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Through a Bird's Eye – Exploring Avian Sensory Perception

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ABSTRACT

For too many birds their environment includes airfields and aircraft. Knowing avian sensory abilities, researchers can design experiments and develop new devices and techniques to deter birds from aircraft on and away from airfields. How birds perceive the world about them determines many choices, including foraging, predator avoidance, and flight. Most experiments to investigate the sensory abilities of birds have been developed and analyzed using only human sensory capabilities, which often differ markedly from those of birds. My objective is to review and synthesize what is known and what is unknown about avian sensory capabilities. Compared with humans, birds can distinguish more colors and detect ultraviolet and polarized light directly. Their range of auditory sensitivity is narrower than humans but some species can hear sounds at least as high pitched as humans. Their chemical sensitivity is similar to humans in most cases but varies seasonally and can approach that of rodents. Avian vestibular sensitivity appears to be similar to other vertebrates but has received little investigation. There is a great deal we do not know about avian sensory perception that we need to know to make aircraft more obvious to birds and improve the effectiveness of dispersal techniques for individual species of birds.

For too many birds their environment includes airfields and aircraft. By knowing the sensory abilities of birds, researchers can design experiments and develop new devices and techniques to deter birds from aircraft on and away from airfields. How birds perceive the world about them determines many of their choices, including where to forage, what to eat, detecting and avoiding predators, and where to fly to avoid hitting objects. Most experiments to investigate the sensory abilities of birds have been developed and analyzed using only human sensory capabilities, which often differ markedly from those of birds. My objective in this paper is to review and synthesize what is known and what is unknown about avian sensory capabilities.

Sensory perception can be subdivided into sensory transduction and cognition. The subject of this paper is primarily sensory transduction, converting physical phenomena to the nervous system. The nerve cells making the conversion are sensory receptors. They respond to a change in the physical signal by increasing or decreasing their rates of firing. These "firings" or nerve spikes are action potentials and the primary way that nerve cells communicate with one another. An Action Potential is an "all or nothing" response produced when the stimulus to the cell reaches the cell's threshold. In special cases, subthreshold responses can be communicated to other neurons but most communication requires the production of an Action Potential. This should be regarded as the first step in the bird's decision making process; if the receptor cell doesn't reach threshold, the information doesn't make it to the higher levels of the brain. If our objective is to cause birds to avoid aircraft, we must make sure that their receptors are stimulated enough to reach their thresholds. To make sure that objective is achieved, we have to know what those thresholds are.

SENSORY RECEPTORS

VISION – The receptors of the avian visual system are the rods and cones of the retina. The dual input to the visual system results from each type of receptor being specialized for a range of light intensities. As with mammals, rods are the most sensitive to light and are the primary receptor for vision in dim illumination. The visual pigment in avian rods is rhodopsin and has a sensitivity similar to that of mammalian rhodopsin, with a peak sensitivity around 500 nm (green). The transition from scotopic (rod based) vision to photopic (cone based) vision influences not only the sensitivity to light intensity but also affects resolution, contrast sensitivity, and color perception. Birds moving in low light intensities are more sensitive to light but cannot discriminate color and have poorer visual resolution. Consequently, they are less able to distinguish the shape of an object at night or in dim light. For comparison, the Tawny Owl (*Strix aluco*; Martin 1982, 1986; Martin and Gordon 1974) and the Great Horned Owl (*Bubo virginiana*; Bite 1973) are about 2.5 times more sensitive to dim light than humans and 100 times more sensitive than the pigeon (*Columba livia*; Blough 1955)

The cones (photopic vision) are about 100 times less sensitive than the rods (scotopic vision) to dim light but because the cones are smaller and can be packed more densely, scotopic vision allows the bird to differentiate more details of an object or distinguish among objects that are near one another (Tovée 1996). The cones are also the basis of color vision. Birds have four or five classes of single cones and a double cone. The function of the double cone is unknown but it might be involved in detecting polarized light (Delilus et al. 1976) or magnetic fields (Beason and Swali 2001). All of the 20 or so species that have been examined have either an ultraviolet (UV) or violet sensitive pigment. The implication is that all of these species, and probably all species of birds, are sensitive to wavelengths (colors) into the UV (Cuthill et al. 2000). Consequently, their visual sensitivity extends from the UV into the far red (but not infrared). Within that range, they posses four or five classes of cones that are more narrowly tuned than the three human color receptors (Vorobyev et al. 1998, Beason and Lowe unpubl. data). The implication is that birds thus are better able to resolve differences in color than are humans and they can see a wider range of colors than humans.

Avian cones (color receptors) differ from human and mammalian cones in structure as well as number of types. Avian cones (as well as many fish, reptiles, and perhaps amphibians) contain an oil droplet that filters the light before it reaches the visual pigments (Fig. 1). These oil droplets contain

carotene based pigments that act as low-pass filters; that is, they allow light that is of longer wavelength (towards the red end of the spectrum) than the cutoff wavelength to pass. The spectral (color) sensitivity of a class of cones is determined by both the sensitivity of the pigment it contains and the oil droplet filter it possesses. All cone photoreceptors that have been examined contain a single visual pigment. By knowing the spectral characteristics of the pigment and filter, the spectral sensitivity of the cell can be calculated. This is the information that is needed for each hazardous species of bird. There is no reason to expect that all birds or even closely related species will have identical color vision. The 15-20 avian species that have been studied do not have a general color vision design. Because there have been no studies of closely related avian species, we have to look at comparative studies among other taxa. In primates, for example, there are differences in spectral sensitivity among species and even differences in trichromatic versus dichromatic color vision (Toveé 1996).

A further complicating factor of vision is that there is some processing of the sensory information within the retina, before it reaches the brain. There are several types of signal processing that occur within our retinas. One is color processing. There are four primary colors for humans: red, yellow, green, and blue; however, there are only three classes of color receptors (red, green, and blue; Fig. 1). Yellow is produced as the difference between the blue cones and the sum of the red and green cones. What are the "primary" colors for the different species of birds? Are there any colors that are generated by signal processing within the retina? We don't know but it would be useful to find out.

A second area of retinal processing affects visual acuity and the detection of motion; this is the response of ganglion cells. The avian retina has received little study but it is thicker than mammalian (and human) retina and logically has similar types of cells and connections among cells. These connections are responsible for the signal processing that occurs before the information is sent to the brain. In humans this results in many of the optical illusions that we perceive. A ganglion cell receives input from several photoreceptors. These inputs are categorized as center (within a central receptive field) and surround (a receptive field outside the central field but restricted in area). These ganglion cells then respond to light and dark of these two categories with excitation or inhibition. An ON-center cell responds strongest when the central field is illuminated and the surround field is dark. The reverse situation (center dark and surround lit) suppresses the output of the ganglion cell. OFF-center cells show the reverse behavior. These characteristics improve our ability to detect movement (cells respond with a rapid change between high and low levels of activity), sharpen the images sent to our brains (edge detection), and cause us to see patterns that aren't there (optical illusions).

There is behavioral evidence and some disputed electrophysiological data that indicate birds can perceive differences in polarized light (Delius et al. 1976, Coemans et al. 1990). The amount and orientation of polarization varies in the sky and various natural objects reflect specific planes of polarized light. The celestial patterns of polarization can be used by birds and other animals for orientation and navigation. The polarization of objects in the environment makes them more or less obvious to the observer. Rapid changes in polarization can also produce strong flickering patterns that are rapidly detected by the retina. Although it is known for invertebrates and some fish, the mechanism used by birds to detect the polarization of light is unknown. One idea is that the double cones might be involved (Delius et al. 1976). The orientation of the visual pigments in vertebrate photoreceptors is perpendicular to all possible planes of polarization for incoming light. Consequently, differences in the angle of polarization do not cause any differences in the amount of energy absorbed by the visual pigment. The double cone could detect the orientation of polarized light by using the scattering produced by the common cell membrane and the resulting polarization that occurs. The polarization could then be determined by the visual pigments because different polarizations would result in different amounts of energy transferred to the pigment (Fig. 1).

The ability of a bird or other animal to determine the distance to an object through stereoscopic vision requires that the object be in the binocular field of vision. Many species of birds have their eyes laterally and, consequently, have a limited binocular field. For some species, the binocular field is extensive enough to include the bill so they can visually guide their feeding. In other species, such as the Mallard (*Anas platyrhynchos*) and Woodcock (*Scolopax rusticola*), the bill lies in the periphery of the

visual field (Martin 1986, 1993), perhaps because their feeding is tactilely guided. This also results in each eye having a 180° view and no resulting blind spot behind the head. Species with the frontal binocular field have a blind field behind the head that differs among species.

The visual acuity of raptors is more than twice that of humans (Fox et al. 1976, Reymond 1985). The American Kestrel (*Falco sparverius*) can discriminate 2 mm insects from the top of an 18 m tree. However, this acuity is dependent on bright light and decreases dramatically under dimmer illumination (Reymond 1985).

AUDITORY – The receptors of the avian auditory system are the hair cells, which resemble the hair cells of other vertebrates in both structure and function. The length of the cilia of each hair cell and the cell's location on the basilar membrane determine the frequencies to which it is most sensitive. Hair cells with the longest cilia and on the thickest part of the basilar membrane respond best to low frequencies and those with shortest cilia and on the thinnest part of the membrane respond best to high frequencies. Each hair cell has a characteristic set of responses to different frequencies that are termed its tuning curve. These cells are connected to cochlear ganglion cells. Birds hear very well over a limited range between 1 and 5 KHz but avian hearing extends to higher and lower frequencies. Some species are more sensitive towards the lower end of the range and other species towards the higher end (Konishi 1970, Hienz et al. 1977). The most sensitive range for pigeons is 1-2 KHz, with an absolute upper limit of about 10 KHz (Goerdel-Leich and Schwartzkopff 1984). Large nocturnal owls differ in that they have a good sensitivity over a wide range of frequencies (Konishi 1973). No avian species that has been tested has shown sensitivity to ultrasonic frequencies (> 20 KHz). Sensitivity to low frequencies has not received much attention but young domestic chickens (*Gallus domesticus*) are sensitive to sounds as low as 10 Hz (Warchol and Dallos 1989); other species might be also. For most species data on sensitivity below 200 Hz is lacking although the species that have been tested showed moderate sensitivity (50 dB SPL) at 200 Hz (Theurich et al. 1984).

Infrasound (sound with a frequency of less that 20 Hz) has been demonstrated behaviorally in the pigeon (Yodlowski et al. 1977, Kreithen and Quine 1979) and the Guinea Fowl (*Numida meleagris*; Theurich et al. 1984) but was unsuccessfully attempted in the Black-headed Gull (*Larus ridibundus*; Theurich et al. 1984). Guinea Fowl demonstrated sensitivity down to 2 Hz (Theurich et al. 1984) and pigeons to less than 0.05 Hz (Kreithen and Quine 1979, Klinke 1990, Schermuly and Klinke 1990). One species of grouse even produces infrasound as part of its vocalizations and, presumably, can detect the infrasound (Moss and Lockie 1979). Unlike responses to auditory frequencies, there are no hair cells in the inner ear that respond uniquely to infrasonic frequencies. Instead, the low frequency sensitive cells respond to infrasound by bursts that are synchronized to the phase of the sound (Theurich et al. 1984, Klinke 1990, Schermuly and Klinke 1990).

In general, frequency discrimination in birds is only about one-half or one-third as good as humans, at least within the 1-4 KHz range (Dooling 1982). The Barn Owl (*Tyto alba*) is atypical in that it has hearing that is as good or better than a cat from 1-7 KHz but has a sharp cutoff about 8 KHz and its frequency discrimination is as good as mammals within that range (Konishi 1973, Quine and Konishi 1974). The Budgerigar (*Melopsittacus undulatus*) also shows good frequency discrimination from 1-4 KHz (Dooling and Saunders 1975). At infrasound frequencies, pigeons can detect a 1% difference at 20 Hz and 7% at 1 Hz (Quine and Kreithen 1981); however, at 500 Hz they can detect only differences of at least 10% (Bräucker and Schwartzkopff 1986).

The tall hair cells of the avian basilar papilla are directly connected to one another in the young chicken, starling (*Sturnus vulgaris*; Fischer et al. 1991), and pigeon (Takasaka and Smith 1971). These contacts appear to be typical for the tall hair cells but rare for the short hair cells. Because the tall hair cells are most sensitive to low frequency sounds, the physiological consequences of these connections would be expected to be manifested with low pitched sounds, perhaps infrasound. The effects of these connections on frequency discrimination, sensitivity, or acuity are unknown.

A problem that birds suffer that is similar to humans is damage to the hair cells from loud noises. The effect, the intensity that produces damage, and the amount of damage differs depending on the species. Unfortunately, little work has been conducted and all of that on domestic songbirds (Ryals et al. 1999). As anyone working around ramps, flight lines, and runways knows, the intensity of sounds produced by jet engines in these areas is intense. If the birds residing in these areas have been constantly subjected to sound pressure levels that continually damage their hearing receptors, then auditory alerts to the birds must be at frequencies that are undamaged by the noise.

Electrophysiological recordings from cells of the cochlear ganglion in the starling (Gleich and Narins 1988) and the Red-winged Blackbird (*Agelaius phoeniceus*; Woolf and Sachs 1977) show phase locking of cellular responses to the stimulus up to 3-6 KHz. Individual cells responded to only one part of a sinusoidal signal. Interestingly, the preferred phase was delayed as the frequency increased.

Because most birds have small heads with ears that are close together, neither interaural time differences nor acoustic shadows are thought to be useful in determining the direction of a sound's source. Unlike mammalian ears, the tympanic membranes of birds are connected by air filled cavities in the skull. These interaural pathways allow birds to measure the differences in sound intensity at each ear and use those differences for sound localization (Lewald 1990). Interaural intensity difference is used by pigeons to determine the direction above 2 KHz but was less useful at lower frequencies.

CHEMICAL – Chemical information can be divided into two categories: contact and media (wind or water) borne. Contact chemoreceptors, taste receptors, are located on the upper and lower jaws and the tongue (Berkhoudt 1985). As with other avian sensory systems, only a few species have been examined, mostly the chicken (*Gallus domesticus*), Mallard, and pigeon. The number of taste buds range from 24 in the Blue Tit (*Parus caeruleus*; Gentle 1975) to 375 in the Mallard (Berkhoudt 1977). The sensory information travels to the brain by way of the lingual branch of the glossopharyngeal nerve, the palatine branch of the facial nerve, and perhaps the chorda tympani nerve (Berkhoudt 1985).

Some birds appear to have a well-developed sense of taste. Sanderling (*Calidris alba*) and Dunlin (*Calidris alpina*) can distinguish between sand where worms had been crawling before the experiment and sand where no worms had been (van Heezik et al 1983). Hummingbirds can distinguish different types of sugars and solutions with different concentrations of sugar (Hainsworth and Wolf 1976). Many birds are tolerant of acidic and alkaline solutions, which might permit the exploitation of otherwise unpalatable food resources, such as unripe fruit (Mason and Clark 2000). Although birds posses capsaicin taste receptors, they do not feel the pain-producing effects of the chemical (Jordt and Julius 2002).

Historically, birds have been thought to have little or no olfactory sensitivity. Comparative anatomy at the macroscopic and microscopic levels shows that avian olfactory systems are similar to those of other terrestrial vertebrates (Roper 1999). Consequently, it seems reasonable to expect that their sense of smell is not absent or rudimentary. There is increasing behavioral evidence to support the conclusion that birds use smell for many purposes, including avoiding chemical repellents (Mason et al. 1989).

Olfaction differs from gustatory responses, which include taste and chemesthesis, in its ability to detect airborne chemicals. Olfaction is capable of detecting chemical stimuli long distances away from the source. The other sources require contact with the chemical source (taste) or must experience high concentrations of the chemical (chemesthesis via the trigeminal nerve). The olfactory receptors are located in the olfactory chamber of the nasal area. The receptors connect to the olfactory bulb of the brain by way of the olfactory nerve. The olfactory bulb is connected with other parts of the brain, although some information processing might take place in the bulb.

Birds have been tested for receptor responses to many different odorants (reviewed by Roper 1999; Table 1) but most of these are not ecologically relevant. Exception to this are the compounds tested by Clark and Mason (1987, 1988). They tested the sensitivity of the European Starling to the odors

of green plant material the birds selected for their nests. The sensitivity to these odors showed seasonal differences, with the greatest sensitivity during the breeding season (Clark and Smeraski 1990). The Crested Auklet (*Aethia cristatella*; Hagelin et al. 2003) and domestic chick (Fluck et al. 1996) demonstrate avoidance of mammalian predator odors. The auklet also shows attraction to two chemicals (*cis*-4-decenal and octanal) that are found on their feathers naturally (Hagelin et al. 2003). (To humans these odors smell like tangerine.) Smell has been shown to be used by seabirds to locate their nests (Grubb 1974, Shallenberger 1975, Minguez 1997) and by pigeons to navigate home (Waldvogel 1989, Papi 2001). There is strong anatomical, physiological, and behavioral support for olfactory abilities in birds and it should not be ignored as a potential avenue for deterrents.

The ability of vultures to detect odors has been argued for over a century (McCartney 1968). Stager (1964) showed that Turkey Vultures (*Cathartes aura*) but not Black Vultures (*Coragyps atratus*) are capable of locating carcasses based on smelling the ethanethiol (ethyl mercaptan) produced by the rotting meat. The Greater Yellow-headed Vulture (*Cathartes melambrotus*; Gomez et al. 1994) and the Lesser Yellow-headed Vulture (*C. burrovianus*; Houston 1988) also seem to use smell to locate carcasses in tropical forests but the King Vulture (*Sarcorhamphus papa*) cannot do so (Houston 1984).

Although methyl anthranilate is an aversive chemical to birds (Marples and Roper 1997), it is detected by way of the trigeminal system rather than the olfactory (Mason et al. 1989). Some of the avoidance of methyl anthranilate and similar repellents might involve detection of olfactory cues but their irritant function does not involve the olfactory system (Clark 1996, Clark and Shah 1992).

VESTIBULAR – The avian vestibular organ is very similar to that of mammals and other vertebrates, and based on three fluid filled canals. Although the avian anterior semicircular canal is much larger than the other two, the biological significance of these differences is unclear. The receptor of the vestibular system is the hair cell, allowing it to detect angular and linear acceleration and changes in position. There are six vestibular receptor structures: one in each of the semicircular canals, two in the utricle, and one in the saccule (Smith 1985). The semicircular ducts probably detect changes in angular momentum and the utricle and saccule organs determine linear acceleration and gravity but there is some interaction among these organs (Smith 1985). Vestibular information is carried to the brain by the vestibulocochlear nerve (VIII cranial nerve), along with auditory information.

Birds obviously use their vestibular system to maintain their orientation during flight as well as walking and swimming. Based on anecdotal accounts, birds become disoriented under conditions similar to those that disorient human pilots. The most obvious of these are fog and flying within clouds. Bright lights on the ground seem to enhance the disorientation under such conditions. It appears that the birds might be interpreting the bright lights as the moon (the only natural source of bright light at night) and fly directly towards the light (Beason 1999). Under natural conditions, such behavior would result in the birds flying above the fog or low clouds and away from obstacles such as trees or hills. Such flying should also put them above the conditions that are limiting their visibility.

MAGNETIC – Birds have three magnetic receptor systems: a light dependent, wavelength sensitive system that appears to serve the magnetic compass; a magnetite based system that appears to provide positional information such as a map; and a light dependent system in the Pineal Gland that influences circadian and perhaps circannual rhythms (Beason and Semm 1991). The receptor for the avian magnetic compass appears to require light and be sensitive to the color or wavelength of that light (Beason 2003) but the responses to the wavelength of light does not appear to be consistent among species. Blue light has no effect on orientation and red causes disorientation in all species tested. However, the effects of intermediate wavelengths depend upon the species being tested; some are disoriented, some have a change in orientation, and some are unaffected (Table 2). These differences might indicate differences in some aspect of the receptor among species. The magnetite based receptor is associated with the Ophthalmic branch of the Trigeminal nerve. It is much more sensitive to changes in intensity of the magnetic field than the light dependent system and can detect changes of 50 nT (0.001 change in the Earth's magnetic field; Semm and Beason 1990, Beason unpubl. data). Treating birds with a brief, high-intensity magnetic pulse changes the direction of the birds' orientations (Wiltschko et al.

1994, Beason et al. 1995) but the effects of the treatment can be negated by blocking the Ophthalmic nerve (Beason and Semm 1996). The magnetic sensitivity of the avian Pineal Gland is independent of other magnetic sensors (Semm et al. 1982, 1987) and appears to involve synchronization of the animal's daily and annual clocks (Cremer-Bartels et al. 1984).

TACTILE – Birds are sensitive to touch and pressure as are other vertebrates, and use four types of mechanoreceptors to transduce the information: Herbst corpuscles, Grandry corpuscles, Merkel Cell receptors, and Ruffini endings (Gottschaldt 1985, Necker 2000). The most common and widely distributed mechanoreceptor in birds is the Herbst corpuscle, which resembles the Pacinian corpuscle of mammals. It is composed of a sensory nerve ending within a corpuscle enclosed by cells that form a lamellar arrangement around it. The number, size, and structure of the lamellae are functions of the location of the receptor and the species and age of the animal (Gottschaldt 1985). The mouth and forehead are well supplied with Herbst pressure receptors, whose information is carried by branches of the Trigeminal (V) nerve. This type of receptor is very sensitive to vibration and acceleration. Herbst and Merkel receptors are scattered on the surface of the skin and associated with the feathers. These mechanoreceptors appear to detect feather positions and are used in flight. These receptors respond to stimuli in three different ways: slowly adapting amplitude sensitivity, rapidly adapting velocity sensitivity, and rapidly adapting acceleration sensitivity (Iggo and Gottschaldt 1974, Gottschaldt 1985). They respond, respectively, to constant pressure or position, changing pressure or position, and the beginning and ending of changes. Merkel cell receptors are primarily found in the bill and on the tongue of nonaquatic birds but have been reported in other locations (Necker 2000). Grandy corpuscles are found only in the bill of aquatic birds and are most numerous in the tip (Gottschaldt and Lausmann 1974, Berkhoudt 1980, Gottschaldt 1985). Although Ruffini endings are well documented in mammals there are only a few studies of avian Ruffini endings, and those are in the bills of geese and Japanese Quail (*Coturnix japonica*; Necker 2000).

TEMPERATURE – Temperature receptors are located in the skin and concentrated in the beak and tongue. Thermoreceptors have a spontaneous rate of firing depending on an animal's body temperature. As with mammals thermoreceptors are free nerve endings in the skin and respond to increases (warm receptors) or decreases (cold receptors) in temperature by increasing their rates of nerve firings. In birds cold thermoreceptors are more common than warm receptors (Necker 2000).

NOCIOCEPTION – Nociceptors respond to mechanical and heat stimuli that could potentially damage the feathered skin or the mouth. High threshold mechanoreceptors or heat nociceptors are located in the skin and respond to strong pressure (increasing force) and heat (from about 45° to 55° C (Necker 2000). Nociceptors of the mouth detect chemical irritants (pH, etc.) and connect to the brain by way of the Trigeminal (V) nerve. Stimulation of nociceptors results in increased blood pressure and heart and respiratory rates (Gottschaldt 1985).

CENTRAL PROCESSING

Information from each type of sensory receptor undergoes some type of processing downstream from the receptor. In many cases the first processing that takes place is to compare the inputs from adjacent receptors. In the retina, for example, the ganglion cells compare adjacent photoreceptor outputs to detect edges and movement. Similar processing occurs in the auditory and other sensory systems. This initial processing usually helps the animal to "refine" the information it receives and extract the signal from the background noise. Some of this initial processing takes place in the periphery, depending on the sensory system.

The next stage of processing typically takes place within the central nervous system. This can be thought of as the animal's attempt to "pigeon-hole" the stimulus and identify its source. There are a multitude of interconnections that occur within the brain and spinal cord of the bird. These connections result in brain nuclei exchanging information with one another This type of accumulation and exchange of information serves as the decision making process for the bird.

CONCLUSIONS

Clearly, there is a great deal that we do not know about the sensory capabilities of birds in general. More specifically, there is little that we know about the visual, auditory, and chemical sensitivities of species that are hazardous to aviation. My objective in this review has been to summarize what we know on the topic so that we will know where to focus our research in the future. By knowing what the limits are of avian sensory transduction we can develop new devices and management techniques to reduce the number of birds on airfields and to alert birds to the presence of aircraft on and away from the airfields. For example, can we paint aircraft or their undersides in such a way that they are more visible or even repellent to birds, but still attractive to passengers?

Similar knowledge gaps are present for the auditory capabilities of birds. We know the range of hearing for a few species but almost none are species hazardous to aviation. We know nothing about the cognitive abilities of birds for sounds. Humans have specific harmonic relationships that we find pleasant, some that are strange, and others that are offensive. Is the same true for birds? We are making our aircraft engines quieter but some have very distinctive sound signatures. Can we exploit that? Can we put sound projectors on aircraft that broadcast a narrow beam supernormal alarm call ahead of the plane to warn of its approach? If we do, what frequency or combination of frequencies do we use? We have no idea.

Can we make chemical repellents more effective by using a combination of odors and irritants? Or perhaps associating visual or auditory cues with the "punishing" effect of the chemicals? There are an almost unlimited number of possibilities but we need to know the sensory abilities of birds to limit our inquiries to those that are potentially profitable.

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Table 1. Olfactory sensitivity thresholds of birds to various non-ecological compounds. Summaried from Roper 1999.

	Amyl acetate	Benz-aldehyde	Butan-ethiol	Butanoic acid	Butanol	n-Butyl acetate	Cyclo-hexanone	Ethan-ethiol	Ethyl butyrate	Heptane	Hexane	Methol	F
Rock Dove	1	1	6	2	1	1		6		1	2	1	
Chicken										1	1		
Northern Bobwhite										2	2		
Magpie			6					5				1	
Turkey Vulture				1				1					
Black-tailed Gull	1												
European Starling							2						
Cedar Waxwing							2						
Tree Swall9ow							3						
Brown-headed Cowbird									1				
Catbird							3						
Eastern Phoebe							3						
European Goldfinch							3						
Great Tit							3						
Black-capped Chickadee							3						

Sensitivity categories: 1: < 1.0 ppm; 2: 1-10 ppm; 3: 10-100 ppm; 4: 100-1000 ppm;5: 1000-10,000 ppm; 6 > 10,000 ppm

Table 2. Magnetic orientation of avian species to monochromatic light. Based on data from Beason unpubl. data; Wiltschko and Wiltschko 1995, 1998, 1999; Wiltschko et al. 1993.

	Red	**Orange-Yellow**	**Green**	**Blue**
Pigeon	Disoriented			Normal
European Robin	Disoriented	Disoriented	Normal	Normal
Australian Silvereye			Normal	Normal
Bobolink	Disoriented	Bimodal Rotated	Disoriented	Normal

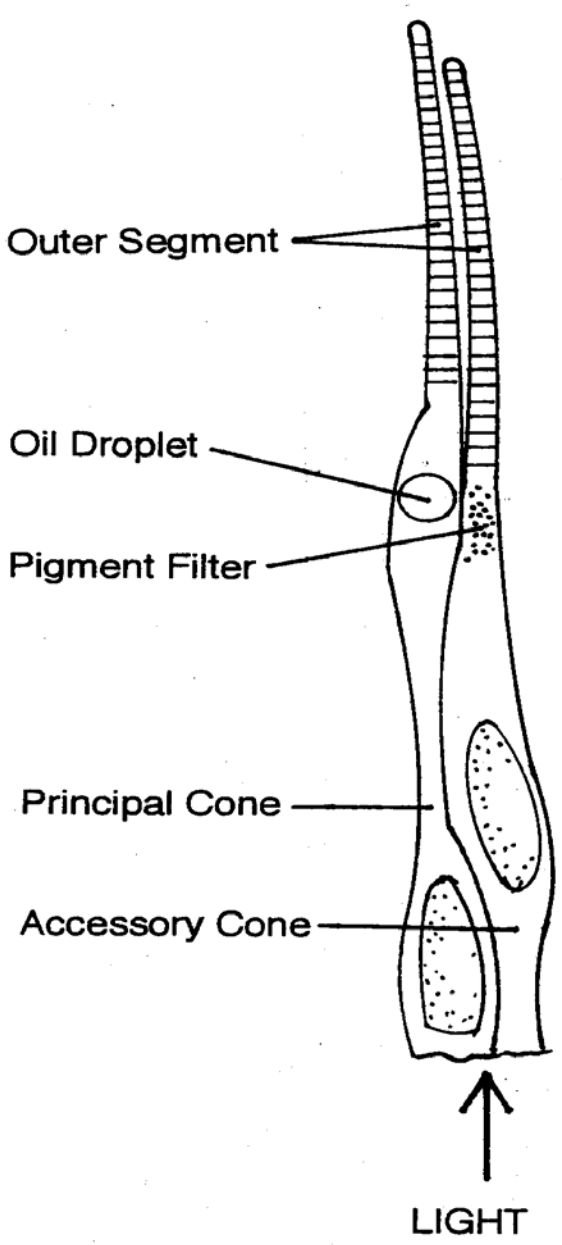

Figure 1. Schematic of an avian double cone showing the relationships of the oil droplet, visual pigment, and common membrane. The avian single cone resembles the structure of the Principal Cone.