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Sensory and Cognitive Ecology of Bats

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Abstract

We see stunning morphological diversity across the animal world. Less conspicuous but equally fascinating are the sensory and cognitive adaptations that determine animals' interactions with their environments and each other. We discuss the development of the fields of sensory and cognitive ecology and the importance of integrating these fields to understand the evolution of adaptive behaviors. Bats, with their extraordinarily high ecological diversity, are ideal animals for this purpose. An explosion in recent research allows for better understanding of the molecular, genetic, neural, and behavioral bases for sensory ecology and cognition in bats. We give examples of studies that illuminate connections between sensory and cognitive features of information filtering, evolutionary trade-offs in sensory and cognitive processing, and multimodal sensing and integration. By investigating the selective pressures underlying information acquisition, processing, and use in bats, we aim to illuminate patterns and processes driving sensory and cognitive evolution.

1. INTRODUCTION

Nearly three decades ago, Leslie Real (1993) coined a term to describe a nascent field that had begun to gain momentum: cognitive ecology. He recognized a critical gap between researchers who exclusively examined mechanistic processes and those who investigated functional explanations for behavior. It was becoming clear that neither field on its own could explain the diversity of behaviors we see in nature (Real 1993). Interest in the integration of these then-disparate fields was reflected by a growing number of empirical studies and solidified in a foundational book edited by Reuven Dukas, *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making* (1998). Since then, several excellent syntheses have been published (e.g., Dukas & Ratcliffe 2009, Healy & Braithwaite 2000, Ratcliffe & Phelps 2019), as well as numerous experimental studies. At approximately the same time that Real launched the field of cognitive ecology, Dusenbury published *Sensory Ecology* (1992), synthesizing studies of how animals use their senses to acquire and respond to environmental information. Pioneers in sensory ecology included Donald Griffin, who discovered echolocation in bats (Griffin 1958), and Kenneth Roeder, who investigated ultrasonic hearing in insects as a defense against bats (Roeder 1963). An integrative approach developed over time, joining the fields of sensory mechanism and function (e.g., Stevens 2013).

We argue that sensory and cognitive ecology are united fields that gain scientific value when considered together. Both examine how selection by an animal's environment shapes nervous system structure and function. Sensory ecology focuses on the acquisition of information, while cognitive ecology focuses on information processing. An integrative understanding of both processes is key. For example, the sensory structures and cells of an animal's nervous system serve as initial filters, allowing for the perception of a selective subset of the total amount of environmental information available to an individual, thus limiting the information for cognitive processing. Just as sensory features evolve in response to selection and reflect both evolutionary constraints and ecological demands (Dusenbery 1992, Stevens 2013), an individual's cognitive toolkit is shaped by its evolutionary ecology (Dukas 1998). Cognitive processes such as decision-making can influence how animals acquire information through their sensory systems and can select for more specific sensory adaptations. By coupling investigations of the sensory filters and adaptations unique to each animal with the downstream processes of learning, decision-making, and memory, we can more fully understand how ecological pressures can shape the perception of, and responses to, environmental cues and signals.

With over 1,400 species spanning an extraordinary range of ecological and behavioral diversity (see the sidebar titled Bat Diversity), bats are an excellent group for studying the connections

BAT DIVERSITY

The majority of bat species are small mammals that hunt insects in flight using echolocation. Some bat species, however, diverge significantly from these common traits. The family Pteropodidae consists of relatively large, frugivorous species, most of which cannot echolocate. The few pteropodid species that can echolocate produce sounds by tongue clicking (lingual echolocation) or wing clapping, whereas bat species in all of the other bat families call with their vocal cords (laryngeal echolocation). The Phyllostomidae is the most diverse of all bat families, with species that eat fruit, nectar, insects, vertebrates, and blood. Carnivory is known from species in four bat families (**Figure 2**). Many bat species catch prey in flight (aerial hawking), others pick their food off surfaces (gleaning), and some species flexibly do both. Some bats listen to prey-generated sounds to locate prey in vegetation, and at least one bat species uses echolocation for this purpose. Bats in the family Mystacinidae, endemic to New Zealand, crawl on the ground to find prey. Bats in two families hunt by dragging their feet through water (trawling). These are just a few examples of the broad ecological, morphological, and behavioral diversity across bats. between sensory and cognitive ecology. Ideal study systems for these fields should have a wellestablished phylogeny; show high diversity in ecology, behavior, and sensory systems; and include detailed knowledge of the molecular and neural bases for behavior. Bats tick all of these boxes. Major advances in phylogenetics (Teeling et al. 2005) have provided a stable phylogeny for developing and testing hypotheses about the evolution of bat sensory systems (Jones et al. 2013). Bats are ecologically and behaviorally diverse, providing the variation needed to test hypotheses about the evolution of information processing. Bats also possess a wide variety of senses. In addition to the five senses commonly studied in vertebrates, bats can possess less studied sensory capabilities, such as echolocation, magnetoreception, and thermoperception (**Figure 1**). Variation in the capabilities of bats across these sensing systems offers a platform for comparative research.

f Hearing and echolocation



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Figure 1 (Figure appears on preceding page)

In addition to the five senses common across vertebrates (touch, vision, taste, olfaction, and hearing), bats possess less studied sensory capabilities, including echolocation, magnetoreception, and thermoperception, and vary in their capabilities across these sensing systems. Bat sensory systems reflect trade-offs, with matched filters allowing only ecologically relevant sensory stimuli entry to the nervous system. (a) Touch is illustrated by a scanning electron microscopy image of a somatosensory hair on the wing surface (Sterbing-D'Angelo et al. 2011). (b) Vision is illustrated by the neurophysiological thresholds for light detection in four bat species. Higher threshold values indicate lower visual sensitivity, with laryngeal echolocators showing poorer visual detection ability than bats with lingual or no echolocation. Note the trend across taxa: Larger eyes correlate with increased visual ability (data from Liu et al. 2015). (c) Bats are able to taste sweet and bitter flavors but not umami. (d) Olfaction is illustrated by diffusible iodine-based contrast-enhanced computed tomography scans of the nasal passages and turbinates (green and yellow structures) of four bat species, with the olfactory epithelium highlighted by yellow dotted lines (Yohe et al. 2018). (e) Thermoperception is illustrated by showing differences in surface temperature on the face of the common vampire bat (Desmodus rotundus), with darker shading indicating cooler skin temperature (Kürten & Schmidt 1982). (f) Hearing is illustrated by the auditory threshold curves for four bat species (data from Heffner et al. 2013, Koay et al. 1997, Long & Schnitzler 1975, Schmidt et al. 1984). Photographs in panels b and f provided by M. Tuttle (copyright MerlinTuttle.org). Panel e reproduced with permission from Kürten & Schmidt (1982). Panel f adapted with permission from Heffner et al. (2013), Koay et al. (1997), and Long & Schnitzler (1975). Abbreviations: HDC, high duty cycle; LDC, low duty cycle; SPL, sound pressure level.

Critically, a rapid increase in research across bat species has improved our understanding of the molecular, genetic, neural, and behavioral bases for sensory ecology and cognition.

Past reviews have covered advances in understanding bat sensory systems (Altringham & Fenton 2003), the molecular basis of bat sensory biology (Jones et al. 2013), comparative neuroanatomy (Dechmann & Safi 2009), and the sensory and cognitive ecology of specific subgroups [e.g., Phyllostomidae (Thiagavel et al. 2020)] or subdisciplines [e.g., social learning (Wright 2016)]. Our review examines the properties that emerge when integrating sensory and cognitive ecology studies for bats as a whole. Our synthesis is not intended to be an exhaustive summary of the literature but rather an exposition of three ways in which bats inform our understanding of the links between sensory and cognitive ecology. First, we describe evidence for and functions of sensory matched filters in bats. Sensory matched filters refer to the matching of an animal's sensory system sensitivity to the specific range of the sensory modality that has the greatest relevance to an animal's fitness, such as the sound frequency of a species' mating call or the color of a profitable food item. Sensory matched filters help animals detect signals and cues of interest by filtering out the enormous amounts of information associated with environmental features that do not significantly affect an animal's fitness (von der Emde & Warrant 2015). Second, we examine sensory and cognitive trade-offs. Evolutionary trade-offs occur in response to resource limitations, with selection for increased investment in certain traits resulting in fewer resources available for other traits. Third, we consider how bats integrate information across multiple sensory modalities. Past research has provided valuable understanding about the functions of individual sensory systems, but more recent research has provided fascinating insights into how information from multiple sensory systems is processed in the brain. By investigating one taxonomic group in detail, we aim to illuminate broadscale patterns and processes, helping us better understand sensory and cognitive evolution across the animal world.

2. SENSORY MATCHED FILTERS

Animals gain information about their environment through their sensory systems. Sensory structures, neurons, and circuits, however, encode information about only a subset of the wide array of potential cues and signals in their environments, such as certain frequencies of sound or certain wavelengths of light. Sensory systems are typically tuned to detect only the aspects of the environment that are most important to an animal's fitness, thus serving as sensory matched filters

filter: a match between the tuning of an animal's sensory system and the sensory stimuli most important for that animal's fitness Trade-off: a negative

Sensory matched

Trade-off: a negative relationship between two traits over evolutionary time driven by resource limitation and relative fitness costs and benefits (von der Emde & Warrant 2015). This simple adaptation—manifest in diverse ways across taxa and sensory modalities—addresses two selective pressures at once. First, sensory filters specifically matched to ecologically important stimuli improve detection and processing by reducing the amount of extraneous stimuli entering the nervous system. For example, echolocating bats are sensitive to the ultrasonic frequencies of sound used for echolocation, whereas humans, who do not communicate in the ultrasound or have predators or prey that produce ultrasound, cannot hear these frequencies. Second, by allowing only a small subset of available stimuli entry, sensory filters reduce the expensive neural tissue required for information acquisition and processing, decreasing energetic costs (Niven & Laughlin 2008, von der Emde & Warrant 2015). How sensory filters are matched to ecologically relevant information is a cornerstone of sensory ecology. Here, we review sensory matched filters in bats for echolocation, hearing, taste, and olfaction.

2.1. Echolocation as a Sensory Matched Filter

Echolocation was a key adaptation that allowed bats to orient and forage in darkness. To echolocate, bats emit sounds and gain information about target location, shape, and movement from the temporal and spectral properties of the returning echoes (Griffin 1958, reviewed in Moss & Surlykke 2010). The acoustic properties of echolocation calls vary across bat species, with the type of sound produced affecting the information received in echoes. These differences in echolocation call properties are adapted to the specific demands of a species' ecological niche (Denzinger et al. 2018, Schnitzler & Kalko 2001). Unlike passive sensing systems, in which stimulus reception is the focus of study, investigations into the sensory ecology of active sensing systems such as echolocation must consider how both signal production and reception contribute to adaptive sensory filters (Moss & Surlykke 2010).

Our understanding of the evolution of echolocation illustrates the benefits of bats as a model system in sensory and cognitive ecology. Most bat species echolocate by producing sounds with their vocal cords (i.e., laryngeal echolocation). Only one family of bats, the Pteropodidae, is incapable of this form of echolocation. This, combined with anatomical traits related to body size and the visual system, led taxonomists to believe that this family evolved independently of other bat lineages (Simmons & Geisler 1998). However, recent genetic research supports the current consensus that bats indeed form a monophyletic group (Teeling et al. 2005) (**Figure 2**). In addition, the family Pteropodidae falls within the suborder Yinpterochiroptera and is more closely related to the echolocating superfamily Rhinolophoidea than echolocating families in the suborder Yangochiroptera (Teeling et al. 2005). This evidence suggests that the ancestor of all bats used laryngeal echolocation, but that echolocation was lost in the ancestor of the Pteropodidae (Teeling et al. 2005). Fascinatingly, several species in the Pteropodidae can echolocate in a very different way than other bat species, using tongue clicking (lingual echolocation) (Yovel et al. 2010) or wing clapping (Boonman et al. 2014), indicating that echolocation re-evolved in this group in a different form from other bats.

Echolocation strategies can be divided into two main categories, low duty cycle (LDC) echolocation and high duty cycle (HDC) echolocation (summarized in **Supplemental Appendix**, reviewed by Fenton et al. 2012). Species that are LDC echolocators produce short calls at long intervals and listen for echoes between calls. Species that are HDC echolocators can hear echoes at the same time as calling by using Doppler-shift compensation and a unique hearing specialization to separate call and echo in frequency. Many LDC bat species produce calls that sweep from higher to lower frequencies, but the extent of the frequency modulation varies enormously from narrowband calls that sweep only a few kilohertz to broadband calls sweeping 50 kHz or more. Open space aerial-hunting bats emit long, low-frequency, narrowband calls, which are effective over long distances but provide poor information about exact positions and shapes of objects. **Ultrasound:** sound waves above the frequency range of human hearing, typically defined as frequencies above 20 kHz

Passive sensing:

gaining information about the environment without emitting a probing signal, typical of most sensory systems

Active sensing:

gaining information about the environment by emitting a probing signal and detecting its interaction with the environment

Laryngeal

echolocation: the use of the vocal cords to produce sounds for echolocation

Lingual

echolocation: the use of tongue clicking to produce sounds for echolocation

Low duty cycle (LDC) echolocation:

the production of short echolocation calls with echoes detected during the long intervals between calls

High duty cycle (HDC) echolocation:

the production of long echolocation calls with call emission and echo detection occurring simultaneously



Figure 2

Phylogeny, diet, foraging mode, and sensory and cognitive abilities for families of the order Chiroptera. Foraging modes are classified into four broad categories: aerial hawking airborne insects in flight (hawk), extensive walking on the ground to capture food (ground), gleaning food from surfaces in flight (glean), and trawling food from the water surface (trawl). For an explanation of LDC and HDC echolocation in bats, see **Supplemental Appendix**. Bats in the family Pteropodidae either do not echolocate at all or use a rudimentary form of echolocation, using wing claps or tongue clicks as opposed to the laryngeal echolocation found in the rest of the order Chiroptera (indicated by the crossed circle). Bats that have retained their short-wavelength opsin (SWS1) have dichromatic vision and can see color; those that have lost SWS1 function have monochromatic vision and are color-blind. Families with dots in both categories contain both monochromatic and dichromatic species. Eavesdropping on the echolocation calls of other bats is a behavioral strategy found irrespective of diet, foraging mode, echolocation type, or visual sensitivity. The limited distribution of this behavior across the phylogeny likely represents sampling bias, underlying the need for behavioral studies of underrepresented groups (see also **Supplemental Table 1**). Abbreviations: HDC, high duty cycle; LDC, low duty cycle. Figure design by D. Kyllo.

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Information about target position in the vertical and horizontal domains is enhanced by comparing spectral differences between the call and echo at each ear, making broadband calls more informative about precise positions than narrowband calls. Species that forage in habitats with many obstacles, such as forests, typically have short, higher frequency, broadband and lower intensity echolocation calls that allow them to gain detailed information about locations of targets and obstacles, at the cost of reduced range.

In addition to the acoustic properties of echolocation calls, auditory sensitivity and tuning contribute to sensory filters. Audiograms (hearing threshold curves) demonstrate how bat hearing is adapted to preferentially detect sounds of greatest importance for each bat species, specifically the particular sound frequencies used for echolocation and acoustic communication within each species (**Figure 1**) (Lattenkamp et al. 2021). In many species, there is an additional range of sensitivity to frequencies lower than those used for echolocation. Such low-frequency hearing may have evolved to allow bats to hear pup isolation calls, the sounds that young bats produce before they are capable of flight that allow mothers to find their offspring in the roost (Bohn et al. 2006, Lattenkamp et al. 2021). Bats that hunt by attending to prey-emitted sounds are also sensitive to the lower-frequency sounds produced by their prey (Geipel et al. 2021, Page & Bernal 2020) (see Section 2.2).

The most specialized matched filter for echolocation is seen in HDC bats (Fenton et al. 2012). HDC bats can both glean (take prey off surfaces) and catch flying insects very close to vegetation. Whereas LDC bats are sensitive to the wide range of ultrasonic frequencies that they use for echolocation, HDC bats show good hearing in the low ultrasonic range but become less sensitive at higher ultrasonic frequencies, except for a very small range of frequencies to which they are very sensitive (**Figure 1**). HDC bats emit echolocation calls at slightly lower frequencies (to which they are insensitive) such that they receive Doppler-shifted echoes at the higher frequency to which they are most sensitive when approaching their target in flight. Therefore, unlike LDC bats, HDC bats can perceive prey even when their calls and echoes overlap in time (**Supplemental Appendix**).

2.2. Auditory Filters for Environmental Sounds

In addition to listening for the echoes of their echolocation calls, bats use hearing to detect environmental cues, including sounds from other bats and prey. Echolocation-as an active senseprovides public information perceptible to other hunters and prey. As a bat attacks its prey in flight, it produces a feeding buzz by drastically decreasing the time between successive calls to obtain precise information on its prey's location (Griffin 1958). Feeding buzzes can indicate food availability, attracting eavesdropping con- and heterospecifics (Fenton 2003). Eavesdropping on the echolocation calls of others is a widespread strategy in bats, especially among aerial insectivores that capture prey in flight in dense, ephemeral prey patches like insect swarms. Not all bats, however, are attracted to echolocation calls (e.g., Jonker et al. 2010; reviewed in Gager 2019). Among bats known to eavesdrop on the echolocation calls of others, attention seems to be selective; individuals are differentially attracted to the calls of species that share an ecological niche or have calls that are acoustically similar to their own (Dorado-Correa et al. 2013, Hügel et al. 2017) (Supplemental Table 1). Because acoustic and ecological similarity are often confounded, it is difficult to know whether differential attraction is due to sensory filters, making similar-sounding bats more conspicuous, or to higher-level processing such as learning and memory, allowing bats to exploit the most relevant types of public information. Recent experiments suggest that bats integrate multiple streams of information when eavesdropping on echolocation calls, weighing the costs and benefits associated with approaching foraging con- and heterospecifics (Lewanzik et al. 2019).

Feeding buzz: a series of rapidly repeated short echolocation calls produced during the final stage of a hunting attack

Echolocation also provides information to potential prey. Many insects have ultrasoundsensitive ears and perform evasive flight when they detect bat calls (ter Hofstede & Ratcliffe 2016). Some eared moths talk back to bats when they detect echolocation calls (reviewed in Conner & Corcoran 2012). The mechanism by which this behavior defends moths depends on the signal's duty cycle (proportion of time during a signal that contains sound). In response to bat calls, some moths produce almost-continuous broadband, ultrasonic clicks that overlap with the frequencies of bat echolocation calls and are in the bats' range of greatest auditory sensitivity, jamming the echolocation of the approaching bat (Conner & Corcoran 2012). Many chemically defended moths also produce ultrasonic clicks in response to bat calls but at a lower rate. These sounds act as acoustic aposematic signals, warning the bat of the moth's toxicity (e.g., Barber et al. 2009). In addition to producing sound frequencies that tap into the bats' sensory biases, moths time these clicks to the approach phase of the bat attack, making them a more salient cue (Ratcliffe & Fullard 2005). Although low click rates might not jam bat echolocation, the sounds could be startling or distracting and thus more easily associated with noxious prey (Ratcliffe & Fullard 2005). Therefore, in addition to exploiting bat sensory biases, moths are likely exploiting cognitive biases as well.

Most bats have poor low-frequency hearing (1–10 kHz) (Lattenkamp et al. 2021). Bat echolocation and communication calls are typically high frequency, and to our knowledge, predators of bats do not produce low-frequency acoustic cues predictive of an attack. Therefore, insensitivity to low-frequency sounds filters out low-frequency sounds that are not relevant to a bat's survival or reproduction. Exceptions are found in bats that listen for low-frequency prey-generated sounds, such as rustling noises or mating calls. These bat species typically have better low-frequency hearing than other bat species (Geipel et al. 2021, Page & Bernal 2020) (**Figure 1**). The most extreme example is the vampire bat, which is sensitive to frequencies as low as 1 kHz and uses this sensitivity for detecting the breathing sounds of mammalian prey (Gröger & Wiegrebe 2006, Heffner et al. 2013).

2.3. Sensory Filters in Taste Reception

The examples of acoustic sensory filters described in Sections 2.1 and 2.2 above likely arose due to positive selection on advantageous changes in these traits, resulting in both increased sensitivity to cues of interest and reduced sensitivity to cues that might interfere with detecting cues of interest. Alternatively, sensory sensitivity or function can be lost over evolutionary time due to relaxed selection (Niven & Laughlin 2008). The loss of gene function due to relaxed selection can be a neutral change when there is no net benefit or cost or it can be favorable if it provides energetic savings by reducing neural activity for detecting and processing information that provides no fitness benefits. Genetic studies on bitter, sweet, and umami taste reception in bats demonstrate both positive and relaxed selection on different taste genes, resulting in different sensory filters for taste perception depending on the ecology of the species (Jones et al. 2013).

Bitter taste receptors inform animals about potentially toxic food. Most mammal species have multiple taste receptor genes for encoding the sensation of bitter because many plants and animals produce or sequester a variety of toxic compounds for defense. For example, unripe fruits often contain bitter compounds to deter consumption by frugivores (Schaefer et al. 2003). Many insects sequester toxic plant compounds, rendering themselves distasteful to animals, including bats (Hristov & Conner 2005). Even carnivores can benefit from bitter taste reception: the fringe-lipped bat (*Trachops cirrhosus*) uses gustatory cues to reject prey coated with poisonous toad secretions (Page et al. 2012). The number of functional bitter taste receptor genes varies across mammals and bat species (Jiao et al. 2018, Liu et al. 2016), likely reflecting dietary variation. The insectivorous genus *Myotis*, for example, experienced positive selection for bitter genes and

has many more functional bitter receptor genes than other groups of insectivorous bats, perhaps contributing to its high diversity and worldwide distribution (Jiao et al. 2018).

Sweet and umami each have a single but different gene responsible for taste reception. The *TAS1R2* gene, which is specific to the sweet taste receptor, is functional and under purifying selection in both frugivorous and insectivorous bats (Zhao et al. 2010). Surprisingly, a functional *TAS1R1* gene, which is specific to umami, was not found in any of 31 bat species tested across the phylogeny, suggesting a possible complete loss of this taste sensation in bats (Zhao et al. 2012). Most carnivores have umami taste receptors (Sato & Wolsan 2012), reflecting its importance in detecting protein, and one might expect this would be important for insectivorous animals as well. Certain amino acids and proteins, however, can also activate sweet taste receptors, so the loss of umami receptors in bats possibly maintained selection for sweet receptors to detect the protein composition of insects.

More study is needed to understand the relationship between diet and sensory filters in taste reception, but work with vampire bats (*Desmodus rotundus*) suggests how dietary specialization can affect this sense. Vampire bats feed exclusively on blood, which varies little in composition and palatability between animals. In addition to lacking the umami taste gene, vampire bats lack a functional sweet receptor gene and have a significantly reduced number of functional bitter genes (Jiao et al. 2018; Zhao et al. 2010, 2012). Vampire bats also show cognitive limitations for this sense. Conditioned taste aversion is the learned association of a taste with illness and subsequent avoidance of food with that flavor. It is a widespread phenomenon and likely evolved in response to strong selective pressure to avoid the consumption of poisonous foods. Of all taxa in the animal kingdom tested to date (including the frugivorous bats *Artibeus jamaicensis* and *Bracbyphylla cavernarum* and the insectivorous bat *Eptesicus fuscus*), the vampire bat is the only species that does not show conditioned taste aversion (Ratcliffe et al. 2003). Together, sensory and cognitive shifts in vampire bats may reflect relaxed selection for toxin detection, given their unusual obligate blood diet.

2.4. Sensory Filters in Olfaction

Olfaction plays a significant role in the social lives of bats, including sexual signaling, colony cohesion, and mother–pup recognition (Chaverri et al. 2018). In addition, plant-eating bats use olfaction for foraging (Rieger & Jakob 1988). Scents are perceived when odorant molecules bind to olfactory receptors on the membranes of receptor cells in the nasal passages, triggering neural signaling to the olfactory lobe in the brain. The perception of a specific scent depends on the activation of a particular combination of olfactory receptors. Therefore, the number of different functional olfactory receptor genes influences olfactory discrimination ability and provides the basis for olfactory sensory filters. Studies on the specific olfactory receptor gene repertoires across bats show that that frugivorous bats from the Phyllostomidae and Pteropodidae families have distinct olfactory receptor gene repertoires compared to their nonfrugivorous relatives (Hayden et al. 2014). Since frugivorous species use olfaction while foraging, whereas insectivorous bats apparently do not, these studies suggest convergent evolution on olfactory receptor genes for frugivory.

In addition to using olfaction to locate food, frugivorous bats can learn about food sources from olfactory cues on roostmates, making communal roosts potential information centers for new food sources (Ward & Zahavi 1973). This may be particularly advantageous when food sources, such as asynchronously fruiting trees, are unpredictable and widely distributed. Studies show that after interacting with demonstrator bats in the roost, naive bats indeed prefer flavors of foods these individuals had consumed outside the roost (Ramakers et al. 2016, Ratcliffe & ter Hofstede 2005). Further, bats can discern whether a returning individual ingested a particular food item or merely contacted it and preferentially select foods that roostmates ingested (O'Mara et al. 2014). The

coupling of a food odor with carbon disulfide, a digestive product excreted through the lungs and detected on an animal's breath, likely allows bats to make this distinction. This pathway has been well studied in rats, which learn novel food cues when carbon disulfide on a demonstrator's breath binds to specific receptors in the olfactory bulb; individuals that lack this pathway do not acquire socially transmitted food preferences (Munger et al. 2010).

2.5. Summary

Bats beautifully illustrate how ecological niches shape sensory systems, with diverse examples of matched filters for relevant sensory inputs and corresponding differences in cognitive processing. A long history of studies shows strong relationships between the acoustic properties of echolocation calls and habitat use in bats (reviewed in Denzinger et al. 2018). In addition, the enormous variation in diet and foraging strategies make bats an excellent system for understanding how foraging ecology influences sensory filters in bats. Examples include sensitivity to low-frequency sounds in bats that eavesdrop on prey signals (Geipel et al. 2021); convergent evolution on olfactory gene families in frugivorous bats (Hayden et al. 2014); and the loss of function of olfactory and taste receptor genes in dietary specialists (e.g., Jiao et al. 2018, Simões et al. 2019), including the loss of conditioned taste aversion in vampire bats (Ratcliffe et al. 2003).

3. SENSORY AND COGNITIVE TRADE-OFFS

Evolutionary trade-offs occur when increased investment in one trait results in reduced investment in other traits (Garland 2014). Nervous system tissue is particularly energetically costly compared to other body tissues (Niven & Laughlin 2008), and thus, limitations on energy acquisition in animals can result in trade-offs in the investment in different nervous system components. A negative relationship between two traits is typically used as a first test for a trade-off between these traits, but on its own, it is not sufficient evidence. Phylogenetic comparative analyses and experiments can provide stronger support for evolutionary trade-offs. In the next two sections, we describe how trade-offs between investment in different sensory systems or brain regions have been studied in bats.

3.1. Trade-offs Between Sensory Systems

A large energetic investment in one sensory system during development leaves less energy available for the development and maintenance of other senses. Tests for trade-offs between sensory systems have focused on those that have overlapping functions, since the improvement in one sense can compensate for the reduced functionality of the other. For example, bats use both vision and echolocation for orientation, suggesting that selection might favor reduced investment in one if reliance on the other increases. Tests for trade-offs in bats between these senses typically compare data about visual systems from bats that do not echolocate, bats that use LDC echolocation, and bats that use HDC echolocation. In bats, another sense that is in a possible trade-off with echolocation is olfaction. Olfaction is used by frugivorous bats for finding food, so there is the potential for a trade-off between this sense and echolocation. Studies that compare echolocation strategies and visual system properties support a trade-off between these sensory systems, whereas evidence for a trade-off between olfaction and echolocation is equivocal.

Visual acuity (the ability to resolve detail) increases with absolute eye size, with bat species showing enormous variation in eye size (Veilleux & Kirk 2014). Bats also show tremendous diversity in echolocation call structure, with HDC echolocation considered more effective than LDC

echolocation in dense habitats, as it has the advantage of allowing bats to detect flying insects in echoes that overlap with both their calls and background echoes (**Supplemental Appendix**). Using ancestral-state reconstruction, Thiagavel et al. (2018) inferred that ancestral bats used LDC echolocation and had both relatively and absolutely larger eyes than most bat species today. According to their analyses, the fruit-eating family Pteropodidae lost echolocation and gained larger eyes; the insectivorous family Emballonuridae retained ancestral echolocation call properties and eye size; and other bat groups evolved more derived, and potentially more effective, echolocation strategies and smaller eyes, suggesting a trade-off between echolocation and visual acuity in these animals.

Photoreceptor properties influence visual sensitivity in dim-light conditions. Compared to diurnal mammals, the retinas of nocturnal species have relatively more rod photoreceptors, which are more sensitive to light than cone photoreceptors (Purves et al. 2008). Gutierrez et al. (2018) found that bats retain the highly conserved peak wavelength for rhodopsin typical for terrestrial mammals, likely due to largely consistent ambient-light wavelengths across terrestrial environments and time of day. However, the half-life of a key molecule in the rhodopsin signaling cascade was greater in bats than other mammals, suggesting a visual adaptation for dim light conditions. In addition, the half-lives for bat species suggest a trade-off with echolocation: The half-life was greatest for a nonecholocating pteropodid, medium for an LDC species, and shortest for an HDC species.

Most other vertebrates have better color vision than mammals because they have more opsin genes, each coding for an opsin protein sensitive to different wavelengths of light. From the common amniote ancestor, placental mammals retained only two of the four cone opsin gene families, presumably due to their nocturnal lifestyle (Jacobs 2009). The ancestral placental mammal is inferred to have two cone opsins: one opsin most sensitive to ultraviolet light (SWS1) and one most sensitive to the longest wavelength peak seen in modern mammals (LWS) (Jacobs 2009). In bats, the LWS gene is highly conserved, potentially due to the wavelengths of light that are best reflected by the tapetum lucidum, a layer of reflective material behind the retina that helps improve night vision in nocturnal animals (Simões et al. 2019). The SWS1 gene in bats, however, is highly variable (Simões et al. 2019). While some bat species can see ultraviolet light and have retained the ancestral mammalian opsin complement, others lack a functional short wavelength opsin and are color-blind (Simões et al. 2019 and references therein) (Figure 2). The loss of color vision and evidence of relaxed selection on the LWS gene in the two main HDC bat lineages suggests a trade-off between color vision and the reliance on more derived echolocation (Simões et al. 2019). However, the repeated loss of a functional SWS1 gene in many other species, including some LDC echolocating species and some nonecholocating pteropodid species, corresponds with roosting in dark caves, suggesting an alternative explanation for the loss of ultraviolet sensitivity that is not related to a trade-off with echolocation (Kries et al. 2018, Simões et al. 2019). These two hypotheses are not mutually exclusive, and both cave roosting and reliance on echolocation could contribute to the loss or maintenance of color vision. Additionally, all three vampire bat species have also lost color vision (Kries et al. 2018), suggesting that their reliance on alternative sensory systems for foraging (see Section 4.1) may have reduced their need for color vision. Genetic data for more bat species will improve our understanding of the sensory and ecological factors that influence color vision in bats.

Among bat species, both olfaction and echolocation are used for foraging, with different species relying to different degrees and at different stages of the foraging approach on one sensory modality over the other. Two studies investigating whether a trade-off exists between these sensory systems, using different methods and bat species, came to different conclusions. Using complete proteomes, Tsagkogeorga et al. (2017) found evidence of a contraction of olfactory receptor genes

in ancestral bats and extant insectivorous species, both groups with a heavy reliance on echolocation, suggesting a low reliance on olfaction in these groups. This study also found an expansion of olfactory receptor genes in the family Pteropodidae, frugivorous bats that, with the exception of a single genus, do not echolocate but rely instead on olfaction for foraging. Taken together, these results suggest a trade-off between olfaction and echolocation. This study, however, did not include frugivorous bats from the family Phyllostomidae, which use both olfaction and echolocation for foraging, nor bats from HDC echolocation lineages. Using PCR amplification of olfactory receptor genes and including frugivorous phyllostomids and insectivorous HDC echolocating bats, Hayden et al. (2014) did not find evidence for a trade-off between echolocation and olfactory gene repertoire. Olfaction might be so important for social functions in bats that the number of olfactory receptor genes do not show a strong relationship with echolocation ability.

3.2. Trade-offs in Brain Regions and Brain Size

The trade-offs discussed in Section 3.1 above reflect the high cost of neural tissue and corresponding selection for reduced information intake and processing. Nowhere are these trade-offs greater than within the brain itself. Similar to trade-offs between echolocation strategy and eye traits, Thiagavel et al. (2018) found that the largely nonecholocating frugivorous bats of the Pteropodidae family had relatively smaller auditory brain regions than laryngeal echolocating bats. Planteating bats (bats from the Pteropodidae family and some bats from the Phyllostomidae family) have relatively larger visual and olfactory brain structures than insectivorous bats (Thiagavel et al. 2018 and references therein), reflecting their reliance on visual and chemical cues in foraging. Insectivorous bats, in contrast, tend to rely heavily on echolocation, which provides rapid information about targets in flight, and use vision and olfaction to a much lesser degree in foraging, if at all; correspondingly, insectivorous bat species show relatively smaller visual and olfactory brain regions (Thiagavel et al. 2018). Likewise, in comparison to predatory bats, plant-eating bats have a relatively larger hippocampus, a brain region involved in spatial memory, perhaps aiding in foraging-related memory tasks, such as remembering the location of fruiting or flowering trees (Thiagavel et al. 2018). Habitat complexity may also shape different brain centers in bats. Bats with large wing areas inhabit dense forests and fly slowly but maneuver well; bats with small wing areas fly fast in open space but show poor agility (Norberg & Rayner 1987). Safi & Dechmann (2005) used wing area as a proxy for the complexity of a bat's habitat, and thus the associated sensory and cognitive demands this habitat requires. Controlling for phylogeny and body size, they found that bats occupying more complex environments have larger inferior colliculi, the largest subcortical auditory center, perhaps reflecting greater demands on acoustic processing when foraging in dense, cluttered conditions.

Comparison of whole brains found that plant-eating species exhibit relatively larger brains than animal-eating ones (Eisenberg & Wilson 1978, Pirlot & Stephan 1970). Researchers have argued that plant-eating bats face greater sensory challenges in finding food. While insect eaters often echolocate flying prey in open space, avoiding the sensory challenge of distinguishing overlapping echoes from prey and clutter, plant eaters navigate cluttered habitats and locate food in vegetation, often using multiple sensory modalities to do so. In addition, they must track temporal and spatial variation in food resources, pressures that researchers argue have selected for larger brains in these species (Jones & MacLarnon 2004, Safi & Dechmann 2005). Ancestral-state reconstruction (Safi et al. 2005) and fossil evidence (Simmons & Geisler 1998) suggest that ancestral bats were of average body mass, wing span, and brain size. Brain size has since diverged under apparently bidirectional selection, with relatively larger brain sizes in bats with high wing areas and smaller brains in bats with lower wing areas (Safi et al. 2005, but see Yao et al. 2012). Brain size might have decreased in fast, open-space flyers to reduce weight and energetic costs, factors advantageous for flight. Consistent with this hypothesis, migratory bats have relatively smaller brains than nonmigratory ones (McGuire & Ratcliffe 2011), a pattern also found in birds (Sol et al. 2005). Given that habitat complexity appears to explain increases in certain brain regions (Safi & Dechmann 2005), the broad dietary patterns observed in early comparative studies of bat brain size (Eisenberg & Wilson 1978) might reflect the cognitive, energetic, and sensory demands associated with flight in complex habitats. Similarly, Ratcliffe et al. (2006) found that the bat species that were most behaviorally flexible in foraging (those that could capture prey by both aerial hawking and gleaning) had larger relative brain sizes than those that only aerially hawk flying prey in open spaces.

While comparative neuroanatomy studies provide insight into potential ecological drivers of whole-brain and brain region size, most studies are correlational, and therefore, the results can be highly dependent on the variables included in the statistical analyses (reviewed in Dechmann & Safi 2009). While excellent fodder for thought, results should be interpreted with caution until they can be followed up with targeted empirical and experimental studies (Healy & Rowe 2007).

3.3. Summary

Because neural tissue is energetically expensive compared to other tissues, studies have often looked for trade-offs in sensory structures or brain areas that overlap in function. Research across bat species show that trade-offs indeed occur, with the similarity of the information gained by each system potentially influencing the extent of the trade-off. For example, multiple lines of evidence suggest trade-offs in neural investment in echolocation versus vision, likely due to the similarity of their primary function in orientation (Simões et al. 2019). Evidence for a trade-off between olfaction and echolocation is equivocal, however, despite both being used by frugivorous bats for foraging (Hayden et al. 2014). This is likely because olfaction and echolocation often serve nonoverlapping functions in foraging, one operating at a distance, the other at closer range, and because olfaction is critical in social interactions (Chaverri et al. 2018). Trade-offs reflect not just the energetic costs of the sensory organs themselves but also the additional investment in brain areas for processing information gained from the sensory system, underlying the intertwined nature of the evolution of sensory systems and cognition. Studies on bats have revealed that diet affects brain size, with plant eaters exhibiting larger brains than their insect-eating counterparts (e.g., Eisenberg & Wilson 1978). Although frugivorous species in other mammal groups also have relatively larger brains than nonfrugivorous species within the same group (DeCasien et al. 2017), the reasons for this, either a higher energy diet or more complex decision-making for food acquisition, are usually confounded. Studies with bats suggest that decision-making is an important factor, as insectivorous bats that forage in complex habitats (Safi & Dechmann 2005) and exhibit flexible hunting strategies also have relatively larger brains compared with species foraging in simpler habitats using a single sensory modality (Ratcliffe et al. 2006). This relationship reflects the trade-offs associated with energetically expensive neural tissue but also can be thought of as a cognitive filter, if processing less information is advantageous for decision-making.

4. MULTIMODAL SENSING

In Section 2, we discussed how animals are constantly bombarded with sensory information and the critical role sensory filters play in preventing the entry, and thus the subsequent processing, of extraneous information. Animals do not just encounter sensory stimuli from one sensory modality, however; they usually simultaneously detect stimuli from multiple sensory modalities. Multimodal sensing involves the acquisition of information about a certain aspect of the environment through

Aerial hawking:

a foraging strategy in which flying animals catch flying prey in the air

Gleaning: a foraging strategy in which flying animals catch nonflying prey from surfaces, such as leaves or the ground

Multimodal sensing:

gaining information about the same aspect of the environment through multiple sensory systems multiple sensory modalities. Here, we examine how bats shift the focus of their information acquisition between modalities at different stages of a task, how they integrate information across sensory modalities, and how they recruit information from multiple sensory sources to overcome sensorially challenging conditions.

4.1. Sensory Modality Switching

The most useful source of information can change over time and with proximity to a target. It can be advantageous to obtain environmental information via different sensory channels, which may offer different and complementary inputs. In simple environments, information from a single sensory modality may suffice; for example, echolocation alone is often sufficient for bats flying in open space to capture flying prey. Species that forage in more complex environments, in contrast, often must rely on gaining information from multiple sensory modalities. A bat emitting echolocation calls in a cluttered forest understory, for example, receives a myriad of returning echoes; discerning which echoes are from a target prey item and which are from surrounding vegetation can be a daunting task (Moss & Surlykke 2010). Bats facing such sensory challenges frequently rely on different sensory modalities at different stages of the foraging approach.

Sensory modality switching is seen across bat species that forage in complex habitats. To find *Piper* fruit clusters, the Neotropical frugivorous bats, *Carollia perspicillata* and *Carollia castanea*, for example, initially follow olfactory cues, which have longer transmission distances than their echolocation calls in the rainforest understory. At close range, they rely on echolocation to pinpoint individual fruits (Thies et al. 1998). At a distance, vampire bats use both echolocation (Rodríguez-San Pedro & Allendes 2017) and smell for host localization (Bahlman & Kelt 2007). Upon approach, they may listen for the breathing sounds of their hosts, aided by unusually good low-frequency hearing (Heffner et al. 2013) and specialized neurons that respond preferentially to breathing sounds (Schmidt et al. 1991). Once in contact with their host animal, vampire bats use infrared detecting organs around the nose that sense heat (Kürten & Schmidt 1982) to locate blood vessels close to the skin's surface. Even acoustic specialists such as HDC echolocating bats recruit additional sensory cues to find prey. Experiments suggest that greater horseshoe bats (*Rbinolophus ferrumequinum*) listen for moth courtship songs (Alem et al. 2011) and rustling noises (Lattenkamp et al. 2018) at the initial stages of a hunting approach, then switch to echolocation to determine the prey's exact location (Lattenkamp et al. 2018).

Sensory switching can also occur when foraging conditions change. Fringe-lipped bats (*Tra-chops cirrhosus*) find their prey by following the sounds of frog mating calls. If a calling frog detects an approaching bat, however, it typically stops calling (Tuttle et al. 1982), resulting in increased localization error by *T. cirrhosus* (Page & Ryan 2008). These bats, however, can also use echolocation for localization upon close approach (Rhebergen et al. 2015), and at the final stage of the attack, they use gustatory cues to assess palatability and reject poisonous prey (Page et al. 2012).

4.2. Multisensory Integration

Instead of sequential reliance on different sensory modalities, many tasks require simultaneous processing of multimodal stimuli. In particular, studies on bats have revealed the importance of multiple modalities in locomotion, navigation, and learning and underlie how the relative importance of different modalities changes with context.

An interesting example of sensory integration can be found in the use of multiple sensory modalities by bats in flight. Bat wing membranes have a sparse network of microscopic hairs that activate touch receptors when moved (Sterbing-D'Angelo et al. 2011). These hairs are sensitive to

airflow and their removal alters flight performance and speed, demonstrating the importance of these somatosensory hairs in the regulation of flight (Sterbing-D'Angelo et al. 2011). The vestibular system, part of the inner ear that regulates balance and movement (Purves et al. 2008), also influences flight. Experiments with the big brown bat (*Eptesicus fuscus*) demonstrate that input from echolocation and vision are integrated with vestibular information for orientation and flight regulation (Horowitz et al. 2004). In a series of pendulum experiments, Boonman et al. (2020) show that horseshoe bats perform Doppler-shift compensation in response to movement but without feedback from echolocation. Thus, the integration of internal cues with external cues from multiple sensory modalities is key to the complex task of flight in bats (Boonman et al. 2020).

Long-range navigation poses unique sensory challenges. Studies show that for short-distance flights in familiar habitats, echolocation alone functions well, but longer distance navigation depends on access to visual cues (Williams et al. 1966). Bats appear to use magnetite in their sensory cells to detect the Earth's magnetic field (Holland et al. 2008) and visual cues at sunset to calibrate their magnetic compass for homing (Holland et al. 2010). Greater mouse-eared bats (*Myotis myotis*) are nonmigratory and use the pattern of polarized light in the sky at sunset, not the direction of the setting sun, to calibrate their magnetic compass (Greif et al. 2014). However, experiments using the same methodology in the Nathusius' pipistrelle (*Pipistrellus nathusii*), a migratory species tested during migration, did not support the use of polarized light (Lindecke et al. 2015). Similar context-dependent results have been found in birds, with different compass calibration methods used in the premigratory season compared with during migration, highlighting the need for further study of this topic across contexts (reviewed in Muheim et al. 2006).

The manner in which simultaneously perceived sensory cues from different modalities are integrated depends on their reliability in a given context. The Egyptian fruit bat (*Rousettus aegyptiacus*), for example, uses both vision and lingual echolocation to navigate and forage. At low light levels, when vision is less effective, the bats increase their echolocation click rate and click intensity (Danilovich et al. 2015). When navigating, *R. aegyptiacus* relies more heavily on vision, the sense with better angular acuity, but when approaching obstacles, they increase their reliance on echolocation, which provides better ranging (Danilovich & Yovel 2019). Similar integration of information from different sensory modalities via task-dependent sensory weighing is seen across bat species and sensory modalities (e.g., Höller & Schmidt 1996, Horowitz et al. 2004).

Integrating information across multiple sensory modalities can also influence learning (Rowe 1999). When prey broadcast warning signals communicating their unpalatability to predators in not just one but in multiple sensory modalities, predators learn more quickly to avoid them (Rowe 1999). Big brown bats learn to avoid toxic fireflies (*Photinus pyralis*) using both vision (attending to the fireflies' bioluminescent flashes) and echolocation (attending to echoes associated with fireflies' characteristically slow flight behavior) when presented with each sensory cue alone but learn faster when they integrate information from both sensory modalities (Leavell et al. 2018).

In some cases, sensory integration can result in cross-modal recognition, i.e., stimuli perceived in one sensory modality are recognized in a different sensory modality, enhancing an animal's ability to flexibly switch sensory modalities in different contexts. *R. aegyptiacus* preferentially learns the three-dimensional shape of an object with vision instead of echolocation, but when given access to each sensory modality sequentially, *R. aegyptiacus* shows evidence of cross-modal recognition; it can discriminate objects of different textures that it originally learned with echolocation later using vision (Danilovich & Yovel 2019). Cross-modal recognition between vision and echolocation has been shown in only one other species, the bottlenose dolphin (*Tursiops truncatus*) (Pack & Herman 1995), and hints at how sensory integration might occur in the brain.

Recent neurophysiological advances offer further insight into the integration of multisensory information. Place cells are hippocampal neurons that fire when an individual passes through a particular spatial location (the place field) (reviewed in Moser et al. 2017). Bat place cells fire not just when bats physically move through the environment but also when stationary bats explore the environment through echolocation (Ulanovsky & Moss 2007). The place field mapped by place cells is a function of echolocation call rate: The more actively a bat senses its environment (the more echolocation calls it produces in a given time period), the more refined the place field these neurons encode (Wohlgemuth et al. 2018). When confronted with obstacles in their flight path, big brown bats increase the rate at which they produce echolocation calls, gathering more information for obstacle avoidance. This increase in echolocation call production is coupled with a narrowing (sharpening) of the place field encoded by the bat's place cells (Wohlgemuth et al. 2018). Interestingly, place cells change their firing pattern (or remap) when switching between sensory modalities. The place cells of Egyptian fruit bats flying through a corridor with access to either visual cues (lights on) or echolocation cues (lights off) remap when the sensory modality used to navigate the environment switches. Thus, not only do place cells remap when entering a new environment (spatially mapping a new location), they remap when assessing the same environment with a different sensory modality (Geva-Sagiv et al. 2016). Combined, these studies suggest that while input from multiple sensory modalities is integrated in the brain, integration may be complex, with different neural representations for different sensory modalities.

4.3. Multimodal Sensing and Noise

Noise poses a significant challenge across sensory modalities and behavioral tasks. Numerous strategies have evolved to mitigate the challenges of detecting and localizing signals and cues in noise (Gomes et al. 2021). A common strategy is to leave the noisy area, releasing the individual from the noise's masking effect. The greater mouse-eared bat (*M. myotis*), for example, hunts by listening for faint, insect-generated rustling sounds and avoids foraging in noisy areas where overlap between prey sounds and background noise decreases prey detection ability (Schaub et al. 2008). Likewise, the fringe-lipped bat preferentially approaches pugnosed treefrog (*Smilisca sila*) calls at a distance from waterfalls that mask the calls (Tuttle & Ryan 1982). In turn, pugnosed treefrogs tend to call from waterfall sites with high ambient noise levels, perhaps to protect them from eavesdropping bats (Tuttle & Ryan 1982). When moving away from noise is not possible, some bats alter the structure of their echolocation calls. In the presence of insect chorus noise, insectivorous Brazilian free-tailed bats (*Tadarida brasiliensis*) increase echolocation call frequency, thus reducing signal overlap (Gillam & McCracken 2007). Horseshoe bats (*Rhinolophus ferrume-quinum*) demonstrate the Lombard effect, increasing the amplitude of their echolocation calls in the presence of ambient masking noise (Hage et al. 2013).

Another effective strategy when confronted with noise is to shift to the use of other sensory modalities (Munoz & Blumstein 2012). Fringe-lipped bats typically localize their prey by listening for individual frog calls. But when foraging in loud choruses of multiple species of calling frogs, they increase their reliance on echolocation for prey finding (Rhebergen et al. 2015). In noisy conditions, when given a choice between a model frog emitting multiple sensory cues and one emitting calls alone, they increase their echolocation call rate, and both prefer and show faster attacks on the multimodal model (Gomes et al. 2016).

Noise is a persistent sensory challenge that has confronted animals in their natural habitats for millennia. While many strategies have evolved to reduce noise-driven costs, the Anthropocene has introduced unprecedented rapid change in environmental conditions, including a ubiquitous increase in sensory pollutants (Dominoni et al. 2020). Research reveals the negative effect of often-overlooked sources of pollution; for example, the noise from gas compression stations and highway traffic results in reduced foraging performance in several bat species (reviewed in Gomes et al.

2021). While some species can adjust their behavior to cope with anthropogenic noise, others are less flexible and are detrimentally affected, highlighting the critical need to incorporate a robust understanding of sensory ecology in the implementation of conservation measures (Dominoni et al. 2020).

4.4. Summary

Although we have a good understanding of how individual sensory systems are processed by the brain, we know much less about how information from multiple senses is integrated by cognitive processes and how this helps animals detect signals and cues within noise. Studies have confirmed that information from multiple senses can accelerate and improve learning and memory (Rowe 1999), suggesting integration of this information in the brain. *Rousettus* bats, which both have good vision and use lingual echolocation, can use vision to recognize objects that they had previously encountered only using echolocation (Danilovich & Yovel 2019). Thus, one might expect that information about the environment has similar or the same representation in the brain regardless of sensory origin. The finding that place cells in the hippocampus are remapped when *Rousettus* switches between sensory modalities (Geva-Sagiv et al. 2016), however, suggests that the same type of information might be represented differently in the brain depending on its sensory source.

5. DISCUSSION AND FUTURE DIRECTIONS

Recent advances in neurophysiological research, the genetic basis of sensory differences, and detailed studies on learning and decision-making have deepened our understanding of information acquisition and cognition. Addressing key questions for future research will strengthen our understanding of three critical areas at the heart of sensory and cognitive ecology: sensory filters, trade-offs, and multisensory processing. How do sensory filters facilitate or constrain cognitive functions such as learning and memory? That vampire bats have extremely poor taste perception and cannot learn to associate even a detectable flavor with subsequent digestive illness suggests that reduced reliance on a sensory system results in poor cognitive processing of the limited information encoded by that system. Alternatively, the loss of sensory and cognitive function could occur in parallel and not be causal. Bats provide the diversity in sensory capabilities to assess how the amount of information encoded by a sensory system influences cognitive function and how this might shift when input comes from multiple sensory modalities. Studies on bats point to trade-offs between sensory systems, but how much overlap between sensory information sources is needed to see sensory trade-offs? Likewise, how much do trade-offs depend on the energetic costs of the sensory structure itself compared to that of central nervous system processing? Why are some sensory system genes highly conserved while others experience relaxed or directional selection? How does the brain integrate or compare information about the environment from different modalities? The extreme differences in selection on taste, olfactory, and vision genes across bats provide excellent diversity for answering questions about selection on multiple sensory systems and integration among these systems. We argue that bats are well poised to help us address these issues and should be key players in the fields of sensory and cognitive ecology going forward.

The idea that every individual exists in its own unwelt, or self-world, determined by its unique sensory and cognitive filters was developed early in the study of animal behavior (von Uexküll 1909). The realization that we can never fully know another's world is exemplified in the famous essay by philosopher Thomas Nagel (1974), *What Is it Like to Be a Bat?* While Nagel's lament that truly knowing what it is like to be any other living being—especially one as seemingly foreign to him as a bat—holds philosophical value, we would argue that we now know quite a lot about what it is like to be a bat. We have discussed some of the key discoveries of the last decades, detailing not

only the increasingly well-understood sense of echolocation but also the less studied senses, such as thermoperception, magnetoreception, and somatosensory processing. We have investigated bats' cognitive toolkits and discussed the ecological pressures that shape learning and decision-making in this diverse group. We argue that, while advances in our understanding of the sensory and cognitive ecology of bats may not allow us to perfectly understand a bat's umwelt, we are closer now than ever before. Detailed investigation of the diverse range of sensory and cognitive adaptations and constraints in this group sheds light on the role ecology and evolution play in shaping sensory and cognitive systems.

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