Bugs and bats: Neural analysis of behaviorally relevant sounds in crickets

Gerald Pollack*

*Corresponding author's address: McGill University, Montreal, H3A1B1, Quebec, Canada, gerald.pollack@mcgill.ca

Bugs and bats: neural analysis of behaviorally relevant sounds in crickets. Hearing in crickets is specialized to serve particular behavioral functions, namely intraspecific communication and predator avoidance. Male crickets produce species-specific acoustic signals (songs) that attract distant females, promote copulation, and contribute to agonistic interactions with rivals. Crickets also hear the echolocation calls of aerially hunting bats, which evoke avoidance responses. These clear behavioral functions of hearing, combined with the relative simplicity of the cricket's nervous system, make it possible to address questions about how behaviorally relevant sensory signals are analyzed at the level of single, uniquely identifiable nerve cells. Cricket songs and bat calls differ both in rhythm and in spectrum, and neurons throughout the auditory processing chain are specialized for processing these two sorts of signal. I will focus on specializations that are evident at early stages of auditory processing, i.e. primary sensory neurons and the first-order interneurons with which they interact.

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As for many animals, hearing in crickets is specialized to serve specific behavioral functions, namely, intraspecific communication and predator avoidance. Crickets use acoustic signals, songs, to mediate pair formation, to promote mating, and in agonistic interactions. And, like many nocturnal insects, crickets can detect the echolocation calls emitted by hunting insectivorous bats. The clear behavioral functions of sound, together with the relative simplicity and accessibility of the cricket nervous system, have facilitated the exploration of specialized neuronal processing of communication signals and bat calls even at early levels of auditory processing, i.e. by auditory receptor neurons and the first-order interneurons with which they interact.

CRICKET SONGS AND BAT CALLS

Cricket songs and bat calls differ in both spectral and temporal characteristics. Figure 1 illustrates the mate-attraction song of the cricket *Teleogryllus oceanicus*, and the sequence of echolocation calls emitted by a hunting bat, *Myotis lucifugus*. The cricket song consists of a series of similar sound pulses, with carrier frequency of ca. 4.5 kHz, that are emitted with a species-specific temporal pattern. The bat calls are ultrasonic, and are emitted at an accelerating rate as the bat closes in on its prey. Sound-pulse rates in the cricket song range from ca. 8 to 32 Hz; those in the bat call range from ca. 10 to >100Hz.

![Graph showing cricket and bat call frequencies](image)

**FIGURE 1.** Sonograms showing the calling song of a cricket, *Teleogryllus oceanicus*, and a sequence of echolocation calls produced by a bat, *Myotis lucifugus*. Note the difference in time scales.

POSITIVE AND NEGATIVE PHONOTAXIS

Female crickets walk or fly towards the source of a conspecific male's song, and they fly away from a source of ultrasound. These behaviors are known as positive and negative phonotaxis, respectively. Both the sound frequency and temporal pattern of a stimulus are important in determining responses. Positive phonotaxis occurs only if sound frequency is between ca. 3 and 15 kHz, and only if the temporal pattern of the stimulus is sufficiently similar to that of the species' song (Pollack et al. 1984; Doolan and Pollack 1985; Hennig and Weber 1997; Hennig 2009). Negative phonotaxis is best elicited by sound frequencies above 15 kHz; the temporal structure of the stimulus is relatively unimportant (Moiseff et al. 1978; Pollack et al. 1984).

NEURAL PROCESSING OF ACOUSTIC SIGNALS

The cricket's ears, situated on the front legs, include a group of ca. 65-70 primary sensory neurons. Approximately 75% of these are most sensitive to frequencies similar to the dominant frequency of the species' song, with the remainder most sensitive to higher frequencies (Imaizumi and Pollack 1999). The axons of these sensory neurons terminate in the prothoracic ganglion of the ventral nerve cord, where they synapse with a small group of interneurons that can be recognized, based on their anatomy and physiology, in all individuals, and even between species (Hedwig and Pollack 2007). Three of these, each occurring as a bilateral pair, have been particularly well characterized with respect to their roles in acoustic behavior. The neuron AN1 is sharply tuned to the dominant frequency of calling song. Each AN1 receives excitatory input from cricket-song-tuned receptors of one ear, and their axons project to the brain, where they provide synaptic input to a network of neurons that comprise the filters that allow crickets to respond selectively to their own species' songs (Kostarakos and Hedwig 2012). The AN2 neurons are most sensitive to high sound frequencies, including those produced by bats (Moiseff and Hoy 1983). They receive excitatory input from high-frequency-tuned receptors, again unilaterally, and their
axons also project to the brain. ON1 is responds robustly to a broad range of frequencies, including those characterizing cricket songs at bat sounds (Atkins and Pollack 1986). Its axon projects to the contralateral hemiganglion, where it provides inhibitory synaptic input to the interneurons that are excited by the ear on that side. The circuitry underlying early auditory processing is illustrated in Figure 2.

![Diagram of auditory circuitry](image)

**FIGURE 2.** Early auditory circuitry. LF and HF represent auditory receptor neurons that are most sensitive to the relatively low sound frequencies that are dominant in cricket song (LF) or to high sound frequencies (HF) including those emitted by echolocating bats. AN1, AN2, and ON1 are bilaterally paired interneurons. Synaptic connections from receptor neurons to the interneurons are excitatory; those from ON1 on to contralateral interneurons are inhibitory.

**Neural processing of cricket song**

The temporal filters that underlie recognition of conspecific songs reside in the brain (Kostarakos and Hedwig 2012), but species-specific pre-processing occurs at the earliest levels of the auditory pathway. Figure 3 shows the information about modulations in stimulus amplitude, a measure of the accuracy of temporal coding, that can be extracted from the spike trains of AN1 and ON1. For both neurons, temporal coding is best over the narrow range of AM rates that occur in song (Marsat and Pollack 2004, 2005).

![Graph of relative magnitude vs. AM frequency](image)

**FIGURE 3.** Selective temporal coding. The curves show (normalized) information content of the spike trains of AN1 (cyan) and ON1 (black) in response to a stimulus in which amplitude was randomly modulated through time. The spectrum of the envelope of the species' song is shown in blue. Inset shows an oscillogram of the song.

In many neurons, temporal response properties are shaped in part by the dynamics of K currents. However, the range of AM rates that is best encoded by ON1 is not affected by intracellular injection of TEA or BAPTA, or by extracellular application of 4AP, although the amount of information embedded in the spike train may decrease. Moreover, when ON1 is driven by depolarizing intracellular injection, it encodes a broader range of AM rates than when it is stimulated acoustically. These findings suggest that ON1's intrinsic properties may play little if any role in determining its temporal selectivity, and indicate that this may be due instead to the pattern of its synaptic inputs. Indeed, when ON1 is stimulated acoustically, but its spikes are prevented by intracellular injection of
hyperpolarizing current, selective coding is evident in the pattern of its summed synaptic potentials. Surprisingly, the temporal coding abilities of individual receptor neurons is poor (Figure 4). However, modeling shows that coding approaching that of the interneurons can be achieved by pooling the responses of a population of receptor neurons (Sabourin and Pollack, 2010).

![Graph showing temporal coding by ON1 and cricket-frequency-tuned receptor neurons](image)

**FIGURE 4.** Temporal coding by ON1 (blue) and by cricket-frequency-tuned receptor neurons (red).

**Neural processing of ultrasound**

Negative phonautaxis is triggered by high-rate firing of the neuron AN2 (Nolen and Hoy 1984). When crickets are presented ultrasound stimuli that vary in amplitude through time (a convenient stimulus for investigating neuronal temporal properties), AN2 responds with occasional bursts of spikes, i.e., brief periods of high-rate firing, that are interspersed with isolated spikes. The bursts tend to occur following sharp increases in stimulus amplitude. Behaviorally, crickets respond to these stimuli with discrete, brief, steering responses. Comparison of the timing of AN2 bursts or isolated spikes with the timing of steering responses shows that bursts, but not isolated spikes, elicit steering responses (Marsat and Pollack 2006, 2012; Figure 5).

![Graph showing stimulus envelope, AN2 spikes, and steering responses](image)

**FIGURE 5.** AN2 bursts elicit steering responses. Top trace: stimulus monitor. Middle: AN2 spike train, with bursts highlighted in red. Bottom: steering responses, as monitored by movements of the abdomen. Discrete movements away from the sound source, indicating negative phonautaxis, are highlighted in blue. Steering responses follow bursts, but not isolated spikes. Modified from Marsat and Pollack (2006).

ON1, which responds to ultrasound as well as to cricket-like frequencies, also exhibits bursts of spikes, but only for ultrasound stimuli (Marsat and Pollack, 2007). This carrier-frequency specificity suggests that, like selective coding of the temporal features of cricket songs, bursting might have its origins in the responses of auditory receptor neurons. Indeed, high-frequency-tuned receptor neurons, but not those tuned to cricket-like frequencies, produce bursts, and these are temporally correlated with bursts in AN2 (Sabourin and Pollack 2009; Figure 6).
FIGURE 6. Temporally correlated bursting in a high-frequency-tuned receptor (HF) and AN2. Bursts are highlighted in red. Modified from Sabourin and Pollack (2009).

CONCLUSIONS

The results summarized here show that behaviorally relevant temporal response properties of interneurons, specifically selective coding of species-specific temporal patterns and generation of spike bursts that trigger escape responses, may be established at the earliest possible stage of sensory processing, that of the receptor neuron.

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REFERENCES


