A-LIFE FOR MUSIC

Music and Computer Models of Living Systems

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Artificial Anuran Choruses

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1.1 INTRODUCTION

Frogs and toads (order *Anura*) can be found just about anyplace where water collects regularly. During their large nighttime assemblies, males call out rhythmically, producing loud, washing choruses of advertisement to the unseen and often unheard females. Choruses commonly include a number of different species, each of whose sound signals fill spectral and temporal niches in the available acoustic bandwidth (Krause 1987).

The structure of anuran choruses can be observed on several time scales. The signal interactions of neighboring callers produce pulses of synchrony and alternation as the callers mutually influence the timing of signal production. Groups of callers engage in competitive bouts lasting several minutes, stimulating other groups, which can spread activation over a large area. These bouts concentrate in one or more periods during a twenty-four-hour cycle, influenced by light, weather, and the presence or absence of predators. Over evolutionary time, female preferences move species through sonic fashions, and the choruses change as genetics drift. It is a natural theme and variation that has been performed continuously for millions of years.

Studies of the signal interactions of anurans, as well as those of insects, have led researchers to develop a general model of an individual's calling patterns based on a phase-resettable oscillator. In addition to explaining the empirical evidence of call-timing adjustments, this oscillator model also allows for general predictions of patterns of synchrony and alternation in simulated choruses. The parameters in this model can be tuned to reproduce the choruses of many different species.

Although chorus models can be useful to composers working with agent-based artificial-life (a-life) models in music by providing a mechanism for rhythmic coordination, these models can alternatively be used to produce a different kind of a-life–based music altogether. Rather than a wholesale appropriation of the algorithms for creative inspiration, an artificial chorus can capture and reproduce a musical event from the natural world as a sort of generative nature recording—a literal imitation of life.

1.2 ACOUSTIC COUPLING AND SYNCHRONY IN CHORUSES

For small nocturnal animals such as insects and anurans, using sound to facilitate the business of life has been a winning strategy. In environments where sight is limited by lack of light and vegetation, males and females alike exploit sound in order to advertise reproductive fitness as well as to locate and select mates.

Ideal breeding sites are often the stage of seasonal nighttime choruses where many species of frogs and toads assemble. Even the distant sound of a chorus can attract both males and females to an area (Gerhardt and Huber 2002). As more individuals join a chorus, there is inevitably competition not only for physical space, but also for acoustic space in which to broadcast a signal of advertisement. Although the calls and calling patterns that have developed in the face of acoustic competition vary from species to species, many frogs and toads share some common signaling strategies molded by common female preferences. These signaling strategies are also displayed in the insect order *Orthoptera*, which suggests a more general convergent solution to the problems of acoustic communication (Greenfield 2002).

One particular signaling strategy found in many species is the alternation and synchronization of calls between conspecific neighbors. This strategy is the result of a perceptual bias in females that causes them to preferentially orient themselves toward, and ultimately approach, males perceived to produce leading calls in a sequence (Bosch and Marquez 2002). Males compete to jam each other's signals in an appeal to this psychoacoustic precedence effect in females.

Although the intended target of a signal may be a female, messages are broadcast indiscriminately to anything with the correct receiving equipment, and chorus participants unavoidably eavesdrop on each other's signals. This eavesdropping can be exploited in the competition to be heard first, and consequently, males have evolved to make call-timing adjustments to their own free-running call period in response to competitors in their immediate vicinity. Ultimately this results in a loose acoustic coupling between competing neighbors.

At its most extreme, call-timing adjustments can drive the chorus to lock around a regular pulse, with each member of the chorus apparently coordinating his or her signaling in synchronous or alternating patterns. This synchronous chorusing is not a coordinated effort, but rather an epiphenomenon of the acoustic coupling between the competing males (Greenfield, Tourtellot, and Snedden 1997).

Although the degree to which synchrony or alternation is expressed in a chorus ultimately varies from species to species, common neural mechanisms are believed to underlie its production. Each individual signaler in a chorus is thought to have a neural oscillator, or pacemaker, that is responsible for triggering calls. The seemingly complex sound of the anuran chorus is the result of many small groups of acoustically coupled signalers.
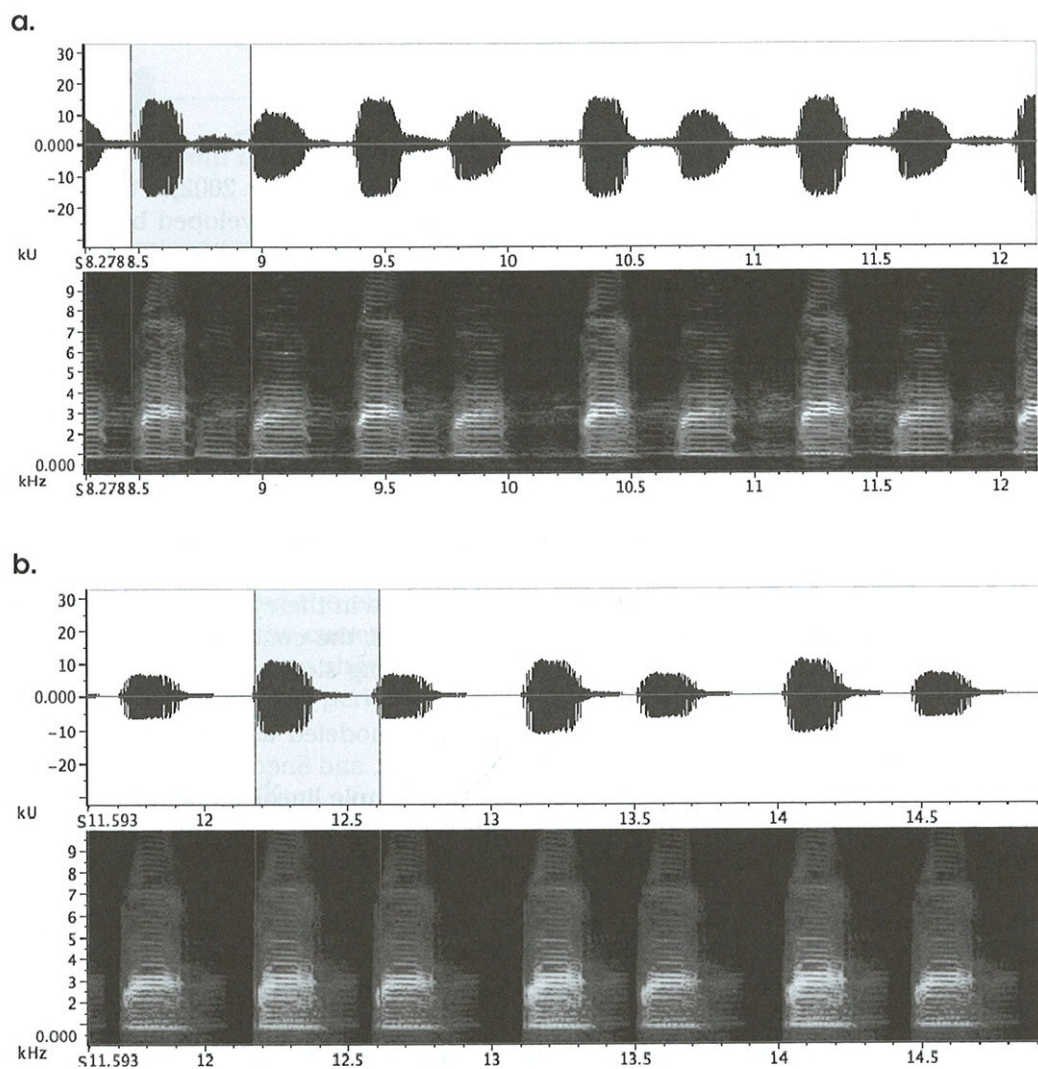
FIGURE 1.1 Spectrogram of (a) natural and (b) artificial green treefrogs alternating.

On the basis of this description, signalers and their interactions can be modeled using a simple network of oscillators that govern the call timing of an individual. It is from one such model that the artificial anuran chorus is built (Figure 1.1).

1.3 THE MODEL

1.3.1 Bodies

The literature on anuran and insect communication describes a number of neural pacemaker models of varying complexity (Gerhardt and Huber 2002). For the following simulations, a basic linear model was used that was developed by Michael Greenfield and his colleagues (Greenfield 2007; Greenfield, Tourtellot, and Snedden 1997) using data collected from playback experiments with the neotropical katydid *Neoconocephalus spiza*. Many other species have since been identified that conform to this model.

I modeled call-timing adjustments by making each anuran in the chorus essentially a sawtooth oscillator with a free-running period T whose phase can be reset by the receipt of a stimulus signal. When the oscillator reaches its peak level, a trigger is sent that results in a call x after a short effector delay t. In the presence of a stimulus signal y the free-running period of the oscillator is reset to its basal level and inhibited for the duration of the stimulus before the oscillator resumes at its natural free-running period. The effect of the stimulus is to either lengthen or shorten the time between calls depending upon where in the cycle the oscillator is reset. If the oscillator is reset on the ascending slope, the concurrent period T' is lengthened. If the oscillator is reset on the descending slope, measured by r, the next call period is shortened (Figure 1.2).

Although this description could conceivably be modeled as a literal sawtooth wave, in a piecewise linear form, Greenfield Tourtellot, and Snedden (1997) have arrived at a computationally efficient and somewhat simple linear model to calculate the modified period T', describing the changes to call timing as influenced by a neighboring caller. The Greenfield timing model is shown below in Equation 1.1:

$$T' = s \left[(d + l/_v) - (r - t) \right] + (T + \varepsilon) + (y - x) \tag{1.1}$$

where T' is the modified call period after the receipt of a stimulus of length y from a neighboring caller. Here, d is the time elapsed since the focal male's last call, l is the distance of the stimulus measured in meters, and v is equal to the speed of sound (344 m/sec). A stochastic element, ε, is added to the call period to better match the reality of imperfect timing in organic pacemakers. The s parameter is the phase response curve (PRC) of the caller, which regresses the response phase against the stimulus phase. It is this s parameter, discussed in the Results section, which has the greatest effect on the development of synchrony or alternation between neighboring callers. Together, the parameters in Equation 1.1 account for effector delay, sound propagation, phase resetting, period inhibition, and oscillator rebounding after inhibition. For a more detailed description of the model, the reader is referred to the original model of Greenfield (1994) and Greenfield, Tourtellot, and Snedden (1997).
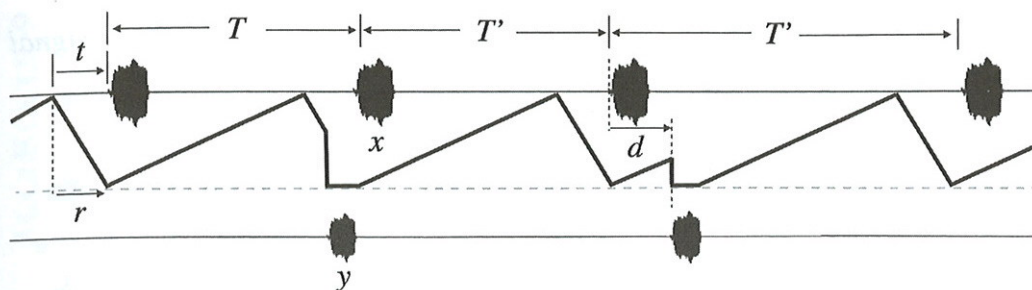
FIGURE 1.2   (a) Phase-resetting inhibitory oscillator showing signal triggering from the focal male and (b) phase resetting and inhibition from an external stimulus.

Of special note here is that when a stimulus is received during the descending slope of the oscillator, or r, the d parameter has a negative value. This is not immediately obvious from Equation 1.1. It is calculated at the time a stimulus signal is received by subtracting the elapsed time since the onset of the last call from the difference between the current call period, T, and the effector delay, t. Thus the effect of a negative d is to shorten the next call period, and that of a positive d is to lengthen the current call period.

1.3.2 The Network

The elegance of the Greenfield timing model is that it describes both the body of the signaler as well as the effect of a stimulus when used in a network of signalers. When simulating a network of signalers using this model, distances are specified for each member of the chorus (given by Equation 1.1), as well as the threshold of sensitivity to the signal of a neighbor. Otherwise the connectivity of the network can inadvertently be quite high, resulting in the continual inhibition of some members of the chorus, which renders them silent.

The sound of the stimulus is modeled to have its intensity decrease with the square of the distance from the source (Di Paolo 2000). In this way, chorus members who are sufficiently far away can be ignored. In fact, there is evidence that each chorus participant selectively attends to no more than a very few neighboring callers—presumably those that are the loudest, closest, or both. Thus, each signaler hears only a few of its closest neighbors (Snedden, Greenfield and Jang 1998).

For a larger chorus, participants are simulated in two-dimensional (x, y) coordinate space, with the "observer" placed in the center of the simulation $(0, 0)$ and reproduced in a stereo field. Signals are panned right and left based on their positive or negative deviation respectively from the center point of the field on the x axis.