Behavioral Ecology

The official journal of the
ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2020), 31(4), 859–867. doi:10.1093/beheco/araa004

Invited Review

Categorical perception in animal communication and decision-making

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Received 14 November 2019; revised 14 January 2020; editorial decision 15 January 2020; accepted 17 January 2020.

The information an animal gathers from its environment, including that associated with signals, often varies continuously. Animals may respond to this continuous variation in a physical stimulus as lying in discrete categories rather than along a continuum, a phenomenon known as categorical perception. Categorical perception was first described in the context of speech and thought to be uniquely associated with human language. Subsequent work has since discovered that categorical perception functions in communication and decision-making across animal taxa, behavioral contexts, and sensory modalities. We begin with an overview of how categorical perception functions in speech perception and, then, describe subsequent work illustrating its role in nonhuman animal communication and decision-making. We synthesize this work to suggest that categorical perception may be favored where there is a benefit to 1) setting consistent behavioral response rules in the face of variation and potential overlap in the physical structure of signals, 2) especially rapid decision-making, or 3) reducing the costs associated with processing and/or comparing signals. We conclude by suggesting other systems in which categorical perception may play a role as a next step toward understanding how this phenomenon may influence our thinking about the function and evolution of animal communication and decision-making.

Key words: **animal communication, animal signals, categorical perception, decision-making, receiver psychology, sensory biology.**

INTRODUCTION

To make decisions, animals must gather and process information from their surroundings. This information may be about the abiotic environment (such as the location of a suitable nest site) or the biotic environment (such as the presence of prey or a predator), including the social environment (such as a signal from a potential mate). Information gathering is achieved by an array of sensory mechanisms that transduce a diverse range of physical stimuli into neural activity (reviewed in Chaudhuri 2011). Sensory transduction is only the first part of the equation, however. Often, an animal's sensory world is overloaded with more information than is needed, and critical information may be obscured. The challenge, then, is for an animal to efficiently process the enormous amount of sensory information it receives and extract what is most relevant to its adaptive decision-making.

This idea is not new. von Uexküll (1934) famously argued that the perceptual world of a tick should be limited to only detecting warmth and the odor of butyric acid, both indicating mammalian skin and, thus, food. What *is* new since von Uexküll's time is the enormous amount that has been learned about how sensory and perceptual systems function. Historically, much of this work focused on sensory cells and sense organs—the nature of physical stimuli to which they respond and how those stimuli are transduced into neural activity (e.g., Nolen and Hoy 1984; Ryan and Wilczynski 1988). These findings gave rise to increasing interest in perceptual processing and receiver psychology (e.g., Guilford and Dawkins 1991; Miller and Bee 2012; Ronald et al. 2012; Rowe 2013; Akre and Johnsen 2014; Bee and Miller 2016) and the underlying mechanisms that allow input from sensory systems to be mapped onto more useful—often simpler—perceptual representations of that information. One such mechanism is categorical perception, in which an animal's perceptual system sorts stimuli that vary in a continuous fashion into a set of discrete categories (Harnad 1987).

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In this review, we first describe categorical perception in the context where it was originally defined: the perception of human speech. We next detail what is known about categorical perception in nonhuman animals (hereafter, "animals"), focusing on its function in animal communication. Finally, we suggest systems in which categorical perception has not yet been described but may play an important role, and we discuss how a deeper understanding of categorical perception might influence studies of animal communication more broadly. Categorical perception was first described more than half a century ago (Liberman et al. 1957), and studies have documented its occurrence in animal communication systems over the last several decades. Recent efforts to develop the concept of receiver psychology and perception in animal behavior more systematically (e.g., Akre and Johnsen 2014; Bee and Miller 2016; Caves et al. 2019), however, lead us to suggest that the time is ripe for a comprehensive review of categorical perception in animals to help identify additional communication systems and decision-making situations in which it may play a functional role and to stimulate further research into its underlying mechanisms.

WHAT IS CATEGORICAL PERCEPTION? ORIGINS IN HUMAN SPEECH RESEARCH

Categorical perception refers to a process by which stimuli are responded to as being similar or different depending on whether they do or do not fall into a presumptive perceptual category (Harnad 1987). A functional definition—one that is amenable to experimental quantification—is based on two main features that characterize categorical perception (Harnad 1987): 1) the labeling of a range of potentially discriminable stimuli as being the same (i.e., responded to in some functional context as though they are the same) with stimuli outside this range labeled as different and 2) the "category boundary effect" (sensu Repp 1984; Nelson and Marler 1989) in which stimulus pairs that fall across a putative category boundary are more readily distinguished as compared with equally differing stimulus pairs that fall on the same side of the boundary. Categorical perception does *not* imply that stimuli falling within a category cannot be distinguished at all but rather that there is enhanced performance on discrimination tasks (e.g., faster response times or fewer errors) for stimulus pairs that lie across a category boundary as compared with pairs within a category (Studdert-Kennedy et al. 1970; Macmillan et al. 1977).

Categorical perception was first defined—and is best explained—in the context of the perception of human speech sounds. Consider the sounds /b/ and /p/. To an English speaker, these sounds are perceived as quite distinct even though they are very similar acoustically. In fact, there is only one key difference between them: when the sound /b/ is produced followed by a vowel (e.g., say "ba"), the initial broadband consonant sound resulting from opening the lips (a "plosive") is followed almost immediately by vibration of the laryngeal vocal folds ("voicing") as the vowel sound is produced. By contrast, when /p/ is produced followed by a vowel (say "pa"), there is a gap between the plosive and the onset of voicing during which time there is a breathiness caused by air passing through the vocal tract without the vocal folds vibrating. This feature is referred to as "voice onset time" (VOT), with /b/ having little or no VOT and /p/ having a VOT lasting several tens of milliseconds. A similar contrast occurs between /d/ and /t/ and between /g/ and /k/ (Lisker and Abramson 1964).

While VOT is the feature that distinguishes /b/ and /p/, there is considerable variation in the range of VOTs associated with both sounds, depending on the speaker and where in a word the sound occurs (Lisker and Abramson 1964). This variation is continuous and creates a potential overlap between the VOT ranges associated with both sounds: /b/s are sometimes produced with long VOTs that may come close to /p/s having shorter VOTs. Humans do not notice this variation in their perception of speech sounds, however. If VOT is below a boundary, we hear the sound as /b/; if VOT is above that boundary, we hear the sound as /p/. Further, if tested with pairs of sounds that differ equally in VOT, our ability to discriminate between them is enhanced for pairs that cross the boundary between /b/ and /p/ as compared with pairs that fall on the same side of the boundary (Liberman et al. 1957; Liberman et al. 1961; Studdert-Kennedy et al. 1970).

This canonical example illustrates both hallmarks of categorical perception: 1) labeling of a stimulus continuum (here, the VOT continuum) as lying in discrete categories and 2) enhanced discrimination of stimuli across a category boundary as compared with stimuli within a category, even for stimulus pairs that vary by the same magnitude (Harnad 1987). Later, we discuss the importance of categorical perception in animal communication, but this example clearly shows its relevance to human speech. It is important to discern whether someone says they want to "pat" you or "bat" you!

An underlying assumption of categorical perception is that stimuli falling within a category *could* be discriminated by whatever sensory mechanisms are involved. For example, the temporal resolution of human hearing should easily allow us to discriminate differences in the durations of sounds or silent gaps on the order of tens of milliseconds, such as the range of within-category VOTs associated with /b/ and /p/ (Moore 1989). Indeed, experimental data show that human subjects are better at discriminating within-category differences than predicted based on the results of labeling tests (Liberman et al. 1957). That is, it is not the case that stimulus pairs falling on one side or the other of a VOT categorical boundary are completely indiscriminable. But for VOT variation listened to in the context of speech, we are significantly more accurate at perceiving differences that cross the perceptual boundary between /p/ and /b/ than differences that do not cross this boundary (Liberman et al. 1957; Mattingly et al. 1971; Repp 1984).

Categorical perception is only one of several mechanisms that can contribute to the broader phenomenon of categorization, which occurs when animals, including humans, treat a range of entities—usually differing in many dimensions—as similar. Categorical perception of a single stimulus dimension can underlie the categorization of more complex, multivariate stimuli (Harnad 1987). For example, the amplitude rise time of a synthetized musical sound (a single stimulus dimension) can determine whether that sound is perceived as one of two more complex stimuli—either a plucked guitar string (a fast rise time) or a bowed violin string (a slow rise time); the categorical boundary between these stimuli is as sharply defined as has been observed for phonemic discriminations, such as between /b/ and /p/ (Cutting and Rosner 1974). Categorization refers broadly to a wide range of processes by which animals sort nonidentical things into groups, the members of which are treated similarly. Categorical perception, by comparison, is most typically invoked in contexts where a single, continuous stimulus dimension plays a predominant role in how something is categorized as is the case for /b/ versus /p/.

NOT JUST SPEECH: CATEGORICAL PERCEPTION IN OTHER ANIMALS

Although initially thought to be a mechanism uniquely associated with human perception of speech sounds (Liberman et al. 1957), categorical perception is now understood to play a role in the processing of sensory input across a variety of animals and behavioral contexts. Much of the information animals need to act on—for example, signals from conspecifics or cues from the environment—varies in a continuous fashion. Under some circumstances, categorical perception may provide an efficient way to recode that information into a set of functionally more useful categories.

An early challenge to the idea that categorical perception is a unique specialization associated with human speech came from the demonstration that chinchillas (*Chinchilla laniger*) categorically perceive speech sounds along a VOT continuum at the same point as humans do (Kuhl and Miller 1975). Similar results were obtained from rhesus macaques (*Macaca mulatta*) (Morse and Snowdon 1975). Human infants also show a categorical boundary in VOT when discriminating speech sounds at ages well before they themselves begin to produce speech (Eimas et al. 1971), even if they have been raised in a language environment lacking sounds distinguished by such VOT differences (Streeter 1976). These and similar findings from tests with avian species suggested that categorical perception did not evolve as a special mechanism for coding speech but rather that speech sounds take advantage of the way vertebrate auditory systems naturally parse acoustic information (Kuhl 2004; Kriengwatana et al. 2014).

Subsequent research across a range of animals revealed that categorical perception can play a role in the perception of a species' own acoustic signals. A first demonstration came from work on Japanese macaques (*Macaca fuscata*; Figure 1a), which produce a variety of acoustically similar "coo" vocalizations in different behavioral contexts (Green 1975). In one of these contexts, juveniles coo when they have lost visual contact with group members; another type of coo is produced by females during courtship. The coos made by juveniles and females in these two contexts differ primarily in the position of a frequency peak (where frequency shifts from rising to falling; Figure 1b). Juvenile coos, on average, have a peak in the initial two-thirds of call duration, whereas, in female coos, this peak occurs in the latter one-third (Green 1975). There is sufficient variation in frequency peak location, however, to suggest a role for categorical perception in providing receivers a consistent rule for differentiating juvenile from female coos. To test this idea, May et al. (1989) trained macaques to release a bar to receive a food reward when they were presented with one of the coo types but not the other. By subsequently testing them with an array of natural and synthetic coo sounds, they found that the macaques labeled the frequency peak continuum as lying in two categories: coos having a peak position less than 125 ms in a 300-ms call were categorized as one type (corresponding to the juvenile call) and coos with peak position greater than 125 ms were categorized as the other (the female courtship call; Figure 1c). Further, discrimination was enhanced at the category boundary: macaques were best at discriminating between coo exemplars that were equally different

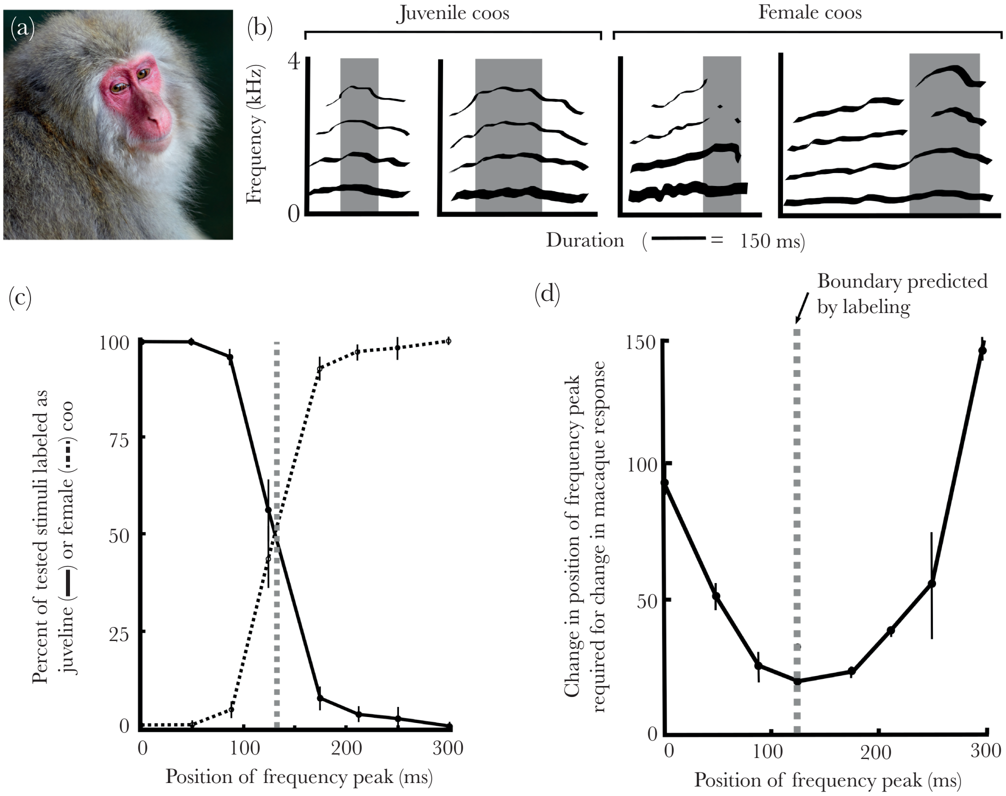

Figure 1

Categorical perception of "coo" vocalizations in (a) Japanese macaques. (b) Spectrograms of vocalizations with frequency peaks (gray boxes) lying in the first two-thirds of call duration (left two examples, corresponding to juvenile coos) or the last one-third of call duration (right two examples, corresponding to female coos). (c) Labeling: macaques labeled most stimuli as juvenile coos until the frequency peak reached ~125 ms in the duration of a 300-ms call (gray dotted line), after which a sharp change in response occurred and most stimuli were treated as female coos. (d) Discrimination: at the boundary predicted by labeling (gray dotted line), macaques required the lowest change in frequency peak position to identify a call as lying in a different category, revealing best discrimination. (a) from Wikimedia commons; (b) adapted from Green (1975); (c) and (d) adapted from May et al. (1989).

in the timing of the frequency peak position if that difference crossed the 125-ms boundary (Figure 1d). A subsequent study failed to replicate the results of May et al. (Hopp et al. 1992), although this later work synthesized test stimuli differently and tested subjects using a same–different task rather than a categorization task (Le Prell and Moody 2000). In their synthesis of research on this topic, Le Prell and Moody (2000) suggested that categorical perception was one, but not necessarily the only, mechanism underlying the way Japanese macaques perceive coo calls.

In another early demonstration of categorical perception in animal communication—one in which natural, not trained, responses were elicited—Nelson and Marler (1989) showed that swamp sparrows (*Melospiza georgiana*; Figure 2a) perceive variation in the acoustic elements that comprise their songs in a categorical fashion. This species' songs last about 2 s and are composed of a repeating sequence of one to five "notes" (Figure 2b). These notes are short, pure-tone frequency sweeps, and they fall into a limited number of population-specific note types (Marler and Pickert 1984; Lachlan and Nowicki 2015). Nelson and Marler (1989) found two of these note types (types "1" and "6") to be especially similar in acoustic structure, differing primarily in duration: type 1 notes have durations less than 13 ms and type 6 notes are longer than 13 ms (Figure 2c). The distribution of durations is bimodal but with overlap (Figure 2d). This raised the question—just as for humans with variation in VOT or Japanese macaques with variation in the position of a frequency peak—whether categorical perception functions in how swamp sparrows differentiate type 1 and type 6 notes. To test this, Nelson and Marler (1989) played conspecific songs to territorial males in the field until their aggressive response habituated, at which point they switched to playing a version of the song that had its type 1 notes substituted with a new note having either a duration within the distribution of the type 1 category (i.e., shorter than 13 ms) or a duration that crossed the boundary (i.e., longer than 13 ms). Comparable trials were done with type 6 notes substituted in a reciprocal fashion. If birds noticed a change when the substitution was made, they would again respond aggressively, recovering from habituation. The sparrows showed this dishabituation response most strongly when the note substitution crossed the 13-ms boundary, showing heightened discrimination across this boundary and, thus, categorical perception of this continuum (Figure 2e; Nelson and Marler 1989). Subsequent work demonstrated that neurons in the "song system" of the sparrow brain also respond in a categorical fashion to note type variation (Prather et al. 2009).

Comparative work on categorical perception has also been extended to color vision. It has long been known that humans perceive color in a categorical fashion as anyone who has seen a rainbow—in which continuous variation in the visible light spectrum is experienced as discrete bands of color—will attest. Similar to the categorical perception of speech sounds, categorical color perception in humans was initially presumed to be associated with language given that the number and type of color categories in some cultures have been linked to the number and type of color terms in those cultures' languages (Davidoff et al. 1999; Roberson et al. 2000). This view has been challenged more recently, however. For example, prelingual infants perceive colors categorically as determined by behavioral testing (Skelton et al. 2017) and by direct measurement of brain activity (Yang et al. 2016). Results such as these indicate that language production, at least, is not essential for categorical color perception. Animals across an array of taxa, including macaques (Sandell et al. 1979), pigeons (Wright and Cumming 1971), and chicks (Jones et al. 2001), have been shown to generalize colors into categories, although, perhaps surprisingly, none of these studies has demonstrated categorical perception per se by showing both labeling of color in categories and enhanced discrimination of color differences across a categorical boundary. Recently, however, Caves et al. (2018) provided evidence for both labeling and enhanced discrimination across a color category boundary in a songbird.

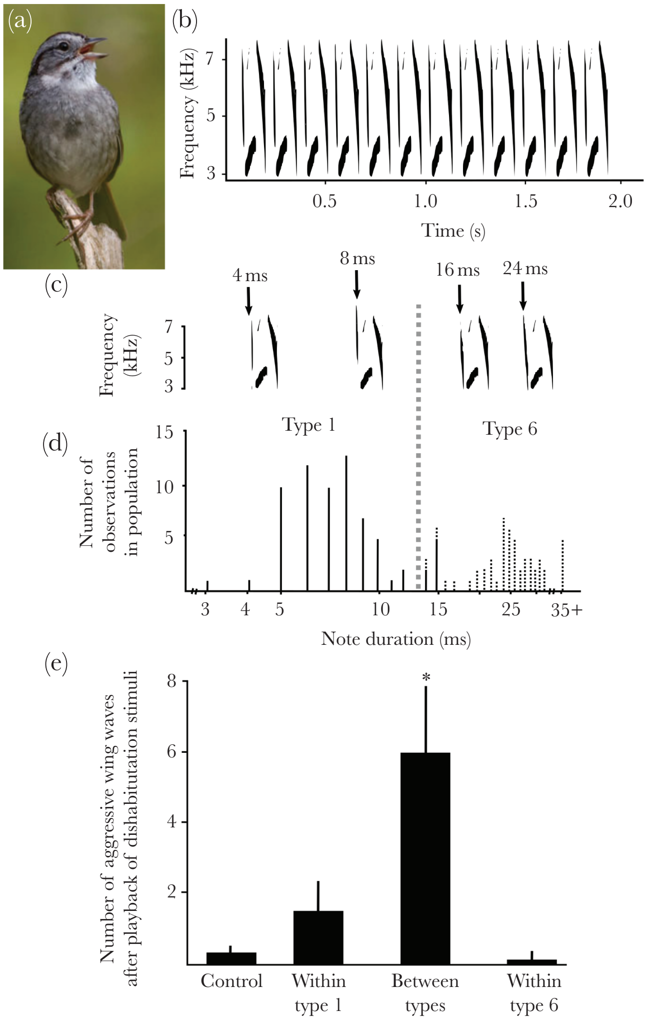

Figure 2

Categorical perception of note type duration in (a) swamp sparrows. (b) Spectrogram of swamp sparrow song, showing repeated syllable elements. (c) Type 1 and type 6 notes can both occur at the beginning of a syllable (arrows) but are differentiated by duration. A bimodal distribution of note type duration (d) suggested a boundary at ~13 ms (gray dotted line). (d) The distribution of note type durations in the sampled population; solid lines represent type 1 notes and dotted lines represent type 6 notes. (e) Discrimination: after being habituated to one note type, sparrows showed the strongest dishabituation response to note types that crossed the category boundary. (a) courtesy of Rob Lachlan; (b) and (c) courtesy of Susan Peters; (d) and (e) adapted from Nelson and Marler (1989).

In this study, female zebra finches (*Taeniopygia guttata*; Figure 3a) were trained to remove colored discs covering food rewards. Only bicolor discs (showing two different colors) were rewarded, whereas solid colored discs were unrewarded. After training the birds on bicolor discs showing colors at the ends of an orange–red continuum (Figure 3b), Caves et al. (2018) varied the colors on the discs along

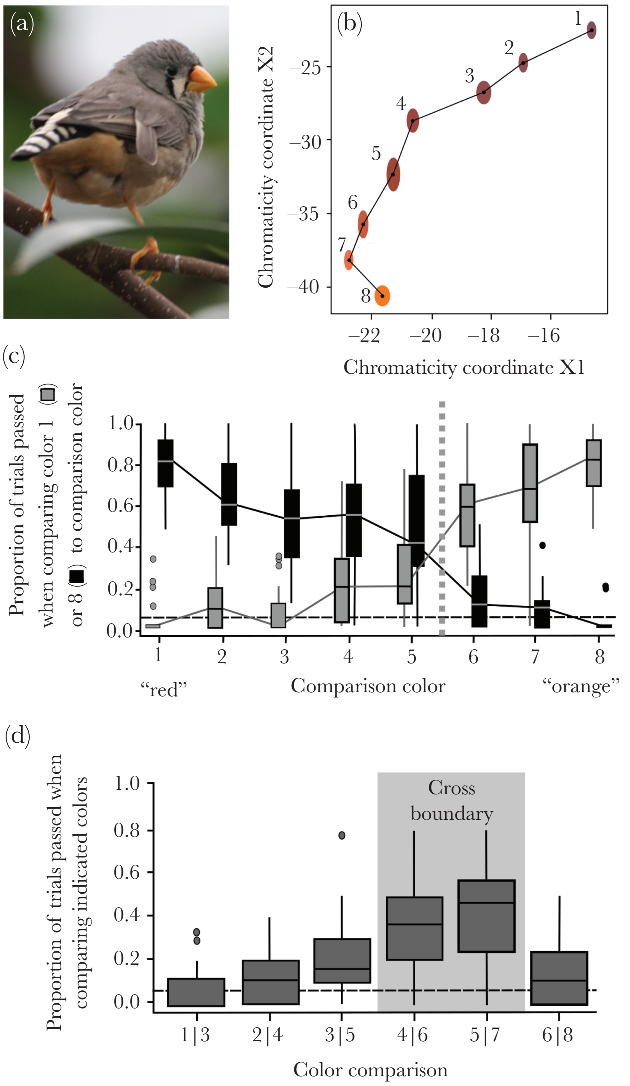

Figure 3

Categorical perception of color variation in (a) female zebra finches. (b) Eight colors were selected along a continuum of red–orange color variation. Colors were approximately equally spaced according to the receptor noise-limited model of color vision (Vorobyev and Osorio 1998). (c) Labeling: females showed a sharp change in proportion of trials passed when color variants crossed between comparison colors 5 and 6 (gray dotted line), suggesting a category boundary. (d) Discrimination: females showed the highest pass rate when color comparisons crossed the 5|6 boundary (gray shaded region), even though distance between colors was approximately equivalent. (a) from Wikimedia Commons; (b), (c), and (d) adapted from Caves et al. (2018).

the spectrum, testing both labeling and discrimination abilities by quantifying how reliably the birds removed both bicolored discs before any solid disc. Female zebra finches labeled the eight colors along this orange–red continuum as lying in two discrete categories (Figure 3c). Furthermore, while females could discriminate color variation within labeled categories to some degree, their ability to discriminate colors that were equally different (in an avian color space derived from the receptor noise-limited model of color vision; Vorobyev and Osorio 1998) was about 25 percentage points better when those colors crossed the category boundary (Figure 3d). This study was the first outside of humans to show categorical perception of color variation. Notably, it also shows categorical perception of colors potentially relevant to a natural communication system: the orange–red colors used in this study match the range of male beak coloration, a signal involved in mate choice in this species (Collins and ten Cate 1996; Blount et al. 2003).

THE ROLE OF CATEGORICAL PERCEPTION IN ANIMAL COMMUNICATION

In preceding sections, we identified examples of categorical perception, moving from its definition in human speech perception to work on color perception in a songbird. Although these examples seem disparate, they are connected by their potential function in communication. Here, we describe additional examples organized around roles categorical perception may play in communication and decision-making systems. In doing so, we suggest conditions under which categorical perception might act as a mechanism for parsing continuously variable information. Specifically, we suggest that categorical perception might be favored in systems where there is a benefit to 1) setting a consistent behavioral response rule in the face of variation and potential overlap in the physical structure of signals, 2) especially rapid decision-making, or 3) reducing the costs associated with processing and comparing signals. We also discuss how categorical perception might reveal new insights into signal function. These drivers of categorical perception are not mutually exclusive and several may be in play in a given signaling system. Importantly, we are not suggesting that categorical perception evolves specifically as an adaptation on its own but rather that it may be selected for in contexts where communicative and decision-making behaviors benefit from enhanced discrimination of a perceptual boundary.

Categorical perception may help receivers more consistently assign a signal to a functional category when there is considerable variation in signal form and the potential for structural overlap in signals having different functions. The coo calls produced by Japanese macaques provide a case in point. These calls are acoustically similar across types and variable within types, with subtly different versions used in at least 10 different contexts (Green 1975). The coo calls produced by separated juveniles and by estrous females are particularly similar but are differentiated in a categorical fashion based on a single distinguishing feature: the location of a frequency peak along the duration of the call (Figure 1; May et al. 1989). Of course, setting a boundary such as this inevitably results in some number of misclassifications; some juvenile coo calls having frequency inflection points closer to what is typical for female coo calls will be responded to incorrectly as though they were females coos and vice versa. Based on the distribution of variation in these call types, however, and the relative costs of incorrect identifications in either direction, signal detection theory suggests that there will be a boundary that optimizes the benefits of having more consistent assignments of call exemplars to one type or the other (Wiley 2006).

Another example of categorical perception's role in providing a mechanism for setting consistent responses comes from work on túngara frogs (*Physalaemus pustulosus*, Figure 4a). The mating calls of this species and a closely related heterospecific (*Physalaemus coloradorum*) differ along a continuum that combines both frequency and duration (Figure 4b). Overlap in these parameters between species could present a problem for females, who should orient toward conspecifics and away from heterospecifics. Using two-choice tests, Baugh et al. (2008) showed that categorical perception facilitates

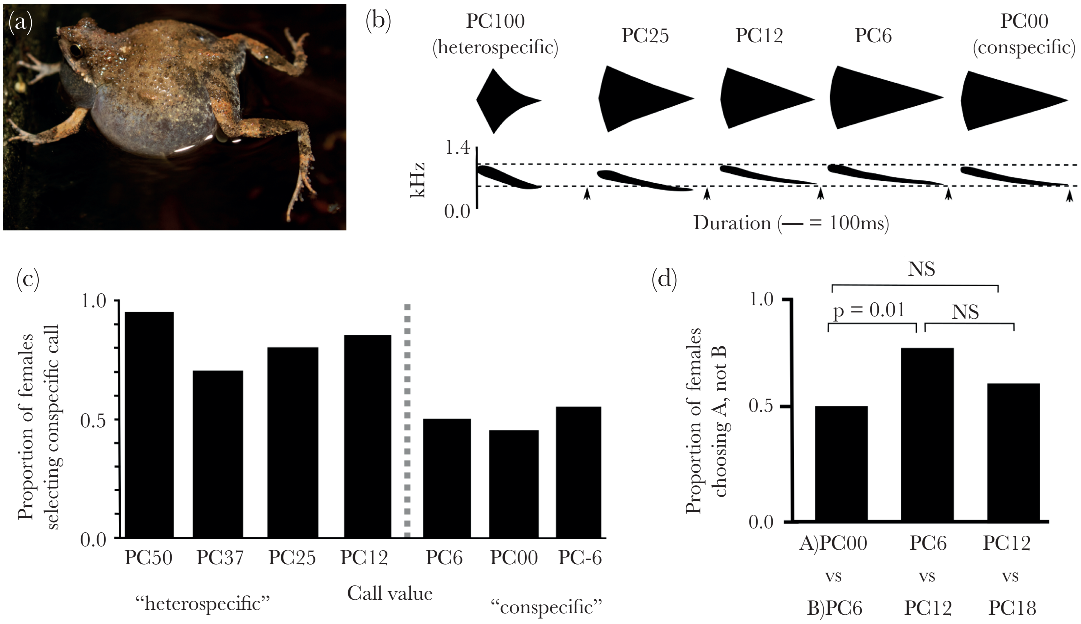

Figure 4

Categorical perception of mating calls in (a) túngara frogs. (b) Oscillograms and spectrograms of call variants that vary in multivariate structure from conspecifics (PC00, right) to heterospecifics (PC100, left). (c) Labeling: in two-choice tests, female túngara frogs sharply increased their rates of choosing conspecific calls once call value (*x* axis) moved from PC6 to PC12, suggesting a boundary (gray dotted line). (d) Discrimination: females showed a strong preference for conspecific calls only when compared against calls that crossed the perceptual boundary (PC6 vs. PC12). (a) from Wikimedia Commons; (b), (c), and (d) adapted from Baugh et al. (2008).

the choice of conspecific mates. Females showed a sharp discontinuity in their response to a continuum of variation in call acoustic structure; that is, they labeled mating calls as lying in either a "conspecific" or "heterospecific" category (Figure 4c). Furthermore, there was evidence of enhanced discrimination across the category boundary. Specifically, females showed a stronger preference for, and quicker response to, conspecific calls when played alongside calls in the heterospecific category as compared with those falling within the conspecific category. This was the case even though all calls differed by the same magnitude (Figure 4d; Baugh et al. 2008). As with the macaque coo call example, mistakes will occasionally be made, but signal detection theory suggests a boundary exists that optimizes the trade-off between the costs of making such mistakes ("false alarms") and the costs of missing correct assignments ("missed detections"; Wiley 2006).

Categorical perception may also facilitate rapid decision-making in critical contexts. Polynesian field crickets (*Teleogryllus oceanicus*), for example, may be faced in flight with the life-or-death decision of orienting toward a potential mate versus away from a potential predator such as a hunting bat. Although cricket mating calls and bat echolocation calls differ in several dimensions, crickets discriminate between them based on acoustic frequency alone and they do so in a categorical fashion (Wyttenbach et al. 1996). By holding all parameters except frequency constant and measuring the orienting response of tethered crickets, Wyttenbach et al. (1996) demonstrated labeling of calls as either attractive or repulsive, with a boundary between 13 and 16 kHz. They then, used a habituation-recovery paradigm to show enhanced discrimination of stimuli across this boundary. Interestingly, the majority of energy in the cricket's mating calls falls well below this boundary, whereas the majority of energy in the bat's echolocation calls falls well above it. Since the overlap in signal variation is low, why would crickets use categorical perception to discriminate these calls? Wyttenbach et al. (1996) argue that categorical perception has been selected for given the obvious urgency of rapidly and unambiguously distinguishing predators from potential mates.

Rapid decision-making is also facilitated by categorical perception in the context of referential labeling of conspecific alarm calls. Here, quickly discriminating which predator type is being signaled by conspecifics may be essential to avoid becoming prey. For example, Barbary macaques (*Macaca sylvanus*) produce "shrill barks" as alarm calls to alert group mates. These barks vary structurally in a continuous fashion, although multivariate acoustic analysis reveals that different call forms are associated consistently with different kinds of disturbances, for example, a dog versus an approaching human (Fischer 1998). Fischer (1998) demonstrated that macaques more readily labeled call exemplars as different if they were classified as being in different categories by the acoustic analysis as compared with equally dissimilar call exemplars sorted into the same category. The macaques were less good at discriminating among calls recorded from a different population, suggesting that call categorical perception is influenced by learning (Fischer 1998) as is the case for human phonemes (Kuhl 2004) and swamp sparrow note types (Prather et al. 2009; Lachlan and Nowicki 2015). Fischer (1998) also identified significant amounts of overlap in the acoustic features of different alarm calls, suggesting that categorical perception in this case not only facilitates rapid decision-making but also sets a consistent response in the face of potential structural overlap.

Categorical perception may also lower costs associated with comparing signals or, more generally, gathering and processing information. Consider mate choice: in general, if variation in mate quality affects an individual's reproductive success, that individual will benefit from sampling and comparing a large number of potential mates. But searching for mates entails both opportunity costs and risk costs (e.g., Janetos 1980). If the benefits accrued from discerning among potential mates are outweighed by costs associated with finding individuals to compare, then selection may favor a threshold model of mate choice (Janetos 1980; Moore and Moore 1988; Reid and Stamps 1997; Roff 2015), in which choosing individuals simply determine whether a potential mate is above some threshold quality (being "good enough" instead of "the best possible"). Categorical perception could facilitate such mate-choice decisions by acting as a mechanism for setting a threshold. Less obvious but potentially equally important costs are those required for developing and maintaining the neural substrate associated with the cognitive processing and memory necessary to compare potential mates (Sterling and Laughlin 2015). Here again, to the extent that such costs exceed the benefits of finer discrimination among potential mates, categorical perception may serve as a less-costly cognitive mechanism for assessment. Work on the red jungle fowl (*Gallus gallus*) provides an example of threshold assessment in mate choice (Zuk et al. 1990). Females were significantly slower to choose males with combs smaller than a ~78-mm threshold as compared with males with combs larger than this size and, when the same females were presented with a large-combed pair of males (i.e., above the presumed threshold) and a small-combed pair of males (i.e., below the threshold) in two different trials, they mated significantly more slowly—and often refused to mate—when presented with only short-combed males (Zuk et al. 1990).

The finding that female zebra finches categorically perceive a carotenoid-based color continuum representative of male beaks (Figure 3; Caves et al. 2018) raises the question of whether threshold assessment might operate in mate choice here as well. Male beak coloration serves as an assessment signal (Collins and ten Cate 1996; Blount et al. 2003; ten Cate et al. 2006) as has been found for carotenoid coloration in many taxa (Searcy and Nowicki 2005). If females assess beak color categorically, their task in mate choice is much simplified. Instead of having to sample, store in memory, and compare small differences in beak color across males, they only need to register whether a male's beak is "red," presumably associated with a male that is "good enough," or "orange," associated with a male falling below the threshold. Whether or not costs associated with comparing males exceeds the benefit of making finer distinctions among potential mates is not yet known in this case. But finding that females perceive male beak colors categorically in a food-reward task means that we cannot take it for granted that they respond in a continuous fashion to continuous variation in beak coloration in the context of mate choice. Behavioral tests more closely associated with actually choosing a mate are needed to answer that question, while modeling approaches can address the connections between categorical perception, threshold assessment, and signal evolution.

Finally, understanding the role of categorical perception in a signaling system may provide novel insights into signal function. Consider the categorical perception of song elements by swamp sparrows (Figure 2; Nelson and Marler 1989; Prather et al. 2009). The discrimination of similar note types in this species bears striking parallels to the discrimination of similar phoneme types by humans. However, whereas the functional significance of categorical perception of parts of speech is clear (to reduce ambiguity in recognition of speech sounds associated with meanings), the significance of categorical perception of parts of songs is not (given that different song types within an individual's repertoire are, in general, functionally redundant; Catchpole and Slater 2008). One possibility may have to do with how females assess the accuracy with which a male has learned its song. The "developmental stress hypothesis" suggests that female songbirds attend to learned features of male song because how well males learn song indicates how well they fared in the face of early developmental stress and, thus, reflects male quality overall (Nowicki et al. 1998; Peters et al. 2014). Experiments with lab-raised birds demonstrate that the precision with which male swamp sparrows learn their songs is affected by early developmental stress (Nowicki et al. 2002). In laboratory copulation-solicitation assays, female swamp sparrows respond more to songs produced by males experiencing less stress as nestlings (Searcy et al. 2010). They also respond more to songs that are closer to the most typical versions of those songs sung in their population (Lachlan et al. 2014). Discriminating among note types (Figure 2) may help a female identify which of several similar song types a male is singing. Only if the female can determine which song types a male has copied can she assess how well that song was learned in comparison to other males in the population (Lachlan and Nowicki 2012). While this idea remains to be tested directly, it illustrates how knowing that signal variation is perceived in a categorical fashion might inform our understanding of how that signal functions.

FUTURE DIRECTIONS

Since its initial description by speech researchers, categorical perception has been shown across a range of animal taxa and behavioral contexts. Here, we suggest other systems in which categorical perception may function in communication and decision-making as a next step toward understanding the extent to which this phenomenon may play a role in the function and evolution of animal behavior more generally.

One promising example where categorical perception may lead to consistent behavioral responses is self/nonself identification in avian hosts of brood parasites. A recent study identified a potential role for categorical perception in how robins use color cues to differentiate their own eggs from the eggs of cowbird brood parasites. Hanley et al. (2017) found that robins sharply increased their likelihood of rejecting an egg from the nest as egg color shifted along a continuum of blue–green to brown. This threshold response, of blue–green as self and brown as nonself, has not, to our knowledge, been followed by a test of robins' ability to discriminate among egg variants that differ equally in color (in a color space determined by robin visual physiology) but that cross or do not cross the relevant boundary. Testing for categorical perception in this system would extend the results of Hanley et al. (2017) while opening the possibility of categorical perception as a means of avoiding brood parasitism across other bird species.

Another intriguing example comes from work on human face recognition. Humans identify individuals, in part, through categorical perception of facial identity (Beale and Keil 1995; McKone et al. 2001). For example, Beale and Keil (1995) presented human subjects with a continuum of images that morphed from Bill Clinton's face to John F. Kennedy's (JFKs) face. The subjects labeled the continuum as either Clinton or JFK, and their ability to accurately discriminate identity was heightened at the Clinton/JFK boundary (Beale and Keil 1995). In other animal taxa, individual recognition is also important and might be driven by categorical perception. For example, paper wasps use facial markings to identify individuals (Tibbetts 2002) and would be an interesting system to investigate further.

Individual recognition using other signal modalities, including odor that, in some vertebrates, communicates identity through major histocompatibility complex molecules or major urinary proteins (Hurst et al. 2001), could also show evidence of categorical perception. Odor, more generally, is a sensory modality in which humans show categorical perception; animals might also perceive odor in a categorical fashion. For example, humans categorically perceive a variation in the types and amounts of volatile compounds to identify odors, such as "minty" and "woody" (Howard et al. 2009). Other animals that must generalize odors or discriminate among odor variation, such as hawkmoths that use fine-scale discrimination of odor to find flowers (Riffell et al. 2014), might do so in a categorical fashion as well.

Much work remains to more fully appreciate the ways in which categorical perception functions in animal communication and decision-making. As von Uexküll (von Uexküll 1934) observed, one needs to understand an animal's own "umwelt" to make sense of how it behaves. Now, almost a century later, we continue to gain a better understanding of how processes such as categorical perception contribute to how animals experience the world around them.

FUNDING

This work was supported by the Duke University Office of the Provost.

We thank Dr E. M. Caves, S. Peters, the BEAM group at Duke University, Dr Innes Cuthill, Dr Leigh Simmons, and two anonymous reviewers for helpful feedback.

Conflict of interest: Authors declare no conflict of interest.

Data accessibility: There are no data associated with this review.

Handling editor: Leigh Simmons

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