does not appear to be the site of the avian magnetic compass because pinealectomized pigeons orient as well as unmanipulated birds (Maffei *et al.*, 1983) and pinealectomized Pied Flycatchers (*Ficedula hypoleuca*) orient when supplied with melatonin (Schneider *et al.*, 1994). In the newt the orientation of the external magnetic field is hypothesized to affect the efficiency of energy transfer and this efficiency is used by the receptor to determine the direction of the magnetic field. The means by which the receptor determines the efficiency of the energy transfer is unclear. Ritz (Ritz *et al.*, 2000, 2004) and Schulten (1982) have developed theoretical radical-pair models in which the balance between two states of a photopigment, such as a cryptochrome, is influenced by the external magnetic field (Fig. 3). Because of the sensitivity of these pigments to short wavelengths, sensitivity to magnetic fields is predicted to disappear at long wavelengths. The responses of Garden Warblers to RF treatment is consistent with the use of a radical pair reaction as the source of magnetic compass information in this species (Ritz *et al.*, 2004).

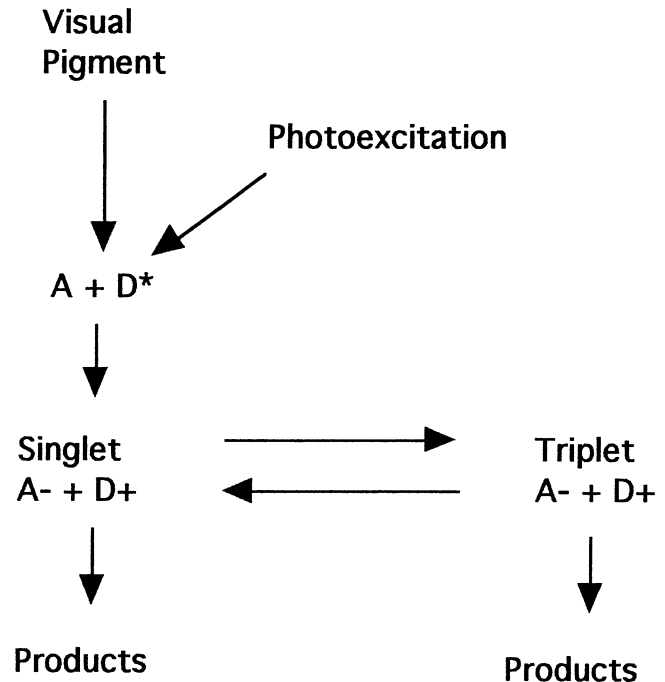


FIG. 3. Effect of the magnetic field on a radical pair reaction in which the equilibrium between the triplet state and the singlet state is affected by the orientation of the ambient magnetic field. (Based on Ritz *et al.*, 2000.)

The avian double cone has also been proposed as the light-dependent, wavelength-sensitive receptor (Beason and Swali, 2001). It is composed of two photoreceptors, each with a different pigment and oil droplet or filter (Fig. 4). Consequently, each receptor has a different spectral sensitivity, similar to the model proposed by Phillips. However, because each pigment is in a different cell, it would be difficult to transfer energy between pigments. Exactly how the double cone could function as a magnetic receptor is unclear but the wavelength sensitivities of the Bobolink correspond to the sensitivities of the two receptors.

MAGNETIC MAP

The second component of navigation is a system by which the animal can determine the geographical direction of its goal from its current location. If such a “map” mechanism was based on variations in the geomagnetic field, its receptors would have to be sensitive to very minute changes in intensity and/or angle of the Earth’s magnetic field (total intensity ~ 50 mT). The intensity of the natural ambient magnetic field changes about 6–12 nT/km along a north-south axis. Overlying this general gradient are several sources of noise or interference. One source of magnetic noise is the generally uniform variation of about 50–100 nT that results from the daily fluctuations in intensity of the magnetic field caused by the day/night cycle of the sun. A second source of magnetic noise is spatial variations in the magnetic field caused by irregularities in the composition of the Earth’s crust. These variations

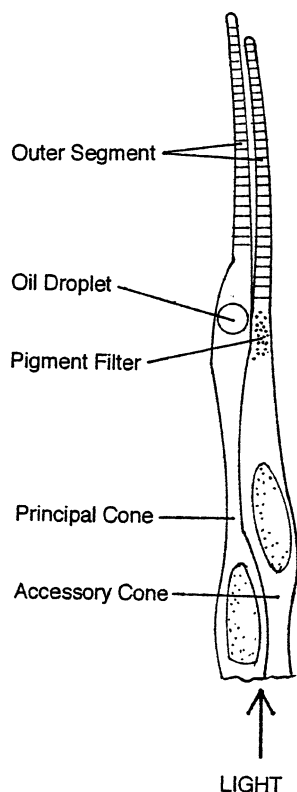


FIG. 4. Structure of the avian double cone. Each member contains a different visual pigment and optical filter or oil droplet.

might interfere with a bird's ability to determine the small intensity changes that occur as it moves from location to location.

Behavioral responses of homing pigeons indicate they can distinguish among magnetic fields that differ in intensity by about 10–30 nT (Keeton *et al.*, 1974; Larkin and Keeton, 1978; Wiltschko *et al.*, 1986; Kowalski *et al.*, 1988; Becker *et al.*, 1991). Pigeons whose eyes are covered with frosted lenses are able to return to within 2 km of their home loft, apparently using only nonvisual cues (Schmidt-Koenig and Walcott, 1978). Pigeons released within a magnetic anomaly appear to be trapped and escape from the anomaly only by chance, after which they fly home (Walcott, 1978). Pigeons released repeated from the same location morning and afternoon show differences in azimuth between the two releases that are correlated with the differences in magnetic field intensity (Becker *et al.*, 1991).

The sensitivities to magnetic field variations are similar to those predicted for a magnetite-based receptor (Yorke, 1979, 1981; Kirschvink, 1983). Because it has a permanent magnetic moment, single-domain magnetite is attractive theoretically for use in magnetoreception (Kirschvink and Gould, 1981). Single domain magnetite has the strongest magnetic moment of any naturally occurring compound and is strong enough to overcome thermal agitation despite the small particle sizes (<1 μm ; Banerjee and Moskowitz,

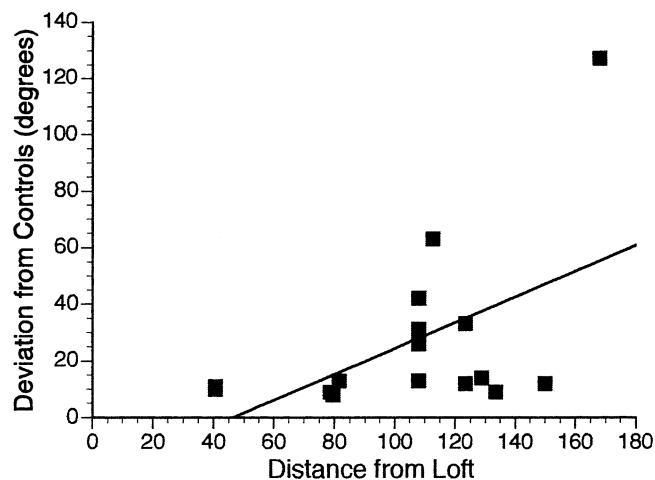


FIG. 5. Deviation of homing pigeons treated with a magnetic pulse from the control birds when released at different distances from their home loft. The response is not fixed but depends on the distance of the home loft from the release site. (Based on data from Beason *et al.*, 1997.)

1985). The sensitivity of such a receptor could be enhanced by arranging the particles into a closely spaced chain. Because it has a permanent magnetic moment, the use of SD magnetite can be tested with remagnetization.

Applying a strong magnetic pulse (0.5 T, 5–10 ms) to pigeons and migratory birds usually results in a change in their orientation, in some cases a 90° clockwise or counterclockwise rotation from the original direction (Wiltschko *et al.*, 1994; Beason *et al.*, 1995, 1997; Wiltschko and Wiltschko, 1995). Because the response of birds to different treatments was to select different directions, this treatment might be interpreted as affecting the magnetic compass receptor. However, the response of homing pigeons to some treatments was dependent on how far they were released from the home loft (Beason *et al.*, 1997). Birds released close to the loft were oriented the same as the control birds. The differences between headings of control and magnetized pigeons increased as the distance between the release site and the home loft increased (Fig. 5). Pigeons released about 200 km away were oriented almost directly away from home and few birds returned home (Beason *et al.*, 1997). A compass receptor's response to the treatment should be similar at all locations and should not be influenced by the distance of the release site from home. Such site independent effects is the response that is seen to manipulations of the sun-compass (Schmidt-Koenig, 1965, 1979; Keeton, 1974).

A second set of experiments also indicates that the magnetization treatments do not affect a receptor for the magnetic compass. Young Tasmanian Silvereyes (*Zosterops lateralis*) show no effect of magnetization treatment during their first migratory journey (Munro *et al.*, 1997) whereas adults do (Wiltschko *et al.*, 1994). Adults are goal oriented in their migration, typically returning to the same locations repeatedly for

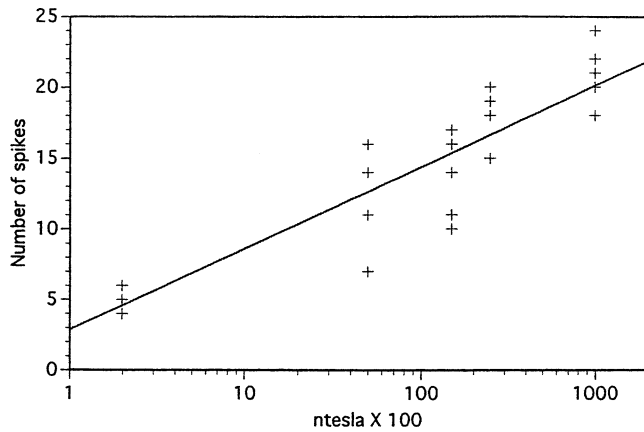


FIG. 6. Logarithmic sensitivity of a fast adapting magnetic receptor cell associated with the trigeminal nerve in the Bobolink to changes in the ambient magnetic field. (Based on Semm and Beason, 1990.)

the nonbreeding season. This ability requires them to use a navigational system analogous to a map. Young birds do not know the nonbreeding grounds because they have not been there. Instead, they use an endogenous program of direction and distance when they leave their breeding grounds. Hence, they do not possess a map, but do possess and use a compass. Although treatment with a magnetic pulse results in directional changes in orientation in adult birds, these changes do not appear to be associated with the magnetic compass. By elimination, the effects must be on a magnetic “map” or some similar location system.

Third, when the ophthalmic nerve of Bobolinks was blocked with lidocaine, the effect of the magnetization treatment was reversed. The birds were not disoriented but selected the same headings they used before being magnetized (Beason and Semm, 1996). Consequently, the birds had a functional magnetic compass receptor that was not associated with the ophthalmic nerve and was not affected by the magnetization treatment.

The nerve block experiments were conducted on the ophthalmic branch of the trigeminal nerve of the Bobolink because electrophysiological recordings indicated the presence of single units that responded to changes in the intensity of the magnetic field around the bird. The responses can be divided into fast adapting units and slowly or nonadapting units. Fast adapting units responded with a burst of action potentials when the intensity of the ambient magnetic field was changed. In the Bobolink these cells show a minimum sensitivity of 30–50 nT and a logarithmic response to intensities up to 50 mT (Fig. 6). These cells also responded to AC stimuli and to a handheld magnet moved towards the bird. Slowly adapting units responded as amplitude detectors. The change in neural activity persisted for several minutes or the duration of the stimulus. The minimum sensitivity of these cells was not tested. Most of the units tested responded to the change in magnetic field intensity with an increase in the rate of firing. Some responded with depressed

activity (Beason and Semm, 1987; Semm and Beason, 1990).

Thus, the sensory capability of the magnetoreceptors associated with the trigeminal nerve can account for the behavioral sensitivity to small changes in the magnetic fields observed in birds and what would be required to use the Earth’s magnetic field for a map or some type of geographic location system. The types of responses indicate the nervous system has the capability to measure small changes in the magnetic field (fast adapting units) and to measure the absolute intensity of the magnetic field (slowly adapting units). These capabilities would allow the bird to determine the intensity of the magnetic field at its location in order to compare the intensity with a remembered value from home. This information would tell the bird which direction along the magnetic gradient to fly towards home. The sensitivity would allow the bird to determine the changes in magnetic intensity as it flew.

Blocking or cutting the ophthalmic nerve of pigeons prevented them from detecting large magnetic anomalies during discrimination experiments (Mora *et al.*, 2004). In these experiments the artificial magnetic fields were several times the strength of the natural Geomagnetic field. To date there is no published documentation of units in the pigeon trigeminal nervous system that respond to changes in magnetic stimuli. However, candidate magnetic sensitive structures have been reported from the ethmoidal region, which receives enervation by the ophthalmic nerve (Fleissner *et al.*, 2003; Walcott and Walcott, 1982; Williams and Wild, 2001).

Single domain magnetite has been reported for the pigeon (Walcott *et al.*, 1979) and the Bobolink (Beason and Brennan, 1986) and superparamagnetic magnetite (SPM) has reported for the pigeon (Fleissner *et al.*, 2003; Hanzlik *et al.*, 2000). The use of single domain magnetite is consistent with the results of the pulse magnetization experiments. Because it possesses a permanent magnetic moment magnetization could reverse the alignment of the particle’s magnetic moment. A particle attached to a membrane or cilia would move in response to changes in the external magnetic field. Such movement would be conducted to the cell membrane, opening or closing ion channels (Kirschvink and Gould, 1981; Semm and Beason, 1990). Remagnetization would produce different responses from the receptor than before treatment. Superparamagnetic particles, on the other hand, would use a different mechanism because the magnetic moments are not permanent, they orient with the external field. One theoretical mechanism has been proposed based on several SPM particles contained within a capsule-like structure (Shcherbakov and Winklhofer, 1999). The size of the capsules would change as the orientation of the surrounding magnetic field changes. The proposed structures closely resemble those reported in association with nervous fibers in the pigeon (Fleissner *et al.*, 2003).

The theoretical sensitivity of a receptor based on

TABLE 1. *The types and sources of physical information birds might use for migratory navigation. Each is identified by whether it would serve a map or a compass function.*

| | Compass | Map |
|------------------------|------------------|----------------|
| Visual | Landmarks | Landmarks |
| | Sun Compass | |
| | Magnetic Compass | |
| Nonvisual Photopigment | Magnetic Compass | |
| Magnetite | | Magnetic Map |
| Olfaction | Specific Odors | Odor Gradients |
| Auditory | Infrasound | |
| | Auditory Sound | Auditory Sound |
| Tactile | Feather Movement | |

single domain magnetite is sufficient to account for both the behavioral and physiological sensitivities observed in pigeons and migratory birds (Yorke, 1979, 1981; Kirschvink and Gould, 1981). The sensitivity of a SPM magnetite-based receptor appears to be adequate to measure the intensity for a compass mechanism (Shcherbakov and Winklhofer, 1999; Hanzlich *et al.*, 2000) but not for a magnetic map receptor.

FUTURE WORK

Based on behavioral and physiological data, birds have the capacity to detect features of the Earth's magnetic field that would allow them to use it for both a compass and a map or a similar geographical positioning system. However, birds are not limited to magnetic cues for navigation. They use a variety of visual and nonvisual sources of directional information. Different species appear to weight sources differently, some use the magnetic field as a primary reference to calibrate visual cues, other species calibrate the magnetic field based on celestial rotation (Able, 1993). Further work is needed on the interaction and hierarchical relationships among the different cues used for navigation.

The cognitive mechanisms birds use to determine location and directional information from geophysical sources is unknown. Only preliminary work has been conducted on the neural integration of sensory information used for navigation. We do not know where and how the various sources of compass and map information come together in the brain. A bird must compare among the various compass mechanisms and establish the most probable direction for north; similarly, the sources of location information must be compared and the direction for flight determined (Table 1, Fig. 7).

The mechanisms by which the magnetic field is transduced to the nervous system remain incompletely determined. Magnetite seems to be involved with the more sensitive system associated with the bird determining its geographical location relative to its goal. There is evidence for the presence of single domain magnetite and superparamagnetic magnetite in birds. These two forms are not mutually exclusive but the mechanisms that have been proposed to convey infor-

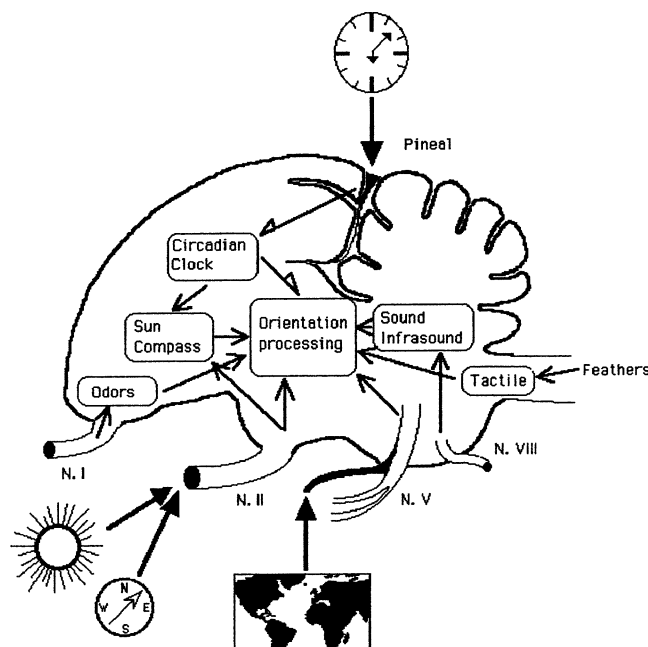


FIG. 7. Sources of sensory information used for navigation and potential neural interconnections.

mation about the magnetic field to the nervous system are radically different. In neither case has a definitive magnetic receptor structure been identified, although candidate structures have been.

Several mechanisms have been proposed to account for the characteristics of the wavelength-sensitive magnetoreceptor. To date no tests have been developed to definitively discriminate among the models. At this time such tests will be difficult to construct because the general models make similar predictions regarding wavelength sensitivities. Until the photopigments that are used for the process and the cells containing those pigments are known, developing test paradigms will be difficult. Species might differ in the photopigments they possess resulting in different critical wavelengths for different species. More importantly, none of the proposed models provide a mechanism by which the change in the magnetic field affects the membrane potential of the receptor neuron. Physiological recordings from the central nervous system indicate that the response is almost immediate with a very short latency. Hence, the effect is most likely on a receptor itself rather than involving a second messenger system.

CONCLUSION

We know homing pigeons and migratory birds possess magnetic compasses and probably some type of geographical location or map system at least partly based on the magnetic field. The characteristics of the map receptor are consistent with the predictions of a magnetite-based mechanism and the magnetic compass receptor fits the predictions of a photopigment-based mechanism. However, in no case do we have a structure that we can point to and say "This is an avian

magnetic receptor.” Herein lies the challenge for future research. Behavioral, anatomical, and physiological work gives us an idea of what we might be looking for but we have not conclusively identified it yet. Electrophysiological and microanatomy techniques will be needed to answer the challenge.

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