Synchrony in Cricket Calling Songs: Models of Coupled Biological Oscillators

T. G. Forrest¹, Joel Ariaratnam², Steven H. Strogatz³

¹Department of Biology, University of North Carolina at Asheville, Asheville, North Carolina 28804
²Theoretical and Applied Mechanics, Cornell University, Ithaca, NY 14750

Abstract: Snowy tree crickets produce a rhythmic acoustic signal composed of short chirps. The chirp rhythms are very regular and dependent on temperature. When signaling in groups, males synchronize their chirps. The rhythmic signals of these tree crickets were used as a model of a 'biological oscillator'. We measured the phase responses of males to single probe stimuli similar to the male calling song. The phase response curves (PRC) of males showed both strong (type 0) and weak (type 1) resetting. PRCs differed depending on amplitude, duration and frequency of the resetting stimulus. In other experiments, males could adjust their periods by as much as 15% when phase-locking (1:1) to an entraining stimulus. Signaling behavior of males was compared with a simple model of coupled oscillators. The phase resetting was not consistent with the simplest resetting model in which a male's phase shift is completed after one cycle of the chirp period. In addition, a simple iteration of the PRC could not stimulate the phase-locking observed in the entrainment experiments indicating that the acoustic coupling between males differs from a simple resetting model.

INTRODUCTION

The loud, conspicuous acoustic displays of crickets, katydids and cicadas have attracted the attention of biologists for centuries. The signals are produced by males and function to attract sexually responsive females for mating. Males often signal in groups and compete with neighbors for the attention of the females. As a result of this competitive situation specialized chorusing behavior has evolved in a number of species (1). The interactions among neighboring males often maintain very precise phase relationship between their calls (2).

The snowy tree cricket, Oecanthus fultoni, is a common species found throughout much of North America. Males call from shrubs or trees emitting a rhythmic chirp and close neighbors synchronize their song. The males maintain synchrony by shortening or lengthening their chirp period. The changes in period depend on the phase at which their neighbor's songs are heard (3). Thus, a chorus of snowy tree crickets can be considered a group of coupled oscillators. Each male is an oscillator having a particular rhythm, but his rhythm is acoustically coupled to the rhythms of neighboring males. We investigated the mechanisms of synchrony and the acoustic coupling between male tree crickets using techniques commonly used to understand coupled biological oscillators.

METHODS

All recording and playback experiments were controlled using a personal computer and TDT A/D and D/A converters. The playback stimulus simulating the crickets' chirp was generated using custom software. The digital signals were played back at a sampling rate of (50 kHz) from a Motorola piezoelectric speaker. The responses of the males were recorded using a B&K or Sennheisser microphone (10 cm from male) and amplifier. The output of the microphone amplifier was digitized (sampling period 65μsec) and stored on computer for later analysis.

Phase Response. We measured the phase response of individual males to a single probe stimulus. An isolated male sang in a small (10x10x10 cm) screen wire cage within a larger cage designed to reduce noise and acoustic reflections. We recorded 2-4 chirps prior to broadcasting the stimulus and 4-7 chirps after the playback. For each presentation we varied the phase of the stimulus relative to the male's period (Δϕ) and we measured the phase shift of the male as a function of the phase of the stimulus probe is the phase response curve (PRC).

Entrainment. We also wanted to quantify the response of a male to a series of stimuli delivered periodically one after the other. For each presentation, we first recorded 3-5 chirps to determine the male's current chirp period. While the male continued to call, we then played a series of chirps at a particular rate. We digitized the male's song and entraining stimulus and measured the phase of each of the male's chirps relative to the period of the stimulus. We varied the rates of the entraining stimulus to see if males could be entrained by a rhythm faster or slower than their current rhythm.
Model. We wished to test whether the PRC of a male could predict the empirical results from the entraining experiments. In the simplest instance of resetting by a single stimulus, the phase shifts are completed by the first cycle after the stimulus is delivered. There are no subsequent phase shifts, i.e. the oscillator immediately regains its original period but shifted by the amount indicated on the PRC. Given an immediate return, conventional PRC theory indicates that the response to periodic stimulation, like those measured in the entrainment experiments, can be predicted by iterating the phase response (4). We used the PRC measured for a male and tried to predict his entrainment data using this simple model.

RESULTS AND DISCUSSION

Phase Response. Males showed strong (type O) and weak (type 1) resetting to a single chirp stimulus (4). Individuals could show type 0 or type 1 resetting depending on the stimulus conditions. Sismondo (5) found that a tropical katydid switched from strong to weak resetting depending on the level of the stimulus. In addition, we found that stimulus level influenced the magnitude of the phase shift in the PRC, and that the frequency and duration of the probe stimulus changed the PRC.

Entrainment. Males are able to maintain a constant phase relationship (1:1 phase locking) to an entraining stimulus when the period of the stimulus differs from that of the male’s by about 15%. When the stimulus was about 6% slower than the male’s rhythm, his phase remained constant at 0.8 of the stimulus period (Fig. 1B). At a rhythm 13% slower than the male’s period, the male phase-locked at 0.6 of the stimulus period (Fig. 1C). Interestingly, the male did not phase lock to stimulus rates that were faster than his own.

Model. We compared the model’s predicted phase locking with the phase locking observed for a male (Fig. 1). Iterating the PRC did not simulate the male’s entraining data. The model only phase locked with the stimulus when the rate of the stimulus was about 6% slower than the rhythm of the model oscillator (Fig. 1E). The cricket was able to phase lock to stimuli having a much greater range of periods. The inability of the model to mimic the behavior of the cricket is in part related to the assumption that once stimulated the oscillator returns immediately to its original period. The PRCs of many of the males showed significant phase shifts in several chirps subsequent to the stimulus. We are currently working on ways to incorporate these effects into our model.

ACKNOWLEDGMENTS

Supported by National Science Foundation (Grant #DMS-9627189) and by a UNCA Faculty Research Fellowship.

REFERENCES


Figure 1. Each panel shows the phase of the oscillator as a function of the number of stimuli presented. A-C. Male tree cricket entraining. D-F. Model based on PRC of male in A-C. The different panels represent different stimulus rates. A&D Stimulus rate was 0.99 of the oscillator’s rate. B&E. Stimulus rate was 1.06 times the oscillator’s rate. C&F. Stimulus rate was 1.13 times the oscillator’s rhythm.