

Pseudo-synchronization Leads the Pack:

an examination of psuedo-synchronization in *Pholidoptera griseoptera*

Charlie Chapman¹

*School of Physics, Georgia Institute of Technology, Atlanta, Georgia 30332,
USA*

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Alternation and Synchronization behaviors between the sexual communications of insects, arise as a response to the female preference to 'leaders'. As a response to this, *Pholidoptera griseoptera*, the dark bush cricket, has developed an interesting response model of imperfect alternating and synchronizing, or psuedo-synchronizing (P-S), for gaining the lead in a chorus of chirps. This P-S behavior model, results in an increased rate at which the bush cricket can take lead of a chorus and produces a larger lead gain, than conventional phase response models for alternation and synchronization behavior.

I. INTRODUCTION

A. Alternation and Synchronization

There are many known species of insects, where signal interactions between males of the species result in neighboring males entering collective phase relationships, such as synchronizing (phase angle $\approx 0^\circ$) or alternating (phase angle $\approx 180^\circ$). Signal interactions, in this instance, are defined as phase adjustments a male makes to its sexual advertisement call, in response to other males². This phenomenon has been well studied in choruses of crickets^{1,3,4}, Katydid calls⁵, and the flashing of fireflies⁶.

The general behaviors of synchronization

and alternation in insects has been attributed to the mating preferences of females of the species. Where antecedent studies have shown that, when in the presence of pairs of synchronizing males, females show preference to the male whose signal leads most often². Other evolutionary explanations for these phenomenon include the preservation of species-specific temporal patterns⁴, and the concealment of calls as a response to acoustically orientated predators⁷.

The majority of mathematical models describing this type of behavior do so by viewing the insects as coupled biological oscillators, which follow a phase response curve^{2,8}. Males will compete for the lead position in the chorus by shifting their position on the

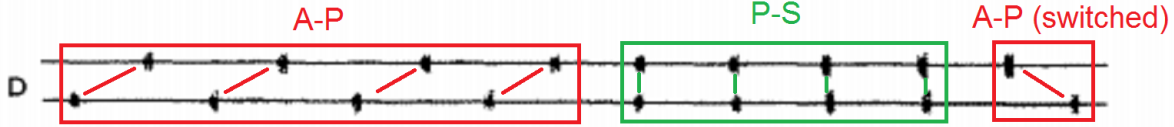


FIG. 1. Interaction pattern between two dark bush crickets, as observed by M.D.R. Jones¹. There is an initial alternating phase (A-P), followed by a phase of pseudo-synchronization (P-S), and finally a shift back to an alternating phase, in which the leading cricket has switched.

phase response curve slightly, resulting in them firing sooner and chirping, and, if successful, taking the lead⁸.

B. A Peculiar Behavior

One species, which exhibits a very unique relationship arising from signal interactions, is *Pholidoptera griseoptera*, the dark bush cricket. When within proximity, males of this species will alternate their chirps, then synchronize for several iterations, before alternating once again¹. The stage of synchrony observed is not perfect however; analysis of choruses has shown that there is always a partial overlap of the signals. In the case of two crickets, one will always be slightly leading the other in time³. This has been termed pseudo-synchronization (P-S), as audibly, it appears to be synchronization between the two crickets.

This complex behavior currently cannot be described according to models using a basic phase-response curve. The closest that

a phase response model can come, is through phase drift, where a phase difference between two crickets signal rates would result in their signals gradually overlapping before moving apart again. However, there are two observations about the bush crickets behavior, which refute this as mere phase drift phenomena. First of all, as observed by Jones¹, the shift from alternation to synchronization, between two crickets, is done in clearly discrete steps, not smoothly as would be expected if this was due to phase drift. Secondly, the amount of chirps for which the two crickets synchronize is highly variable, as opposed to the stable number we would expect from phase drift - over a 4 minute period, Jones was able to observe anywhere between 1 to 6 chirps per synchrony for the same two crickets¹.

The data collected in Jones' research also brings forth another significant feature of the P-S behavior. Looking at two crickets of similar chirp rate, which have just undergone a synchrony event, it can be seen that the lead position always switches between crickets af-

ter such an event (FIG. 1).

C. The Pseudo-Synchronization Model

The culmination of this information lends to the idea of a model in which crickets seem to carefully calculate their moves while attempting to overtake the lead position in the chorus. There are several inherent features of this type of model, which pose significant evolutionary advantages for a cricket. First of all, a cricket can more reliably gain the lead position in this model, as opposed to a basic phase response model, as it isn't sporadically shifting its phase either up or down in the chance of taking the lead. It is making a calculated move into a P-S state, and then shifting forward into the lead. The second major advantage for a cricket following this type of model, is that when it does take the lead in this model, it will be by a maximum phase shift of roughly 180. In the basic phase response model, there is a maximum phase shift which can be achieved if a cricket were to start from a position near P-S. However, in most cases, a cricket following a phase response model will not start from this ideal position, but in a range of unideal positions (FIG. 2).

The remainder of this paper focuses on a presentation of evidence comparing the favor-

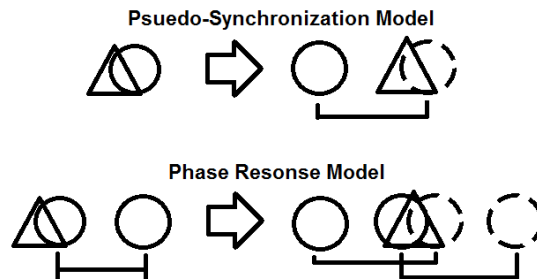


FIG. 2. The triangle represents the lead cricket, and the circle represents the follower. As can be seen, the follower in the P-S model will always achieve a maximum possible gain when overtaking the leader, whereas most values of the gain in the phase response model will be less than optimal.

ability, of a P-S model versus a basic phase response model, for gaining the lead position. Favorability in this context, is defined as the rate at which a following cricket is able to overtake a leading cricket.

II. METHODS

Due to the fact that a mathematical model accurately describing the P-S behavior does not yet exist, data from live *Pholidoptera griseoptera* was analyzed in order to determine the favorability. In Jones' data of live cricket interactions, he notes the total duration of a recording, the chirp rate of each cricket, the number of times a synchrony occurs, as well as the length of the synchrony (in chirps). Using this information, the syn-

chrony occurrence ratio for live crickets was determined, and, under the assumption that all synchrony events do in fact lead to lead-switches, used as a measure of the favorability.

In order to be able to compare crickets controlled by a P-S model to crickets controlled by an alternative phase response model, specialized electronic crickets (SynCricks) were used. Each SynCrick consists of a microphone and a speaker, routed through a dedicated sound card, which is controlled through Matlab, where the particular phase-response model is defined. For the purpose of this study, the phase response model for coupled biological oscillators, as described by Mirollo and Strogatz⁸, was used. It must be noted, that due to instabilities within Matlab while analyzing a live audio feed, the base chirp rate of the SynCricks had to be slowed to 1 chirp per 5 seconds, as opposed to a more natural 0.5-1 chirps per second.

For the data collection, two SynCricks were arranged in a master-slave relationship; the master was preordained as the leader and made to chirp at a constant rate, whereas the slave started $\approx 180^\circ$ out of phase with the master, and was allowed to regain the lead, following whichever model it employed. The start time of each SynCricks chirp was recorded to an excel spreadsheet for later analysis. As with the live crickets, data from

the SynCricks was used to find the lead-switch occurrence ratio, used as a measure of favorability.

III. RESULTS

From the more than 90 minutes of Jones' recordings of *Pholidoptera griseoptera*, 594 synchrony events were analyzed and used to determine the lead-switch occurrence ratio. These recordings occurred over several temperatures, and because crickets vary their chirp rate with temperature⁴, this was accounted for in all calculations. The synchrony occurrence ratio, and thus lead-switch ratio, for Jones' cricket recordings was found to be 0.088.

The model employed by the SynCricks allowed for a variable parameter of the coupling constant, so a range of realistic values of this constant were sampled and used to determine an average lead-switch ratio (FIG. 3). As with the live crickets, this data was used to find the measure of favorability of the behavior controlling model, in the form of the lead-switch ratio. This value was found to be 0.042 for the Mirollo-Strogatz phase response model.

The value of the lead-switch ratio is time independent, and thus should not be affected by the time scaling of the SynCricks chirp rate, for comparison purposes. In addition,

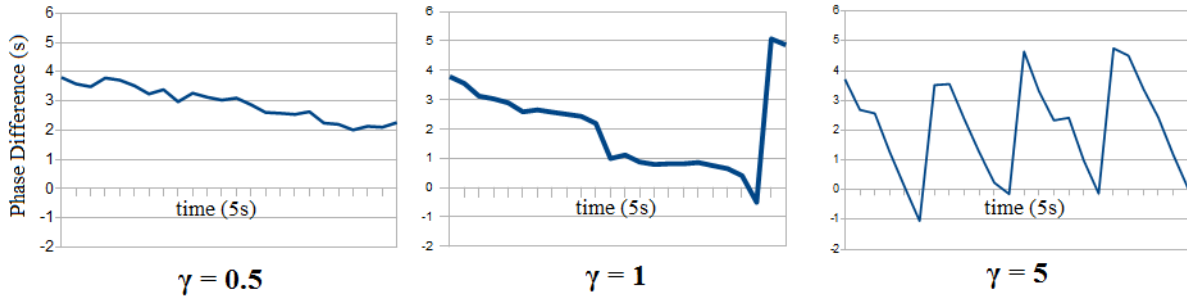


FIG. 3. Phase difference versus time, for varying coupling constants (γ) controlling the SynCricks behavior. Points where the phase difference ≤ 0 represent lead switch events.

there was a recorded 7% error between trials in Matlab, possibly due to the same reasons that required the chirp rate scaling.

IV. DISCUSSION & CONCLUSION

A comparison of the lead-switch ratios of the live crickets and the SynCricks, immediately poses a significant finding. The live crickets, assumed to be following the P-S model, had nearly double the lead-switch events within a sample than the SynCricks following a phase response model. Even accounting for the 7% error between trials, this result is significant in supporting the evolutionary favorability of a P-S model. This type of model allows crickets to fastidiously gain the lead position in a chorus, which thus increases their chances of attracting females and propagating their progeny.

However, this result leaves much room for further study of the P-S model. Determining the relative favorability of other, more ad-

vanced models of biological oscillators, would be necessary, as this research only tested one of the simplest cases. Possible such models include the Kuramoto phase response model, as well as oscillator timed automata⁹. Another point of interest would be obtaining the mathematical formulation of the P-S model, which would require the collection of more data from live bush crickets; both to increase Jones' original sample size, as well as to get chirp interactions at a higher time resolution than was available to Jones in 1966.

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