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3aAB8. Auditory object formation in Cope's gray treefrogs (*Hyla chrysoscelis*)

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Hearing and acoustic communication in 'real world,' multi-source environments require animals to group sound elements produced by the same source into perceptually coherent 'auditory objects.' However, research on nonhuman animal communication rarely investigates perceptual processes involved in forming auditory objects of communication sounds. We tested the hypotheses that spectral and spatial proximity promote the sequential integration of temporally separated sounds produced by the same source into coherent auditory objects of acoustic signals. Male gray treefrogs produce a pulsatile advertisement call; females prefer longer calls (= more pulses) to shorter calls and discriminate against calls missing pulses. We gave females a choice between a short but spectrally and spatially coherent call (25 pulses) and a longer call (35 pulses) in which alternating groups of 5 pulses had different frequencies (ΔF , 0-12 semitones) and came from different locations ($\Delta\theta$, 0° or 90°). Females generally preferred the longer call at smaller values of ΔF and $\Delta\theta$, indicating a role for spectral and spatial proximity in sequential integration. Under some conditions, however, subjects showed a surprising willingness to integrate pulses despite large ΔF s. Together, these data shed light on the perceptual cues that receivers exploit to form coherent auditory objects of communication sounds.

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INTRODUCTION

Many animals communicate acoustically in large and noisy social aggregations. In these environments, the overlapping sounds of competing signalers combine to create a single waveform that impinges on the receiver's ear, and which the auditory system must then parse (reviewed in Hulse, 2002; Bee, 2012). This process is made especially difficult because signals can be complex in both spectral and temporal structure. To compare and discriminate between signals, receivers must perceptually integrate or *group* sound elements from a single source (e.g. syllables composing words) across frequency and time into coherent representations. These representations are commonly known as *auditory objects* (Griffiths and Warren, 2004) and the perceptual grouping mechanisms responsible for their origin are sometimes referred to as *auditory object formation*. Very little is known about how animals form auditory objects of their acoustic communication signals (Bee and Micheyl, 2008). In humans, sounds tend to be grouped into the same auditory object when they share commonalities in one or more features (Bregman, 1990). For example, when sound elements are presented sequentially, they tend to be grouped if they have similar frequencies (small *spectral incoherence*), but not if they have very different frequencies (large *spectral incoherence*). The broad aim of this research is to elucidate the mechanisms animals use to group vocal communication signals appropriately in complex acoustic environments. This paper takes up the specific hypothesis that spectral and spatial coherence facilitate auditory grouping in Cope's gray treefrogs (*Hyla chrysoscelis*).

Frogs are an important model system for the study of hearing and sound communication (Ryan, 2001; Gerhardt and Huber, 2002; Kelley, 2004; Narins *et al.*, 2007; Bee, 2012; Schwartz and Bee, in press; Vélez *et al.*, in press). The communication system of Cope's gray treefrog is one of the best understood (reviewed in Gerhardt, 2001; Gerhardt and Huber, 2002). During the breeding season, male gray treefrogs gather in ponds where they broadcast loud, pulsatile advertisement calls composed of ≈ 30 pulses, produced at a rate of ≈ 50 pulses/s (Ward *et al.*, in review). Each pulse has a bimodal frequency spectrum with peaks close to 1.3 kHz and 2.6 kHz (Schrode *et al.*, 2012). Female fitness is strongly tied to the ability to recognize, localize, and discriminate between male calls. Females exhibit strong preferences for particular signal traits and will exhibit phonotaxis (approach behavior) toward preferred calls. In the laboratory, females will show phonotaxis toward synthetic calls, including calls that have a frequency equal to just one of the normal spectral peaks of a call, indicating that they consider these manipulated calls to be relevant biological signals (Gerhardt *et al.*, 2007; Bee, 2010). In two-choice tests, females prefer calls with more pulses (Bee, 2008b; Ward *et al.*, in review), and discriminate strongly against calls where pulses have been replaced with silent gaps (Seeba *et al.*, 2010).

The way that frog ears encode frequency differs from that of most animals in which auditory grouping has been investigated. While most animals have one sensory organ in the inner ear, frogs have two distinct organs, the amphibian papilla (AP) and the basilar papilla (BP) (Geisler *et al.*, 1964). Given this uniqueness, we may find that frogs perform auditory grouping in a novel way compared to those few animals that have been previously studied. In all frogs examined to date, the AP is sensitive to lower frequencies than the BP; additionally, nerve fibers arising from the AP tend to be selective (or tuned) for small frequency ranges (reflecting the tonotopy in the AP), while those from the BP are homogeneously tuned to a broad frequency range (Zakon and Wilczynski, 1988). The frequencies to which the sensory organs are most sensitive often coincide with spectral peaks in advertisement calls (Capranica and Moffat, 1983; Gerhardt and Schwartz, 2001). While these trends in tuning seem consistent across the handful of species that have been studied, the exact tuning properties of the sensory organs in gray treefrogs is unknown. If gray treefrogs have organs selectively tuned to the frequencies in their calls, the AP and BP should be most sensitive to frequencies around 1.3 kHz and 2.6 kHz, respectively. It is likely that intermediate frequencies between 1.3 kHz and 2.6 kHz excite both organs (Gerhardt, 2005).

BEHAVIORAL EXPERIMENTS

Methods

Our general methods followed those described in more detail in our recent studies of Cope's gray treefrogs; readers are referred to these studies for additional methodological details not provided here (Bee, 2007, 2008a, 2008b, 2010; Swanson *et al.*, 2007; a; Bee and Riemersma, 2008; Bee and Schwartz, 2009; Kuczynski *et al.*, 2010; Love and Bee, 2010; Seeba *et al.*, 2010; Vélez and Bee, 2010, 2011, in press; Nityananda and Bee, 2011, 2012; Bee *et al.*, 2012; Schrode *et al.*, 2012).

Subjects

We collected Cope's gray treefrogs from three populations in neighboring counties in eastern-central Minnesota. Frogs were brought to the laboratory and housed short-term for behavioral tests. After testing, subjects were released at their collection site, usually within three days of capture. All procedures for recording, collecting, handling, and testing animals were approved by the University of Minnesota's Institutional Animal Care and Use Committee (#0809A46721 and #1202A10178) and complied with the National Institutes of Health guidelines for animal use.

Protocol

Using two-stimulus phonotaxis experiments (Gerhardt, 1995), we tested the working hypothesis that female gray treefrogs use spectral and spatial coherence to group sequential elements (pulses) of communication signals. We gave females a choice between a short but spectrally and spatially coherent call (25 pulses) and a longer call (35 pulses) in which alternating groups of 5 pulses had different frequencies (ΔF , 0-12 semitones) and came from different locations ($\Delta\theta$, 0° or 90°) (examples illustrated in Fig. 1). Both calls had unimodal frequency spectra, with a carrier frequency matching one of the spectral peaks of a natural advertisement call (1.3 kHz or 2.6 kHz). By using calls with unimodal spectra, we attempted to target just one of the two auditory papillae and potentially identify distinct roles for each in auditory grouping. The long call was constructed by interleaving two "gapped calls" in which groups of five pulses were replaced with silence, one whose pulses had frequencies equal to the carrier frequency of the call (denoted "On Frequency"), and one whose pulses had a frequency 0, 2, 4, 6, 8, or 12 semitones (ST) above or below the carrier frequency (denoted "Off Frequency"). We determined through a series of control tests that females did not show strong preferences for any of the frequencies tested (Schrode *et al.*, 2012). For each carrier frequency we tested females with calls at all levels of spectral incoherence, and we replicated the experiment using signal amplitudes of 85, 73, 61, and 49 dB SPL, for a total of 240 frogs. In all of these tests, the On Frequency and Off Frequency pulses originated from the same location ($\Delta\theta = 0^\circ$). We tested an additional group of females at the 85-dB playback level using 35-pulse calls in which the On Frequency and Off Frequency pulses originated from two different locations separated by 90° around our circular test arena.

We made the following predictions based on previous work in the lab showing that females prefer longer calls over shorter calls (Bee, 2008b) and calls with consecutive pulses over gapped calls (Seeba *et al.*, 2010). If females used spectral and spatial coherence to group sequentially produced pulses into a coherent call, we expected that when the spectral and spatial incoherence in the long call was small, females would group pulses into a single coherent, attractive long call that would be preferred over the short call. As spectral or spatial incoherence increased, however, we predicted females would be less likely to group the pulses of the two gapped calls, instead perceiving

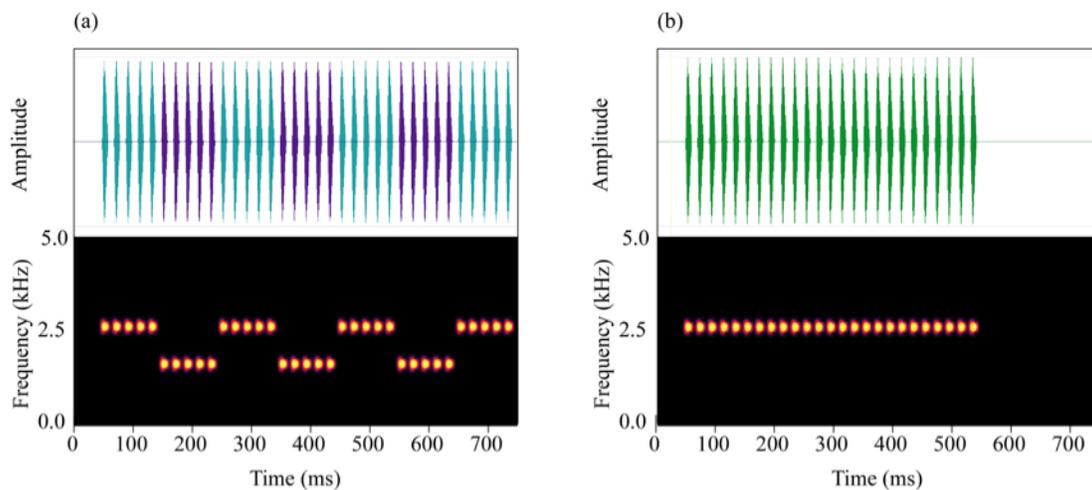


FIGURE 1. Example stimuli used in two-choice tests. An example 35-pulse long call (a) and a 25-pulse short call (b) are depicted in oscillograms (top) and spectrograms (bottom). Long and short calls used in a given test had the same carrier frequency; in this example the long call and its corresponding short call have a carrier frequency of 2.6 kHz (a-b, bottom). Long calls were spectrally incoherent in that they included some Off Frequency pulses (purple pulses in (a) top) that were either above or below the carrier frequency. The example long call has Off Frequency pulses that are 8 semitones below the carrier frequency.

two distinct, unattractive gapped calls, each of which would be less attractive than the spectrally and spatially coherent short call. We tested these predictions after converting the proportion of females that responded to the long call to a continuous measure of response strength in units of dB (based on a separate control experiment not described here).

Results & Discussion

As predicted, response strength to the long call decreased with increasing frequency and spatial separation between the ON Frequency and OFF Frequency pulses. In terms of spatial coherence, females tended to group pulses originating from the same spatial location, though the effect of spatial proximity was not strong (data not shown). Somewhat unexpectedly, the decrease in response strength as a function of frequency separation only occurred when the frequency of Off Frequency pulses was below 1.3 kHz or above 2.6 kHz (Fig. 2; cf. solid lines in regions I, II and III). For clarity, only results fitted to the data for signals broadcast at 85 dB SPL are plotted in Fig. 2, but the general pattern was similar for all amplitudes tested. These results were consistent with the hypothesis that frogs use spectral coherence to group sequential elements of communication signals, at least for some frequency ranges. However, decreased sensitivity of the frog's auditory system to some frequencies could invoke the perception of lower amplitudes for those frequencies. Thus, an alternative hypothesis for our results was that frogs use a level-dependent mechanism to group sequential elements of communication signals. For frequencies between 1.3 kHz and 2.6 kHz, response strength was constant or increased with increasing spectral incoherence. We subsequently hypothesized that increased responsiveness at Off Frequencies between 1.3 and 3.6 kHz may have been due to simultaneous excitation of both sensory papillae by the long call. To test these additional hypotheses regarding level-dependence and simultaneous excitation, we measured auditory sensitivity directly using a neurophysiological method called the auditory brainstem response (ABR), which we describe in the next section.

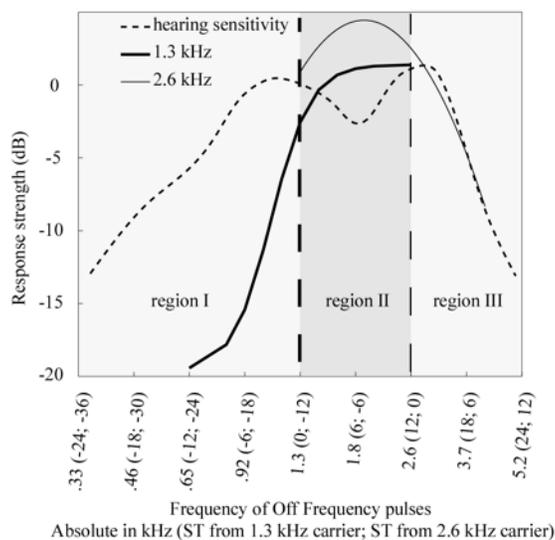


FIGURE 2. Results of two-choice tests and hearing sensitivity. Females were given an option between a short call and a long call with spectral incoherence. Calls had a carrier frequency of 1.3 kHz (dark line) or 2.6 kHz (thin line). Response strength toward the long call is plotted versus the frequency of the Off Frequency pulses in terms of absolute frequency as well as distance of the frequency from the carrier frequency. Response strengths are shown as fitted data. Also plotted is a curve of relative sensitivity of the auditory system (dashed line) constructed from auditory brainstem responses. Compare the slopes of the sensitivity curve to the 2.6 kHz behavioral curve versus the 1.3 kHz curve.

PHYSIOLOGICAL EXPERIMENTS

Methods

Subjects

Cope's gray treefrogs were collected from the same three populations as those used in behavioral experiments. We tested 25 males and 25 females within five days of their collection during the breeding season. Subjects were either released following testing or held in the laboratory for additional experiments. All procedures for recording, collecting, handling, and testing animals were approved by the University of Minnesota's Institutional Animal Care and Use Committee (#0803A28781 and #1103A97192) and complied with the National Institutes of Health guidelines for animal use.

Protocol

Our procedures generally followed those for recording the ABR in small birds and reptiles (Brittan-Powell *et al.*, 2002, 2005, 2010; Brittan-Powell and Dooling, 2004). Experiments took place in a mini-acoustic chamber. For recordings, subjects were first paralyzed with an injection of d-tubocurarine chloride, then placed in a natural position directly facing the playback speaker. Small subcutaneous recording electrodes were placed under the scalp. We broadcast multiple-intensity trains composed of nine 5-ms tone pips in order of ascending level. Level within the train ranged a total of 40 dB with a difference of 5 dB between subsequent pips, although the actual levels used varied between frogs. Frequency was constant within a train, but we tested each frog with randomly-ordered trains of 21 different frequencies, ranging from 0.35 kHz to 5.0 kHz. Responses were averaged over 400 presentations in a single replicate of each train before analysis; thresholds were determined for two such replicates and then averaged.

We determined auditory thresholds (relative sensitivity) for each frog to each frequency. To do so, we plotted responses to each tone pip of a train in order of descending level, then determined threshold to be halfway between the lowest level at which a response occurred and the next highest level at which no response was recorded. For each response, we also measured the amplitude of and latency to the first apparent positive deflection.

Results & Discussion

The relative sensitivity curve (Fig. 2; dashed line) had an "M" shape with two peaks of sensitivity centered at the frequencies in natural calls (1.3 kHz and 2.6 kHz). Sensitivity decreased greatly toward the extreme frequencies tested, and was ≈ 6 dB lower at the frequencies between the two peaks of sensitivity. The shape of the sensitivity curve supported our hypothesis that tuning in this species follows the general trends seen across frogs: peaks of sensitivity centered around the spectral peaks in the natural call, with decreasing sensitivity away from those frequencies. Subsequent analyses of ABR amplitudes and latencies suggest the lower frequency half of the curve (region I and partially region II) reflects responses from nerve fibers arising from the AP, while the higher frequency half of the sensitivity curve (region III and part of region II) reflects responses originating in the BP. The region of decreased sensitivity at intermediate frequencies (1.5-2 kHz; region II) is probably outside the best sensitivity of either papilla; however, since sensitivity at these frequencies is better than at the extreme frequencies, these frequencies likely excite both papillae simultaneously, as well as their corresponding auditory nerve fibers.

By superimposing the physiology data over the behavioral results, as in Fig. 2, we were able to evaluate evidence testing our hypotheses derived from our behavioral data (see above). The high frequency slope (>2.6 kHz) of the sensitivity curve is similar to the slope of the curve for behavioral data with the 2.6 kHz carrier frequency (region III). The match between behavior and auditory sensitivity at high frequencies (region III) suggests that the decrease in behavioral response strength was likely due to differences in the perceived amplitude of these frequencies. This interpretation is consistent with our alternative hypothesis that frogs use a level-dependent mechanism to group high-frequency sounds. This match was not observed for the low frequency slopes (<1.3 kHz) for hearing sensitivity and behavioral responsiveness (region I); instead, the slope of the behavioral data curve was much steeper than that of the hearing sensitivity curve. The mismatch between the curves for lower frequencies (region I) suggests that the decrease in response strength is not due to differences in amplitude, but rather level-independent differences in frequency. This interpretation is not consistent with the alternative hypothesis. These results make sense, given that cells of the AP are narrowly tuned, while BP cells are more broadly tuned. Narrow tuning is conducive to frequency discrimination, because discrete populations of neurons or nerve fibers can respond to each frequency. When tuning

is very broad, on the other hand, a single population is activated by multiple frequencies, thus giving little information about the frequency of the stimulus that is level independent. Therefore, for low frequencies encoded by the AP, frequency may be a more useful cue than for high frequencies encoded by the BP. A level-dependent mechanism of grouping for higher frequencies could compensate for the inability to easily discriminate between these frequencies. The mid-frequency region of the sensitivity curve, which was indicative of simultaneous excitation of both papillae, overlaps with the region of the behavioral data that showed constant or increased response magnitude (Fig 2; region II). This result is consistent with our hypothesis that simultaneous excitation of the two papillae was responsible for the increased response magnitude at these intermediate frequencies.

CONCLUSIONS

Based on the behavioral data we collected, we conclude that females can use frequency cues to group acoustic communication signals appropriately. The physiological data suggest that the gray treefrog AP and BP are maximally sensitive to 1.3 kHz and 2.6 kHz, respectively, with decreasing sensitivity to lower and higher frequencies, and possible simultaneous excitation at mid-range frequencies (1.5 kHz-2.0 kHz). Taken together, our behavioral and physiological data suggest two new hypotheses. First, auditory grouping in frogs is mediated by a level-independent mechanism for lower frequencies, within the putative range of the AP, and a level-dependent mechanism for higher frequencies, within the putative range of the BP. Second, intermediate frequencies excite both papillae and trump the decrease in auditory grouping that was expected at these frequencies. Our next step is to test these and other hypotheses about neural mechanisms using more invasive neurophysiological recordings.

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