Sensory basis of bird orientation

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Summary. Sensory information which may be essential for the complex process of orientation of birds is described in this article. The use of vibrational, visual, chemical, olfactory, magnetic cues and their receptive mechanisms, as far as they are known, are explained. Special reference is given to the behavioral and physiological aspects of magnetic sensitivity.

Key words. Vibrational cues; visual cues; photodetectors; chemical cues; olfactory receptors; magnetic cues; magnetic receptors; vibration detectors.

Introduction

A wide variety of sensory information is available to birds for use as navigational aids. Some of this information can be used directly such as vibrational information (sounds and infrasound), visual information (star patterns, landmarks), magnetic information, and chemical information (odors). Other types of sensory information require compensation for time or movement. The most common and best studied example is the sun compass which results from internal compensation of visual cues (i.e., the movement of the sun).

Visual cues

Homing and migratory birds use landmarks for navigation when they are within a known area. The other commonly used visual cues include the sun compass and stellar cues, all of which involve the use of visual images on the retina. In addition to being sensitive to wavelengths that are visible to humans, birds can also detect ultraviolet light. Hummingbirds, pigeons, and some other species have demonstrated behavioral and physiological responses to UV stimulation[22, 45, 63]. There are also behavioral data which indicate that birds can detect the plane of polarization of polarized light[1, 2, 17, 57]. The mechanism of UV detection is unknown, but may involve special photoreceptors that have transparent oil drops[24]. How birds perceive the plane of light polarization is also unknown, but is thought to involve special double cones. Polarized light detection probably occurs in the UV wavelengths, because the greatest amount of polarization occurs at those frequencies.

Photodetectors

The eyes of birds are both relatively and absolutely large. In most species, the eyes are so large that they are separated only by a thin bony septum in the middle of the skull. The eyes of most avian species seem to function optimally within a narrow range of luminance. As light levels decrease, diurnal species usually roost[53, 81], except during the migratory season when many species of small birds migrate at night. They can probably see well enough to fly high in the air, but not well enough to maneuver through trees and obstacles.

Although extraretinal photoreceptors occur in the brain and the pineal organ, retinal photoreceptors are the primary source of light information to birds. The retina is divided into two major layers, an outer pigmented layer and an inner nervous layer containing the visual cells which are the outer, neuroepithelial layer next to the pigmented epithelium[54].

At least five distinct types of avian retinal photoreceptors have been identified: rods, straight cones, oblique cones, and double cones composed of principal cones and accessory cones[55]. A similar number of photoreceptor types have been described based on ultrastructural differences[58]. Double cones, which are found in some birds, show a pattern on the retina that varies among species[54]. Delius et al.[17] have proposed that double cones may be involved in detecting the plane of light polarization. This idea was further supported by Young and Martin[112], based on their analysis of the oil droplets contained within these cones.

Most cone photoreceptors contain an oil droplet that serves as a cutoff filter, making their associated cones less sensitive to short wavelengths and transmitting light at longer wavelengths[54]. The smallest droplets have no apparent color and therefore are transparent to all wavelengths longer than 325 nm. Pale yellow or greenish, yellow, orange, and red droplets have maximum absorption at individually characteristic longer wavelengths[23]. The role of oil droplets in color vision is influenced by the visual pigments they are found in combination with.

All evidence suggests that rods contain a rhodopsin photopigment[54]. Microspectrophotometric analysis of cone photopigments indicate that some species have at least three pigments, and other species have at least one additional pigment (c.f., Martin[54]). The pigments and oil droplets occur in specific combinations, indicating that up to six distinct cone receptor types occur in some avian species. How these combinations relate to morphological differences in the cones and to color vision is not yet understood.

Color vision in birds appears to be associated with the presence of retinal cones. Color discrimination experiments in the visible and ultraviolet region in the pigeon substantiate this idea[20], but there is some difference of opinion about the sensitivity of pigeons to ultraviolet wavelengths[21].

Unlike other types of transducers, photoreceptors decrease their rate of spontaneous activity with increasing light intensity. This results in a reduced rate of neurotransmitter release, a signal which can cause postsynaptic depolarization or hyperpolarization. Both polarities are observed in light-evoked changes in retinal bipolar cells[5].

The optic nerve provides the sensory pathway for visual information to the brain and is the largest of the avian cranial nerves. It is composed of many central processes of the somatic afferent fibers of the ganglion cells of the optic nerve within the retina[10]. After entering the cranial cavity, the nerve crosses in the optic chiasma on the ventral surface of the diencephalon and becomes the optic tract which enters the visual centers of the mesencephalon[15, 56]. The size of the nerve is especially large in Falconiformes and Corvidae, and smaller in Strigidae and other nocturnal species[85]. In addition, the optic nerve includes efferents to the avian retina, which project from the isthmooptic nucleus to the principal processes of amacrine cells and the junction of the inner nuclear layer and inner plexiform layer. The physiological function of this projection is not clear yet, but may provide a control on light thresholds and pattern discrimination[65].

The fibers of the otpic nerve pass to the optic tectum. The tectum is also linked to several other areas via several fiber tracts[37]. The anterior connections include the rotund nucleus in the thalamic region and some parts of the Wulst. The posterior connections are similar to other vertebrates and located within the rostral portion of the mesencephalon[66]. The rotund nucleus is generally believed to be the avian homologue of the mammalian ventral thalamic nuclei and serves as a major relay station within the central visual pathway[37].

Chemical cues

Several researchers have reported the use of olfactory information for homing by pigeons[61, 94], but there is some dispute as to how important information carried by the olfactory nerve is to pigeon navigation[71, 91, 92, 109] and as to how treatment of the olfactory nerves with local anesthetics affects the information transmitted to the brain[100]. It appears that the importance of olfactory information in homing varies between regions and breeding lines[62, 100]. Several nocturnal species, including the Kiwi and some Procellariiforms, have demonstrated the use of olfactory information for orientation during feeding and homing[30, 31, 34, 36, 96–98].

Good laboratory evidence has been obtained for odor perception from many avian species[96, 99], mostly using laboratory stimuli on pigeons. These sensitivities range from 0.1 to 40 ppm[32, 78, 84, 93], and vary among individuals of the same species[84]. An important, untested problem is the sensitivity of birds to environmentally relevant odors. Another important related question is how many different odors can birds perceive and distinguish[4]? Recent work on the turkey vulture[80] and a corvid[82] indicate some species are more sensitive to specific relevant odors than other species.

Olfactory receptors

Transduction of chemical odors to the nervous system in birds is similar to that of other terrestrial vertebrates. The olfactory capsules lie within the nares and contain the olfactory epithelium. Olfactory receptor cells of the neuroepithelium, stimulated by a chemical, produce an electro-olfactogram, a slow action potential[4, 86]. This information is carried via the olfactory tract to the olfactory bulb where synaptic connections are made. There is a correlation between the diameter of the olfactory nerve and olfactory development[10], and between the number of olfactory receptors and bulb size[4]. The olfactory nerves of aquatic birds (e.g., marine species, waterfowl, and shorebirds) are well developed[85]. Olfactory bulb size and shape vary greatly among species, as does the internal structure[4]. In the pigeon, projections from the olfactory bulb suggest that olfaction is an important element in their behavior[70]. Unfortunately, study of the avian olfactory systems structure and functioning has been very limited.

Projections from the pigeon olfactory bulb are extensive[70], but because the functional anatomy of the avian telencephalon is poorly understood, the functional significance of the various projections are mostly unknown.

Magnetic cues

The use of the earth's magnetic field for orientation has been described in some species of birds (reviewed in Wiltschko and Wiltschko[108]), but magnetic fields also may have other behavioral influences on migrants[3]. Although the use of magnetic information for orientation has been reported most commonly in nocturnal migrants, there are some data indicating diurnal migrants also may use magnetic information in their orientation[60, 83, 101]. The pigeon is the only nonmigratory species whose magnetic orientation has been well studied. These experiments reveal that the pigeons also use a magnetic compass for orientation[108], and, as a first hint of the underlying receptor mechanism, seem to need the presence of light to use the magnetic compass during transportation[106].

Based on behavioral studies, the avian compass is an inclination compass[105]. The birds appear to perceive the magnetic field as a total vector and cannot distinguish its polarity. This type of mechanism distinguishes between 'poleward' and 'equatorward', rather than north and south. The compass operates within a narrow range of intensities, similar to the ambient magnetic field[103], but can adapt to different intensities over a period of days[102].

A second aspect of navigation is the ability of a bird to determine its current position with respect to its goal, i.e., a map component. Use of some aspect(s) of the geomagnetic field as part of a map has been proposed[84, 88, 89]. Use of magnetic information for a map system differs greatly from its use for a compass. While the magnetic compass system is rather insensitive to even moderate (20%) changes in the ambient magnetic field, a map system must respond to slight variations of less than 0.1% of the total field[108]. An additional difference is that a compass system must detect some directional component of the field, while a map system might compare only local intensity with that at the goal. Based on these data, it is quite likely that the mechanism of perceiving the magnetic information for the map component is different from, and independent of that used for the magnetic compass. Thus, two different types of magnetoreceptors have been postulated and there is some preliminary electrophysiological evidence that birds may have two independent magnetic systems (see below).

Magnetic receptors

Convincing evidence for use of the earth's magnetic field for orientation exists for only a few species other than birds. In magnetic bacteria the mechanism of orientation is well understood: the bacteria contain magnetite particles which are suitably arranged to passively align the entire bacterial cell with the magnetic field. With the exception of sharks and rays, which may use their electroreceptors for magnetic detection[36], the mechanism underlying the magnetosensory receptors is unknown for other species.

Four candidate transducer substances have been proposed: magnetite[38], melanin[50], biological radicals[72] and photopigments[48]. The presence of magnetic material, perhaps magnetite (Fe_3O_4), has been reported in a variety of animals, including migratory and nonmigratory birds[7, 87]. In the pigeon the consistent presence of such material is still doubtful[90]. The amount of material which has been reported, if it is single-domain magnetite, may be sufficient to permit the sensitivity needed to detect information for a magnetic map. The upper beak area of the starling and the zebra finch contain melanin (Semm and Holtkamp, unpublished data). Chromatophores containing melanin can respond to magnetic stimulation[50]; furthermore, the complex molecule of melanin can generate radicals which in turn may respond to artificial magnetic fields in the strength of that of the earth.

Electrophysiological investigations reveal that fibers in the ophthalmic nerve of the bobolink (*Dolichonyx oryzivorus*) are responding to magnetic stimulation, mainly to small changes in intensity[8]. Although this nerve innervates the upper beak area, where the iron oxide and the melanin are located, these magnetic responses are not a proof for magnetite and/or melanin being involved in magnetic perception.

Experimental evidence also indicates that the vertebrate visual system and the pineal gland (which in mammals is coupled functionally to the visual system and in birds contains functioning photoreceptors) respond to magnetic stimulation[12–14, 18, 69, 77]. However, the pineal gland is apparently not involved in magnetic orientation[52, 74] but exerts a magnetic influence on the circadian system[19]. With respect to orientation, the gland seems to have an indirect effect by influencing the timing of the use of the magnetic compass in young, inexperienced migratory birds[74].

The model of the inclination compass implies the simultaneous sensing of the orientation of both gravity and the magnetic field suggesting that the two detection processes may be integratively locked together. In order for magnetic and gravity cues to be integrated the vestibular system is likely to receive the magnetic message via the known visual-vestibular projections. Thus, Semm et al.[75, 76] investigated the effects of magnetic stimulation on electrical activity in the nucleus of the basal optic root (nBOR) which has a projection to the vestibular system. The results demonstrate that single neurons in the nBOR can respond to directional changes in the earth's magnetic field. The nBOR is part of the accessory optic system and receives completely crossed projections from displaced retinal ganglion cells. Although it was of course not possible to test all cells in this nucleus, the results of the studies reveal that, in the nBOR, some of the units which respond to directional movements of light and some of the cells exhibiting an axis specificity respond to direction changes of the magnetic field, whereas the cells which respond only to visual movement do not appear to respond. Interestingly, it is these direction selective cells which project to the vestibulo-cerebellum. Most of the cells which were directionally sensitive to light also showed a clearcut directional selectivity to the magnetic stimulus, i.e., they responded to only a distinct part of the total range involved in the complete inversion of one magnetic vector.

Because many cells in the stratum griseum et fibrosum superficiale of the optic tectum are directionally sensitive, the response of these units to magnetic directional changes was investigated. In contrast to the nBOR, the optic tectum exhibits a retinotopic organization. Thus, the occurrence of magnetically sensitive units in this part of the visual system would allow the animal to determine the orientation of the magnetic field. This could be tested by altering the position of the animal relative to the change of the MF.

In the optic tectum spontaneously active cells and initially silent cells, which could be activated by light, were subjected to dynamic photic stimuli. Most of the units showed directional selectivity and were further tested for responsiveness to gradual inversion of the vertical component of the natural MF. Of these cells some showed a clear response to the magnetic stimulus; most were excited and a few were inhibited. In each case an indication of directional sensitivity to the magnetic stimulus, similar to that described for the nBOR units, was observed. It was possible to compare the response of cells to MF stimulation with the animal's head pointing to the four cardinal magnetic compass directions (north, west, south, east). Five of these units showed excitatory responses at all four positions, although the peak of the response occurred at different points during the magnetic inversion. Three units showed no response with the head pointing to the south or east, while the remaining five only responded at two of the four positions.

The investigations in the visual system of the pigeon under earth-strength magnetic stimulation reveal that the magnetic responsiveness of visual neurons in both the accessory optic system (nBOR) and tectum is dependent on the presence of light and an intact retina. The clear correlation between the direction selectivity to both photic and magnetic stimuli observed in the two parts of the visual system suggests that the directionality component of magnetic responses may already be present in the retina itself, since it appears that directionality in the transfer of photic information depends on excitatory retinal photoreceptor 'units' having the same preferred direction as the tectal cells with which they make contact. This in turn implies that the magnetic detection system of the pigeon may function by exploiting the visual sensory organization which allows processing of visually related information. If the occurrence of single distinct peaks in the magnetic response at particular points in the inversion cycle provides information about the direction of the MF stimulus, it follows that the response maximum of an individual unit is unlikely to occur at the same point during the inversion, when the MF is changed with the pigeon's head pointing to different magnetic compass directions. This was not the case for most of the units tested, suggesting that the pattern of response to the MF stimulus could indeed contain meaningful information concerning the direction of the prevailing field relative to the position of the eyes in space.

In both the nBOR and the tectum, magnetic responsiveness disappeared when magnetic stimulation was performed in total darkness or when the optic nerves were dissected. Thus, it might well be that the photoreceptors are also the postulated magnetoreceptors for the magnetic compass. This hypothesis recently received support from intracellular recordings of fly photoreceptors under magnetic stimulation[67]. Although species differences have to be taken into account, these experiments demonstrate for the first time that photoreceptors have in principle the capability of responding to magnetic stimulation. Although it is possible that the avian visual system is receiving magnetic information from a magnetoreceptor located elsewhere, it seems unlikely. The processing of magnetic information may need light, or alternatively the animal may need to see the environment in order to spatially integrate magnetic information.

It is important to note that even following severing the posterior part of the ophthalmic nerve in the upper beak area, the magnetic responses in both the nerve and the visual system persisted. This implies that two different magnetic systems with different receptors are present in the bird's central nervous system.

Vibrational cues

The most obvious (to humans) vibrational cues used by birds are auditory cues. These include nocturnal call notes from flying conspecifics and other birds[24–26], as well as sounds from the ground such as frog calls, rivers, and breaking surf[16, 28, 29]. A less obvious source of vibrational information is infrasound. There is a rich source of navigational information available in frequencies below 10 Hz which are inaudible to humans, but within the detectional abilities of pigeons and probably other avian species[45]. Although binaural localization of the sound could not be used at infrasound frequencies, birds can obtain directional information by flying in a circle and detecting the resulting Doppler shift as they fly towards and then away from the infrasound source. The ability to discriminate such sound frequency shifts is within the capability of some species[45, 68].

Vibration detectors

The inner ear serves two functions in birds: hearing and equilibration. Hearing takes place in the cochlear organ and equilibration in the vestibular organ. The inner ear is inside the skull and is composed of two parts. The bony labyrinth surrounds and supports the membranous labyrinth, with the vestibular and cochlear ducts smaller than their bony counterparts. Perilymph surrounds the membranous labyrinth, filling in the space between it and the bony labyrinth. It serves to conduct vibrations from the tympanum and the columella produced by sound to the endolymph and basilar membrane. The endolymph is contained within the cavity of the membranous labyrinth[79].

To efficiently transform vibrational energy to the nervous system, the middle ear must match the low impedance of air to the higher impedance of the fluids within the cochlea. The transfer of acoustic information from the tympanic membrane to the vestibular window is mediated by only one bony ossicle, the columella. The base of the columella fits into the vestibular window and extends distally to articulate with the tympanic membrane via a cartilage[47]. Attached to the columella is a single middle ear muscle. When the muscle is contracted, the tension on the tympanic membrane is increased and the columella is moved towards the tympanic membrane, moving the base away from the vestibular window[59].

This would result in a decrease in the transformer efficiency of the middle ear, reducing the sound energy transferred to the inner ear[47]. Thus, the columellar muscle serves as a bandpass filter with minimum suppression occurring in the range of maximum auditory sensitivity[46]. This mechanism may allow birds to filter extraneous noise, increasing the signal/noise ratio at the relevant wavelengths. When the cochleas and lagenas were surgically removed from a group of pigeons, the birds no longer responded to auditory or infrasonic stimulation[111]. If just the columella was removed, the birds were less sensitive to low frequency (2–10 Hz) sounds, suggesting that the infrasound transducing mechanism is probably the ear.

Sound transduction occurs in the cochlear organ. The finger-like cochlear duct projects anteriorly from the saccule and is closed distally. Its length varies from 2.75 mm in small species to at least 10 mm in owls[73]. The cochlear duct contains two sensory structures: the basilar papilla and the macula of the lagena.

The method by which vibrational information detected by the ear is transduced to the nervous system involves hair cells within the cochlea. The hair cells form the receptor cell of the auditory and vestibular systems, transducing physical information into the electrical information of the nervous system. Individual hair cells are selectively responsive to a particular set of frequencies, both because of the mechanical properties of their hair bundles and as a result of their ionic channels which serve as an electrical resonator[33]. Vestibular and auditory information is carried in the 8th cranial nerve, the vestibulocochlear nerve. The vestibular part of the nerve is composed of axons from vestibular ganglion cells. The ganglion is located in the vestibular area of the internal acoustic fossa[10]. Vestibular axons enter the vestibular nuclear complex of the medullary segment of the brain stem. Some fibers enter the cerebellum through the 'juxtarestiform body' in the caudal cerebellar peduncle[9]. The cochlear part of the nerve is composed of fibers originating from the bipolar cells of the cochlear and lagenar ganglia. Fibers from these ganglion cells are distributed to the neuroepithelium of the cochlear basal membrane and the macula of the lagena[10].

Localization of the source of auditory sound is accomplished by recognizing the binaural differences of the detected signals. Phase differences, differences in time of arrival, or differences in amplitude between the two ears can be used to distinguish the source of sound. The pigeon's best azimuthal resolution acuity was 4°[51], only slightly less than that of the barn owl's 1–2°[43,64], and better than the songbirds' 16–26°[27,39]. The angular acuity of pigeon hearing is frequency dependent, with the best localization performance in two frequency ranges, 250–500 Hz and 2–4 kHz[51].

Intracellular recordings from afferents of the magnocellular cochlear nuclei of barn owls (*Tyto alba*) show orderly changes in conduction delay associated with their vertical location within the nucleus. It appears that these afferent axons act as delay lines and provide the basis for the neuronal map measuring interaural time differences[111]. These neurons project to the nucleus mesencephalicus lateralis dorsalis (MLD) which contains nerve cells that respond only to specific sound stimulus within a small restricted area in space[43]. The owl's auditory receptive fields are arranged so that the auditory neurons 'project' to a visual-auditory bimodal map in the owl's optic tectum[40]. The auditory map is matched topographically with the projectional visual map. Although these maps are different in origin, they are functionally equivalent[44]. The formation of receptive fields requires binaural information from the environment. Birds cannot localize sound with one ear plugged[42].

Conclusions

The abilities of migratory and homing birds to extract meaningful directional information from their environment is dependent upon a variety of specialized sensory receptors. The receptors for some sensory modalities are well known and their mechanisms at least partially understood. These include the photoreceptors of the retina, the hair cell mechanoreceptors of the auditory and vestibular systems, and the chemoreceptors of the olfactory system. On the other hand, neither the structure nor the mechanism of the magnetoreceptor are known, although there are data to support some of the different hypotheses on magnetic field transduction. Little is known about how or where the sensory information is integrated within the avian brain for its use in navigation. These are areas for future research.

Acknowledgments. Financial assistance was provided to RCB in part by the Geneseo Foundation and NIH (NS2601601), and to PS by the Heisenberg-Program of the German Research Council.

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