

Modelling animal interactive rhythms in communication - Supplement

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Phase response curves and coupling

Phase response curves (PRC) describe the magnitude of phase changes of an oscillator in response to pulse-like perturbations. These curves are already used at many different levels in the field of biology to model circadian clocks, physiological rhythms and of course timing mechanisms in the study of animal communication. In a PRC, the response phase is regressed against the signal phase ¹.

Oscillators have an endogenous or free-running period with a determined period and amplitude. However, the rhythms of these individuals interact with the oscillations produced by others, like in the acoustic communication of katydids, and the synchronous flashes of fireflies ²⁻⁶. A perturbed oscillator will show a change in amplitude and phase. A phase change $\Delta\phi$ can be measured on the PRC when a pulse occurs at phase ϕ . The resulting phase shift, which lies between 0° and 360° , is thus plotted as a function of perturbation time.

The strength of coupling of biological oscillators can be quantified using a PRC. Synchronisation through coupling of oscillators can lead to oscillators with the same period, but with different phases. If the coupling is strong enough, external periodic stimuli can lead to entrainment of biological oscillators. "A p:q (p and q being small integers) frequency ratio implies that after p cycles of oscillator 1 and q cycles of oscillator 2 the initial state is reached again" ¹ (pg. 5). Frequency locking ratios of 1:1, 1:2, 2:3, 3:2, and more have all been detected in animal rhythmic behaviours ⁷. A larger strength of oscillator coupling increases the likelihood of synchronisation, but when the coupling is weak, synchronisation can still happen if the observed frequencies are close to one another.

Inhibitory resetting model

External stimuli in the form of signals from a close neighbour may not only reset a male's rhythm but may completely inhibit their rhythm. In inhibitory resetting, an individual's pacemaker is reset to the basal level at the onset of the signal and remains inhibited at this level until the neighbour's signal terminates ⁸. At this point, the pacemaker returns faster to the trigger level if the PRC slope is less than 1. In the absence of an external signal, the signals emitted are based on the endogenous period of the species in question, and no fast ascent can be observed. It is possible that when an individual is inhibited by a neighbouring signal, such a rebound can happen as a

consequence of energy conserved during the inhibition period. However, this model assumes that an individual cannot be inhibited by conspecifics when signalling because its signal masks the signals of its surroundings neighbours emitted at the same time ⁵. Indeed, some species cannot hear neighbouring stimuli whilst signalling, but others can. This means that in species with a fast free-running period and capacities to discriminate nearby stimuli while signalling, the signal may be inhibited for a long period of time.

The acoustic rhythm in the acridid grasshopper (*Ligurotettix planum*) is controlled by inhibitory resetting ⁹. Playback experiments identified a PRC slope of 0.6, causing the pacemaker to quickly rebound to its trigger level. Two individuals with similar endogenous rhythms adhering to this mechanism are expected to alternate. However, due to random variations in signal period length, alternation would be punctuated by short occurrences of synchrony if the period lengths of each individual diverge from their mean value in opposite directions ⁸. Indeed, changes in signal lengths accompany changes in phase shifts, which constitutes of either a phase advance or phase delay. The example provided here highlights an important trade-off between phase shifts and signal lengths. In addition, synchrony can still occur incidentally after a long silent interval if both individuals start signalling at the same time ⁷. This has also been observed in an amphibian species ¹⁰. Some insects and anurans can time their calls in a synchronous manner with respect to a rapidly delivered signal. However, none of the species so far is capable of interacting with stimuli repeated as frequently as 6 times their natural signalling rate ⁸.

Mechanism meets function: The case of duets

This paper focuses on the mechanisms for rhythmic signalling in collective interactions, and the quantitative models describing them. The evolutionary functions of rhythmic signalling are more difficult to investigate empirically. A number of hypotheses have been proposed, especially for duets. Duetting occurs mostly between males and females, but in some avian species, it can occur between individuals of the same sex. For instance, in lekking blue-backed manakins (*Chiroxiphia spp.*), male-male duos duet to attract females ¹¹. Although some research has been done on duetting in primates, most studies have focused on birds, frogs, and insects ¹²⁻¹⁴. Acoustic duets require precise temporal coordination of signals. A duet is characterised by two main components: a constant time lag between the signals of contributing individuals and a repetitive structure that can be predicted in time ¹⁵.

What is the function of timed duets? Twelve hypotheses for the evolution of duetting were proposed: of these, 4 seem particularly promising ¹³. Duetting functions include mate guarding, preventing a partner from being usurped from its mate, joint resource defence and signalling commitment to one's sexual partner.

In insects, the duet generally starts with the male signalling; an answer from the female follows. Several insect taxa exhibit duetting. Bailey believed that this form of communication evolved independently several times. He went on to develop the following hypothesis, using male advertising calls as a starting point. In non-duetting species, males emit calls to attract females, and females adopt a searching role. The calls emitted by the males provide females with important information on male fitness and allows females to locate the source of the signal. For males, calling out can be costly in terms of energy expenditure, predation risk and inter-individual competition. Females, however, benefit from increased male acquisition. Moreover, as male costs increase, selection pressures aimed at countering these costs may arise. Initially, this may result in the shortening of male calls. Calling for a longer period of time increases the amount of information available for females to choose a mate, but also increases the risk of attracting predators such as parasitic flies or insectivorous bats. This can lead to females adopting different searching strategies in which they emit small sounds and duetting begins. This hypothesis suggests that the evolution of duetting is strongly dependent on sexual selection pressures ¹².

Duetting is characterised by a low variance in the reply latency of females ¹². This short delay can be described as the time between a key element in the male's call, such as a trigger pulse, and the onset of the female's response. This pulse indicates the end of the signal and acts as a cue to which she may reply. The time window within which the female replies is often species-specific ¹⁶. When one sex recognises the other during a duet, it alters its behaviour in response by adopting a different calling strategy or taking on a searching role. In order to critically evaluate current mechanisms involved in duetting, one should consider the costs and benefits of each contributing individual participating in the duet and analyse the importance of having such a high degree of signal coordination ¹⁵.

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