Sensory Biology: How Female Treefrogs Pick Mates at a Noisy Party

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A recent study has found that, despite strong acoustic masking from background noise, female treefrogs are able to select among individual males advertising for mates by taking advantage of small, periodic decreases in the overall noise structure.

Animal brains are constantly bombarded with a dizzying array of complex environmental stimuli. These stimuli must be rapidly sorted and identified, as failure to do so imposes costly fitness consequences [1]. For example, an animal that identifies a different species as a viable mate may waste its considerable reproductive effort (Figure 1). For animals that communicate acoustically, recognizing and discriminating among relevant auditory signals is a critical task. As anyone who has attempted to have a conversation at a noisy party can attest, this task becomes exponentially more difficult with increasing extraneous noise. Like humans, many other animal species communicate amid noise [2] and must solve this cocktail-party-like problem [3]. Although the question of how animals communicate in noise is an old one, the mechanism(s) by which the auditory system accomplishes this task has remained rather elusive; a study of treefrogs by Lee *et al.* [4], reported in this issue of *Current Biology*, provides a critical new insight into one mechanism by which animals may solve this problem.

Male frogs use vocalizations to communicate for reproductive purposes and often congregate in large calling groups, creating a cacophony of overlapping sounds referred to as a chorus [5]. Amid this din of noise, females must recognize members of their own species and discriminate among individual calls to select a mate [6]. Lee *et al.* [4] took advantage of the impressive existing body of knowledge about the communication system of Cope's gray treefrog (*Hyla chrysoscelis*) [7–9] to design a series of clever experiments that uncovered a mechanism for hearing amid noise: the exploitation of statistical regularities in noisy acoustic scenes.

Lee *et al.* [4] first tested the hypothesis that a group of animals vocalizing together will generate comodulations in overall chorus noise. That is, the different frequencies produced in the frogs' advertisement calls exhibit synchronous changes in amplitude (Figure 2). In effect, this produces short, but repeated 'windows' of decreased background noise that the frogs can exploit to improve their ability to listen for individual signals within the noise. Alternative possibilities for chorus noise structure include uncorrelated noise, where changes in amplitudes of the different frequencies occur asynchronously (Figure 2), and unmodulated noise, where there are no significant decreases in sound energy in the background noise. To test their comodulation hypothesis, the authors passed recordings of frog choruses through a series of 'tuning' filters simulated to match the sensitivity of the frog's two inner ear organs. They found that comodulations in the frequencies important to the frog ear occurred with statistical regularity. This portion of the study elucidated an important physical feature of biological noise in this communication system and raised the possibility that the frogs could take advantage of it.

In the next step, borrowing procedures from human psychophysical studies, Lee *et al.* [4] asked if the frogs could exploit this comodulated structure to improve their ability to detect individual calls within the noise. Here they played a single male advertisement call (the signal) to females in one of four treatments: no noise control; unmodulated noise; uncorrelated noise; and comodulated noise. All noise treatments consisted of frequencies within the range of normal calls and thus were likely to generate substantial masking of the target signal. The authors also varied the amplitude of the target signal relative to background noise, altering the overall signal-to-noise ratio. In these phonotaxis tests, female frogs will approach a speaker playing the call if they can detect it, providing a robust assay of signal detection by the animal. The authors found that all noise treatments decreased the ability of the frogs to detect the signal in noise. The frogs performed substantially better in comodulated noise, however, than in the other noise treatments. Thus, they demonstrated that the frogs were able to

Figure 1. Hybrid mating between gray treefrog and squirrel treefrog.
This incorrect mate identification — a small squirrel treefrog male clinging to large female gray treefrog — will result in lack of egg development, a considerable loss of energetic resources for the female.

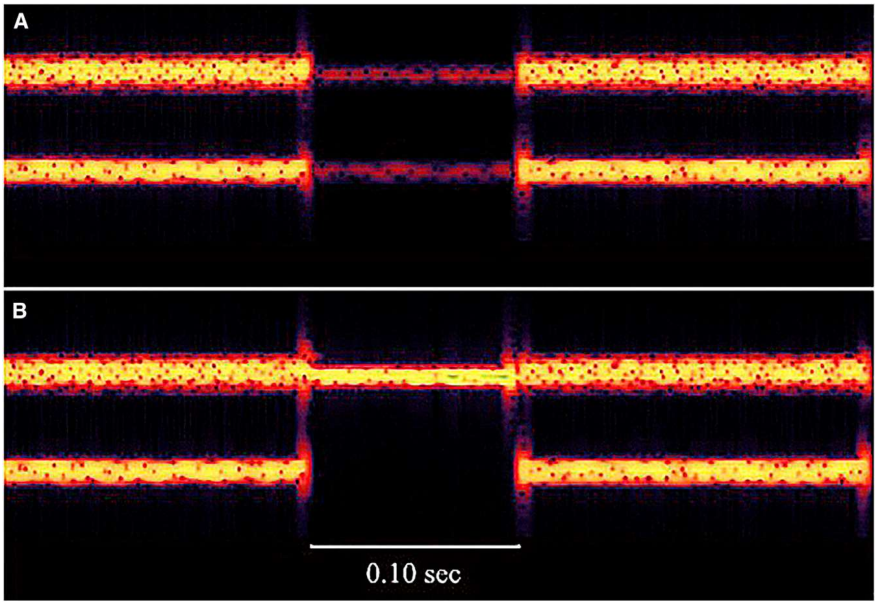

Figure 2. Stylized example of comodulated and unmodulated noise structure.
The x-axis represents frequency; the y-axis is time. Brighter regions indicate more sound energy. (A) Comodulated noise. There are two frequency bands that occur in the natural frog calls. In comodulated noise, the energy in both the upper and lower frequencies decrease together, leaving quieter 'windows' of opportunity for listening to target sounds. (B) Unmodulated noise. In unmodulated noise, the energy in only one frequency band decreases. This results in noise remaining in at least part of the sound, and does not provide the 'quiet windows.' In unmodulated noise (not shown) there is no substantial decrease in sound energy at any frequency.

exploit comodulated noise, improving their ability to detect the signal.

Lee *et al.* [4] performed a second set of experiments where they then asked if the frogs could not only detect a call, but also discriminate between two calls in noise. Here again the authors cleverly exploited a biological feature of this animal's communication system. The Cope's gray treefrog is the sister species to the morphologically identical gray treefrog (*Hyla versicolor*). Males of *H. chrysoscelis*, however, produce calls that have a pulse rate roughly twice as fast as those of *H. versicolor*, and females express strong preferences for pulse rates consistent with their own species. In addition to preferring species-specific pulse rates, female frogs also prefer to mate with males who produce high-effort calls, for example, calls with more pulses [7,10]. In the first experiment, Lee *et al.* [4] asked if females of *H. chrysoscelis* could distinguish between calls of the two species in noise. Noise of any kind increased error rates in distinguishing between the call types. Again, however, the frogs exhibited significantly fewer errors in the comodulated treatment relative to the other noise types. Finally, they asked if the females could discriminate among high- and low-effort calls. Consistent with previous results, all noise reduced the females' ability to distinguish, but they made the fewest errors in comodulated noise.

A continuing enigma in noisy acoustic communication scenes is how individuals are able to sort out any meaningful signal at all. This substantial problem occurs across diverse taxa ranging from insects [11], to frogs [12] to birds [13], and yet evolution has favored this form of communication in multiple independent lineages. Lee *et al.* [4] have provided at least one answer to how the evolution of animal sensory systems has solved this problem.

If the authors had stopped there, the paper would represent an important contribution to our understanding of sensory biology and signal evolution; however, they went on to make two further advances that promise to make it valuable for other fields. First, the authors adopted behavioral methods from psychophysical studies, for example, determining hearing thresholds [14]. This places the work in a broader comparative framework that can be used to understand the physiology and evolution of vertebrate hearing, including applied applications for humans. Second, there is a growing interest in understanding how anthropogenic noise influences the behavior and ecology of acoustically communicating animals [15–17]. The findings here demonstrate that for future studies on this topic, researchers should pay attention not only to the frequency and amplitude of the anthropogenic noise, but also to the actual noise structure itself. In sum, this work represents a broad contribution to our understanding of acoustic communication from both pure and applied perspectives.

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