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Sensory Capacities of Parrots

Jennifer Graham, Timothy F. Wright,
Robert J. Dooling, and Ruediger Korbel

INTRODUCTION

Parrots are gregarious and vocal creatures that communicate in ways we have yet to understand. How do parrots perceive the world? By understanding some of the unique adaptations of avian anatomy, we may better understand parrot behavior. This chapter will discuss the sensory capacities of parrots including vision, hearing, taste, smell, and touch perceptions.

VISION

The majority of birds rely heavily on visual abilities in their daily activities. Visual acuity is enhanced in avian species, approximately two to eight times higher than in mammals, as the avian eye is large in relation to the size of the head, allowing a large image to be projected on the retina.[1–5] Visual acuity is also enhanced because the retina of diurnal birds has a large number of cones compared to humans; for example, the hawk fovea contains around 300,000 cones/mm^2, while the human fovea contains around 147,000 cones/mm^2.[1] In addition, nearly every cone in the avian eye is represented by an individual axon traveling to the brain, while the eye of humans contains six to seven million cones but only one million axons in the entire optic nerve.[1]

While eyes come in different shapes depending on the species of bird, parrots have a "flat" eye. The flat eyeball is characterized by a short axis that projects a relatively smaller image on the retina, decreasing visual acuity compared to other species such as birds of prey.[1] The eyeball of birds is asymmetric, favoring binocular vision.[1] The sclera of the eye is strengthened by ten to 18 small bones called scleral ossicles.[1–5]

Because the eyeball almost completely fills the orbit, the eye movements of the bird are generally fewer than those of mammals.[1] However, birds can move their heads and necks extensively, and this compensates for the small eye movements.[1] Movement of the orbits is independent between both eyes in parrots, in contrast to mammals.[1]

A feature of the avian eye is that the sphincter and dilator muscles of the pupil contain mainly striated fibers, compared to the mammalian counterpart that contains only smooth muscle.[1–5] Because of this anatomic feature, the pupillary opening is under voluntary control in parrots. Rapid dilation and constriction of the pupillary opening is often observed in aggressive or excited parrots.[6] While pupillary light reflexes do occur in birds, complete decussation of the optic nerve axons prevents true consensual pupillary light reflex.[2, 3] The iris is the colored part of the eye that contains chromatophores that can create varying iris colors based on age, gender, and species of the parrot.[1–3]

Unlike the mammalian counterpart, the avian retina is devoid of blood vessels, which decreases scattering of light and shadows.[5] The pecten is a unique vascular structure found only in the avian eye in association with the retina. The function of the pecten is likely to provide nutrition to the eye, as retinal vessels are lacking.[1, 5, 7]

Parrots often turn their head or body sideways when presented with a new toy or object. Behavioral studies in many birds have shown that they prefer the use of a lateral and monocular field to observe distant objects.[5, 8–12] Based on monocular data in pigeons, visual resolution is higher in the lateral field than frontal field, thus explaining this preference.[5, 13]

The lens of the avian eye is softer than that of mammalian species.[1] Unlike the yellow-tinted mammalian lens that filters out wavelengths of light below 400 nm, the clear avian lens transmits wavelengths below 400 nm.[1] Colored oil droplets on the ends of the cones provide protection against the effects of ultraviolet (UV) light.[5, 14] Birds are able to see UV light below 400 nm due to the combined effects of cone oil droplets and visual pigments.[4, 5, 15] While trichromatic color vision in humans is based on three colors (blue, green, and red), the tetrachromatic, or pentachromatic in some avian species, system of birds includes UV, fluorescent, blue, green, and red.[4, 16–24] UV perception of parrots likely plays an important role in behavior. Many parrots' feathers reflect UV and studies have shown that UV reflection of feathers affects mate choice (see Plates 1 and 2 in color section).[4, 16, 25–29] While some parrots are not visibly sexually dimorphic to the human eye, UV reflection from plumage and skin varies between sexes of some birds.[4] Some types of fruits and berries, such as kaki, green grapes, and figs, reflect UV light and ripeness of the food may be determined by this characteristic.[4, 30] Certain flower patterns, insects, and urine and feces of rodents also reflect UV light that can be detected by birds.[4, 30–32] Additionally, highly UV-reflective areas within the oral cavity play an important role in triggering reflexes to feed young birds that demonstrate their oral cavity to their parents. Birds may use UV receptors in combination with color receptors for navigation by detecting sun-based color gradients.[33–35] Fluorescence, which occurs when short wavelength light is absorbed and re-emitted at a longer wavelength, occurs on parrot feathers and may be an important avian signaller.[25, 36]

Birds are able to detect a spatial frequency of around 160 frames/second or hertz (Hz), compared to 50–60 Hz in humans.[37–39] Because most artificial lights produce noncontinuous light at a frequency of around 100–120 Hz, a stroboscopic effect not detectable to humans results and may be detrimental to birds.[4, 39–41] In addition, artificial lights and sunlight passing through windows do not provide full-spectrum light. While studies are currently under way to examine the effects of artificial lights on birds, current recommendations have been made to provide full-spectrum light and high frequency sources that emit continuous light.[37] Suggestions have also been made to consider light source and presence of full-spectrum light when performing ethological studies.[17, 37, 42, 43] Because video or computer monitors have refresh rates of around 50–95 Hz, welfare issues may arise when performing video playback experiments in birds.[39, 44–46]

Familiarity with the unique anatomic and physiologic variations of the avian eye compared to that of mammals is important when assessing behavior alterations in parrots. Behavior changes, such as reluctance to fly or step onto an extended hand, abnormal head posture, inappetence, and others, can certainly result from ocular abnormalities. In addition, permanent ocular problems, such as blindness resulting from cataract formation, are a common occurrence in parrots and can be managed in such a way as to maintain quality of life. Provision of full-spectrum lighting, normal light cycles, and continuous-emitting light sources should be considered when addressing behavioral problems in birds.

HEARING

Birds rely on their hearing ability for detecting predators and prey, orienting in the environment, and communicating with conspecifics. The songs and calls produced by birds are among the most complex auditory signals known,[47] and this complexity has generated much interest in how birds hear sounds.[48] In the case of parrots, many of these vocalizations appear to be learned through experience,[49] which has led to further interest in the connections between perception, learning, and vocal production.

The anatomy of the avian ear presents some marked contrasts to the more familiar mammalian ear. These differences include the absence of an external ear; a single middle ear bone, the columella, in place of the three bones found in mammals; and the much shorter sensory auditory epithelium in the inner ear. In Budgerigars, for instance, the sensory surface of the inner ear, the basilar papilla, is about 3–4 mm in length (compared to around 30 mm in humans). The columellar middle ear and the short auditory sensory epithelium in birds probably both exert limitations on the range of hearing in birds compared to mammals.[50] Another interesting difference between birds and mammals is in the organization of sensory hair cells on the auditory epithelium. Mammals typically have one row of inner hair cells and three rows of outer hair cells across the width of the auditory epithelium, while birds show more rows of hair cells and considerable variation in the structure and orientation of these hair cells.[51] The functional consequence of these differences remains obscure. But, in striking contrast to mammalian hair cells, avian hair cells are known to be capable of regenerating after damage caused by exposure to excessive noise or ototoxic drugs.[52, 53] Here the functional consequences are enormous. Birds regain their hearing when their hair cells regenerate. Many forms of human deafness are related to defects in or loss of hair cell function,[54] and thus the discovery of hair cell regeneration in birds has spurred a renewed interest in avian ear anatomy.

The anatomical complexity of the bird ear is not fully understood and has led to much interest in how well birds are able to detect, discriminate, and learn complex sounds. We are fortunate to know a great deal about the hearing in one parrot species, the Budgerigar, because of its small size and tractability in the laboratory for behavioral studies of hearing. Less is known of the hearing abilities in other parrot species, but what is known suggests that many abilities of the Budgerigar are shared across species. The behavioral methods used for studying hearing involve operant conditioning or training the bird to respond to a sound—or the change in a sound—by pecking a switch in order to obtain food.[55] These methods have been highly successful and have been used in a wide range of studies examining how parrots and other birds detect sounds, discriminate among similar sounds, and classify sounds into perceptual categories.

One of the most basic measures of hearing abilities is the audiogram. The audiogram is a plot of the least detectable amount of sound energy a bird can hear in the quiet at different frequencies over its range of hearing. Figure 4.1 shows audiograms for three parrots—the Budgerigar, the Cockatiel, and the Orange-fronted Conure. These audiograms show that these parrots, like many bird species, hear best at frequencies between about 1 and 5 kHz and less well at frequencies below about 500 Hz and above 10 kHz. The lowest threshold approaches 0 dB in the Budgerigar, 5 dB in the Cockatiel, and 20 dB in the Orange-fronted Conure.[56, 57]

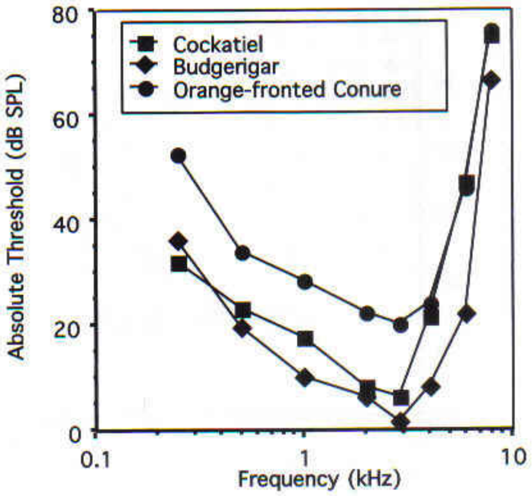

Figure 4.1. Hearing thresholds under quiet conditions for three species of parrot. Figure redrawn from Wright et al. (2003).

In all three species these lowest thresholds in the quiet occur at frequencies between 2 and 4 kHz. This is also the frequency range in which most of the acoustic energy is found in their most common type of vocalizations, the contact call.[57, 58] Contact calls are probably designed for distance communication under more noisy conditions than found in the laboratory. Interestingly, when hearing thresholds are measured in the presence of a masking noise, Budgerigars, Cockatiels, and Orange-fronted Conures also show the best signal-to-noise ratios in this same frequency region. These signal-to-noise ratios (called critical ratios) are shown in Figure 4.2. These critical ratio functions show the level (in decibels) above the background noise that a sound must be in order to be heard. Most birds show a pattern like the Cockatiel; that is, critical ratios increase monotonically at roughly 3 dB for every octave increase in frequency. The Budgerigar and Orange-fronted Conure, by contrast, show a 5–10 dB increase in sensitivity between 2 and 4 kHz relative to the typical avian critical

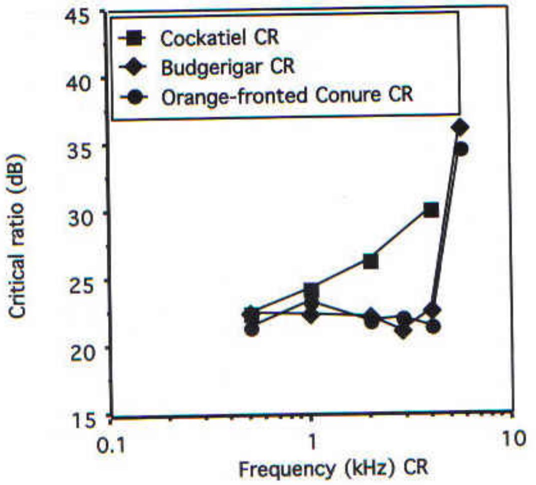

Figure 4.2. Hearing thresholds under noisy conditions for three species of parrot. Thresholds are given as the critical ratio between signal level and the masking noise at the threshold of detection. Figure redrawn from Wright et al. (2003).

ratio function.[56, 57] While the function of this increased sensitivity in these species is uncertain, it is intriguing to note that it corresponds well to the frequency range of maximum energy in their contact calls and may help in discriminating among different calls within large noisy flocks.

Birds in general, with the exception of nocturnal predators such as the Barn Owl, are not very good at localizing sound. Because of their small heads and closely spaced ears, the time difference or intensity difference between sounds arriving at the two ears of a bird is negligible. One parrot, the Budgerigar, has been tested in the laboratory and minimum audible angles are in the range of 22–52 degrees for pure tones and 24 degrees for broadband sounds such as noises and vocalizations.[59]

Hearing is much more than the detection or localization of sounds. In order to communicate, an animal also must be able to discriminate among different sounds with potentially very different meanings. The complex temporal and frequency structure of many bird vocalizations has long prompted suspicions that birds may have particularly good abilities to detect small differences in frequency, amplitude, and temporal characteristics of sound. In some cases this prediction is borne out, while in other areas the abilities of birds are very similar to those of mammals and other terrestrial animals. For example, studies of frequency discrimination in the Budgerigar and the Orange-fronted Conure have shown that, like most birds, they are able to discriminate among tones that differ by about 1% of their frequency.[57, 60] This threshold is roughly in the range of humans and other animals that have been tested. In contrast, these parrots are worse than humans at discriminating differences in the intensity of two tones; humans can discriminate a 1 dB difference in the intensity of pure tones, while birds, including Budgerigars and Orange-fronted Conures, typically require a difference of 2–5 dB.[57, 61] One can imagine that in discriminating vocalizations in the real world, frequency cues might be far more reliable than intensity cues due to degradation of signals during transmission through the environment, so perhaps this is one reason that intensity discrimination abilities are less well developed.

The detection abilities measured using pure tone stimuli may not be perfect predictors of the ability of parrots to distinguish among complex species-specific calls. Several studies have examined the ability of parrots to discriminate among and classify their contact calls. One study compared the abilities of Budgerigars and Zebra Finches to detect the presence of contact calls in a noisy background, and compared these threshold levels to those found when birds were asked to discriminate among the same calls in the presence of noise.[62] Thresholds were 2–5 dB lower for detection than for discrimination among the same calls, suggesting that discrimination is a more difficult task requiring more of the information in the calls to be clearly perceived.

A second study compared the ability of Budgerigars, Zebra Finches, and Canaries to discriminate among a set of stimuli including four contact calls from each species.[63] All three species had more difficulty discriminating between calls from the same species than between calls from different species. Furthermore, all three species could discriminate more easily between calls from their own species than between two calls from a different species. These results suggest that discrimination is more difficult when calls are acoustically more similar (i.e., from the same species) but that different species may have special hearing abilities that aid in the perception of their own calls. Such specializations may arise either through innate differences in auditory capabilities or through learned preferences developed through selective exposure to conspecific sounds as nestlings or fledglings.

A third study examined the ability of the Orange-fronted Conure to form perceptual categories for different individuals based on the acoustic properties of their calls (T. Wright, K. Cortopassi, J. Bradbury, and R. Dooling, unpublished data). Subjects listened to a repeating background of ten calls from a single individual interspersed with calls from different individuals. Subjects quickly learned to avoid responding to the differences between different renditions of the contact call by a single individual and to respond to the differences among calls of different individuals. Their ability to learn this distinction rapidly suggests that they are able to form perceptual categories for the calls of different individuals that allow them to focus on those acoustic features that reliably differ between different individuals. Such perceptual abilities may be critical for acoustic recognition of a variety of social levels in parrots, including individuals, pairs, flocks, roosts, and geographic regions.

TASTE AND SMELL

Taste buds lie on the tongue base in most of the avian species studied such as the chicken, pigeon, swift, raptor, and songbird.[1, 64, 65] In parrots, taste buds are found along the choanal opening on the roof of the oropharynx in association with salivary glands.[1, 65] Compared to mammals, birds have a poor sense of taste; while humans have around 9,000 taste buds, parrots are estimated to have 300–400.[66, 67] Parrots have a higher number of taste buds than most other avian species, such as the chicken with 250–350 and the pigeon with only 37–75.[64, 66, 67] Despite the low number of taste buds found in birds, many studies have shown that flavors can affect food choice and quantity consumed.[66, 68–76] While it has been stated that most birds easily detect salts and acids but sweet substances are not effective stimuli, the response to different flavors varies widely among birds.[1, 76] Some parrots and Budgerigars, as well as other birds, have been shown to prefer sugar solutions over water.[67] Studies in captive Cockatiels examined threshold and preference for water, sodium chloride, potassium chloride, sucrose, glucose, fructose, sodium phosphate buffer, and citric acid buffer solutions.[66, 76] In the Cockatiel studies, all tested compounds added to the water resulted in decreased consumption of the test solution and increased consumption of pure water. No test compound was preferred by the Cockatiels.[66, 76] While future study is needed to determine the significance of taste preference in parrots, there is no question that taste plays a role in food acceptance and avoidance.

The receptors of the nasal cavity that detect odor are generally located on the caudal nasal conchae.[1] Receptor nerve fibers run from the conchae olfactory epithelium to an area within the brain called the olfactory bulb, which is relatively small in the parrot compared to other avian species.[1] Interestingly, the avian orders with relatively small olfactory bulbs have high olfactory thresholds.[77, 78] Compared to mammals such as man, dogs, and rats, birds have proven to have comparable olfactory capacities in conditioning studies.[77, 79–83] Although research into psittacine olfactory abilities is scarce, various avian species use olfactory cues for food location, orientation and navigation, returning to nest sites, reproduction and parenting, and selection of nest material.[81, 84–89]

TOUCH

There are many types of sensory receptors, including those for touch, heat, and pain, located within the parrot beak and skin that give the bird more information about its environment. The different types of touch receptors, or mechanoreceptors, in birds are Herbst corpuscles, Merkel cell receptors, Grandry corpuscles, and Ruffini endings.[90] Herbst corpuscles, which are vibration-sensitive, are the most numerous skin receptors and are found in the beak, leg, and skin.[90, 91] Because they lie in close association with feather follicles and muscles associated with the follicles, Herbst corpuscles relay feather position in relation to the body. Merkel cells are found mainly in the beak of non-aquatic birds, while Grandry corpuscles are present in aquatic birds; both are numerous in the bill tip organ that is important for food prehension.[90, 91] While Ruffini's corpuscles can be found in joint capsules of birds, Ruffini endings have only been identified in the bill of geese and the beak of the Japanese quail.[90, 92–94] Mechanoreceptors are involved with behavioral responses, including the initiation of a feeding response in baby birds upon beak manipulation and the ability of parrots to manipulate food with their beak and feet.[90] The sensitive mechanoreceptors in the feet of parrots may allow them to feel earthquakes that are undetectable to owners.[90, 95] Disorders of the plumage may be detected by mechanoreceptors and stimulate preening behavior.[90, 96] Flight control and patterns may be regulated by mechanoreceptors detecting vibrations caused by air stream turbulence.[90, 97, 98]

Avian thermoreceptors may be free nerve endings and are present in the skin, especially the beak and tongue.[90, 99] Thermoreceptors in the skin assist with body thermoregulation and those in the beak may be used for regulating incubation temperatures in some birds.[100] Pain receptors, or nociceptors, respond to mechanical and thermal stimuli and are present in the beak and skin.[90, 101, 102] Research indicates that birds respond to pain by either a reflex/escape response or by immobility; these responses may be mediated by different types of pain receptors.[103] In addition, beak amputation studies show that birds may experience chronic pain.[103]

CONCLUSION

Parrots experience the world in ways both similar and different to mammals. It is apparent that vision, hearing and vocalization, taste, olfaction, and touch perception play vital roles in the daily life of the parrot. Many of the normal and abnormal behaviors of parrots can be better understood by examining how birds perceive the environment around them. Further research in the area of sensory perception of parrots will expand our knowledge and likely enable us to improve the lives of these magnificent creatures.

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Andrew U. Luescher, Editor

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Andrew U. Luescher, DVM, PhD, is Director of the Animal Behavior Clinic at Purdue University. He established the Animal Behavior Clinic in 1997 and is certified as an applied animal behaviorist by the Animal Behavior Society and is a diplomate of the American College of Veterinary Behaviorists. He has been treating animals with behavioral problems for more than 20 years.

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