

Synchronous and Alternating Choruses in Insects and Anurans: Common Mechanisms and Diverse Functions¹

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SYNOPSIS. Neighboring males in rhythmically calling insects and anurans often chorus in a synchronizing or alternating fashion. Neuroethological investigations of chorusing species reveal that their rhythms are maintained by pacemakers and that a basic interactive algorithm, common to many species, yields the collective synchrony or alternation observed. Traditionally, synchrony has been viewed as a cooperative event. However, recent evidence suggests that a collective synchronous display can also be an incidental outcome of signal "jamming" activities between neighboring males competing to attract females. This arises when female phonotaxis is influenced by a precedence effect in which the first of two or more closely synchronized calls is preferred. Under such circumstances, males are selected to adopt a timing mechanism averting following calls. If males happen to call at comparable rates, the adopted mechanism can yield synchrony as a by-product. Alternation, too, may be produced by a similar mechanism and also represent an epiphenomenon. That alternation, as opposed to synchrony, results may be a mere artefact of the species' solo calling rate, but perceptual constraints may select specifically for alternation in some species.

INTRODUCTION

Comparative studies of acoustic communication in insects and anurans reveal various similarities in neuroethology and behavioral ecology. Of these, some of the most striking cases of shared mechanisms and functions involve signal interactions among chorusing males. Signal interactions are occurrences in which conspecific males mutually adjust the timing of their long-range sexual advertisement calls and generate a characteristic temporal pattern (Greenfield and Shaw, 1983). Such collective patterns assume different formats, the most precise of which exist in those insect and anuran species that produce relatively short calls repeated with a regular rhythm. In these rhythmically calling species it is common for neighboring males to adopt

precise phase relationships between their calls and collectively synchronize (phase angle $\approx 0^\circ$) or alternate (phase angle $\approx 180^\circ$) (Alexander, 1975). Comparable interactions are known in other acoustic animals and in bioluminescent signalers (Carlson and Copeland, 1985; Morin, 1986), indicating that the synchronous and alternating choruses in insects and anurans treated here are examples of a more general phenomenon.

Various synchronizing and alternating insects and anurans can maintain remarkably precise phase angles while calling at rates as fast as 5 s^{-1} (refs. in Greenfield, 1994). This impressive ability has attracted the attention of neuroethologists, and their studies have identified several different phonoreponse mechanisms by which interactive signaling may be regulated. Comparable work on synchronous flashing in lampryid beetles (Buck, 1988) has indicated additional mechanisms that may be responsible for signal interactions. Despite this diversity of explications, some evidence suggests that many insect and anuran cho-

¹ From the symposium *Acoustic Communication in Anurans and Insects: Common Mechanisms in Behavior, Neurophysiology and Evolution* presented at the Annual Meeting of the American Society of Zoologists, 27-30 December 1993, at Los Angeles, California.

ruses are not only outwardly similar, but are generated by the same underlying mechanism. This view is supported here by results from recent playback experiments and reinterpretations of previously collected data which indicate that one basic mechanism with several modifications can generate most of the chorusing patterns observed.

While it is possible that the various patterns of collective signal interactions in insects and anurans are mechanistically similar, the outcomes of these mechanisms can serve a diversity of functions (Greenfield, 1994). Both synchrony and alternation may be cooperative phenomena in which chorus participants adjust their signal timing to avoid "spiteful" behavior while attracting females or avoiding natural enemies. Synchrony and alternation may also represent cooperation between spatially aggregated males who are competing on an inter-group level with other male aggregations for distant females. Alternatively, these chorusing formats may reflect competitive signal "jamming" between rival individuals (Greenfield and Roizen, 1993). In this context, it is even possible that the collective patterns per se are not selected for but instead emerge incidentally as the summation of individual phonoresponses (see Alexander, 1975). Thus, some of the collective displays most apparent to human observers may simply be epiphenomena!

COMMON MECHANISMS IN RHYTHMIC CHORUSING

Neural oscillators

The rhythmic calls of insects and anurans are timed via central nervous system (CNS) oscillators. Such regulation must be appreciated if the more complex mechanisms that control interactive calling are to be understood. Presence of a CNS oscillator or pacemaker is indicated by finding that arrhythmic electric stimulation of specific brain loci can elicit rhythmic effector activity (e.g., Huber, 1965).

Rhythm control by a CNS pacemaker may be depicted with a sawtooth model in which the level of the pacemaker gradually ascends to its maximum level, triggers the call effector, and then suddenly—but not instantaneously—descends to its lowest or basal level

and initiates another cycle (see Buck *et al.*, 1981*a,b*). Calls are not emitted immediately when the pacemaker reaches its trigger level. Due to the finite speed of neural transmission, an effector delay ranging from 50–200 ms necessarily separates triggering of the call and its actual emission. This model of pacemaker regulation of signaling was initially inferred from experiments testing the responses of synchronizing fireflies to single isolated flashes presented at various times during their flash periods (Hanson *et al.*, 1971; Buck *et al.*, 1981*b*). Similar playback experiments with acoustic insects and anurans have corroborated it (see Greenfield, 1994).

An interactive algorithm

A set of playback experiments conducted on the Neotropical katydid *Neoconocephalus spiza* (Orthoptera: Tettigoniidae: Copiphorinae) illustrates both pacemaker control of rhythm and the interactive mechanism that yields collective synchrony (Greenfield and Roizen, 1993). *N. spiza* males produce loud (SPL \approx 80 dB at 1 m; 0 dB re 20 μ Pa), rhythmic chirps for the attraction of females. The chirps are generated by stridulation of the forewings at \approx 150 wingstrokes s^{-1} (at 25°C). A chirp comprises 2–10 "pulses," each pulse corresponding to a complete wingstroke, and lasts from 15–70 ms. Chirp rates range from 1.8–3.6 s^{-1} and vary both within and between individuals, but a given individual usually sustains a relatively constant chirp rate throughout several minutes of solo calling. Unlike wingstroke rates, chirp rates are not temperature dependent.

When a *N. spiza* male calls at the same time as his neighbor(s), he either synchronizes his chirps or interrupts his regular calling for a period and then re-enters the chorus in phase (Greenfield and Roizen, 1993). Therefore, an observer may detect a rise and fall in the loudness of the chorus as the number of participants increases and decreases over successive periods. Recordings of natural choruses demonstrate that *N. spiza* synchrony is quite precise: Absolute phase angles between the rhythms of neighboring males calling without interruptions are invariably $\leq 54^\circ$ (Fig. 1a).

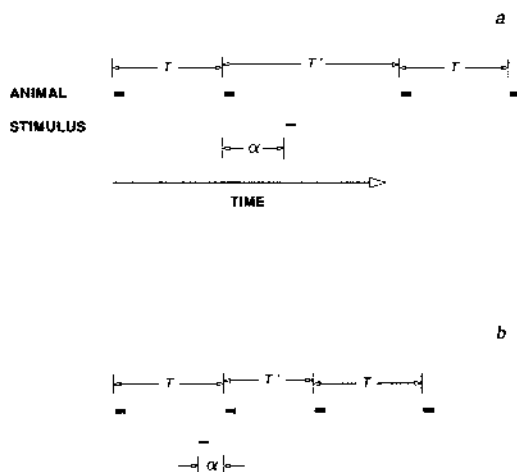
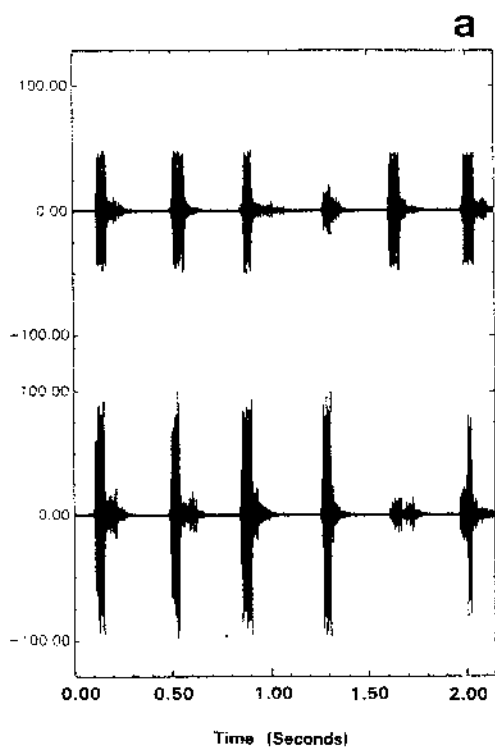


FIG. 2. (a) Period lengthening by an acoustic stimulus in *Neoconocephalus spiza*. (b) Shortening of the subsequent period by an acoustic stimulus in *N. spiza*.

N. spiza males calling in solo alter their call periods (T) predictably when presented with playbacks of single isolated stimulus chirps or series of such stimuli (Greenfield and Roizen, 1993). A single 55-ms stimulus chirp broadcast α ms after the onset of a male's chirp results in a lengthening of his concurrent chirp period to T' ($\approx T + \alpha$ ms; Fig 2a). However, if the stimulus is broadcast shortly before the next anticipated chirp ($-60 < \alpha < 0$ ms), the male does not modify the concurrent period (T), but the first complete period after the stimulus is shortened to T' ($\approx T - |\alpha|$ ms; Fig. 2b). A parsimonious interpretation of these responses is that the pacemaker is reset to its basal level by stimuli such as a neighbor's call and that the point ($\beta \approx T - 60$ ms) at which stimulus chirps no longer lengthen the concurrent period but shorten the next one indicates the beginning of the effector delay. Presumably, stimuli presented after this juncture do not modify the immediate rhythm because the next chirp has already been triggered. Advance of the second chirp

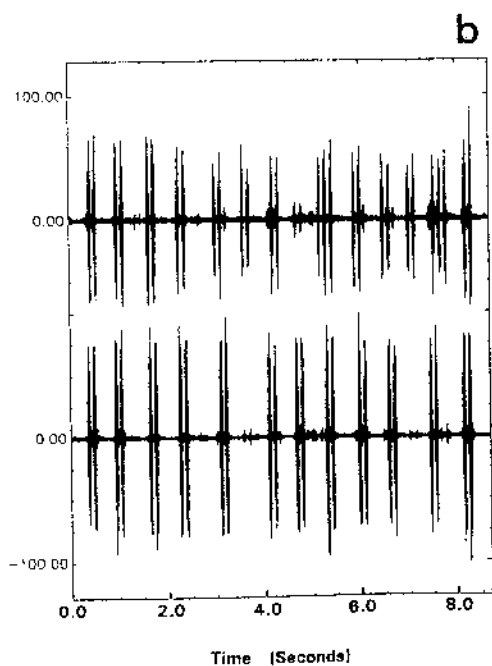


FIG. 1. (a) Oscillogram showing synchrony of two *Neoconocephalus spiza* (Orthoptera: Tettigoniidae: Copiphorinae) males from Gamboa, Panama. (b) Oscillogram showing synchrony of two *Sphyrmetopa femorata* (Tettigoniidae: Agraeciinae) males from Monteverde, Costa Rica.

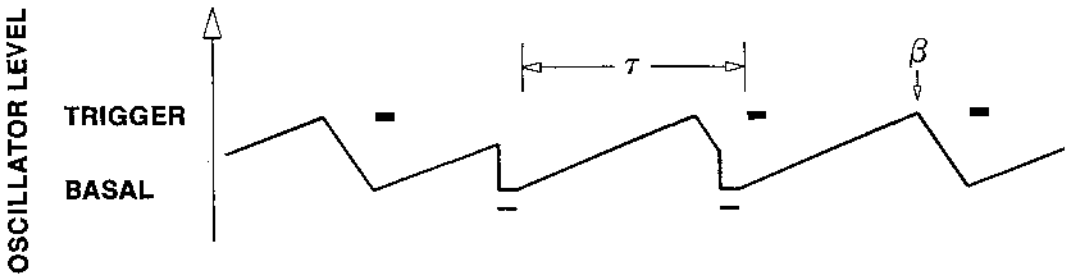


FIG. 3. Sawtooth pacemaker model depicting the phase delay mechanism for interactive calling in *Neoconocephalus spiza*. Thick (upper) and thin (lower) horizontal bars represent the animal's calls and stimuli, respectively, β is the beginning of the effector delay, and τ is the rebound interval. The pacemaker ascends to the trigger level more steeply following inhibition.

demonstrates that the pacemaker is nonetheless instantaneously reset to its basal level by stimuli during the effector delay. Chirp periods that follow the shortened or lengthened one are of normal length (T), indicating that resetting influences one period only and does not affect the insect's free-running rhythm.

Phase delay synchrony

The above responses are illustrated by the sawtooth pacemaker model in Figure 3. This model is adapted from a similar one developed to describe the "phase delay" mechanism of flash synchrony in the Melanesian firefly *Pteroptyx cribellata* (Coleoptera: Lampyridae) (Buck *et al.*, 1981b). When two males signal at similar rates and adhere to a phase delay mechanism, synchrony is attained one period after both individuals begin signaling and is maintained thereafter by continual adjustments every period. Synchrony produced under these circumstances is a default outcome: A male either chirps < 60 ms before or after the onset of another male's chirp—in which case synchrony occurs—or, prior to the triggering of his own chirp, his pacemaker is reset to the basal level by the neighbor's chirp, or vice-versa. The latter outcomes would be consequences of a male's period length increasing or decreasing excessively in the course of normal, stochastic fluctuations.

A phase delay mechanism can also be modelled by a phase response curve (PRC) (see Walker, 1969; Sismondo, 1990) in which response phase ($= ((T' - T)/T) \cdot 360^\circ$) is regressed against stimulus phase ($= (\alpha /$

$T) \cdot 360^\circ$). In the special case where $T' = T + \alpha$, seen in *P. cribellata*, the PRC has a slope = 1 and passes through the origin. The particular stimulus phase ($= (\beta/T) \cdot 360^\circ$) at which a discontinuity in the PRC occurs due to triggering of the next chirp is termed the "transition phase."

Closer analysis of the *N. spiza* PRC and additional playback tests with this insect demonstrated several critical refinements of its phase delay mechanism which influence the nature of synchronous chorusing. PRC slopes in *N. spiza* are ≈ 0.9 , indicating that the insect's first chirp after resetting by a stimulus is delayed by slightly less than T . This may result from steeper pacemaker ascents to the trigger level after resetting or from partial resetting to a point above the basal level. In either case, rapid returns to the trigger level suggest occurrence of the general neurophysiological phenomenon "post-inhibitory rebound" and may reflect "compensation" afforded by the lengthened period since the last call. Rapid returns avert complete overlapping of chirps by chorusing males. Instead, absolute phase angles of $20\text{--}30^\circ$ are typical, and the leading role regularly passes back and forth between the males.

Inhibitory resetting mechanisms

Playback trials using stimulus chirps lengthened by l ms ($l = 65\text{--}305$ ms) with a computer signal-editing program showed that a *N. spiza* male's rhythm is not only reset by an acoustic stimulus but is also inhibited for the duration of the stimulus (Greenfield and Roizen, 1993). At the end

of the stimulus, rapid returns followed by a normal chirping rate are seen as above. These responses are illustrated by PRCs obtained from lengthened stimuli: PRC slopes are parallel to the fundamental PRC obtained with a normal 55-ms stimulus chirp and are each elevated by $(l/T) \cdot 360^\circ$ above that fundamental PRC. This implies that the pacemaker is reset to its inhibited level at the beginning of the stimulus and does not begin its return to the trigger level until the stimulus ends. Phase delay mechanisms that incorporate inhibition as such are termed "inhibitory resetting."

Tests using series of 55-ms stimulus chirps helped clarify the conditions under which synchrony in *N. spiza* occurs naturally. When a male is presented with stimulus chirps delivered at a rate (r) 2–4 times faster than T^{-1} , he remains silent throughout the playback. The sawtooth pacemaker model would explain this as repeated resetting of the male to his basal level before chirps are triggered. If r is reduced to 1.5–2 $\cdot T^{-1}$, the male typically chirps in synchrony with every second or third stimulus chirp. These intermittent chirps are probably emitted when the male's chirp period length happens to fluctuate spontaneously to a low value and his pacemaker rapidly returns to its trigger level, which is more likely after resetting. On the other hand, if the stimulus rate is slower than T^{-1} ($r = 0.6\text{--}0.8 \cdot T^{-1}$), the insect chirps in alternation with the stimuli in a phase-locked manner; *i.e.*, he appears to be entrained to chirp $\approx 0.9 \cdot T$ ms after each stimulus. No evidence suggests that males adjust their chirp rates to synchronize with slower stimulus rates.

The responses to serial stimuli suggest that runs of natural synchrony in *N. spiza* only result when two (or more) males happen to sustain equivalent chirp rates. Otherwise, the faster male would chirp in solo most of the time while the other(s) is repeatedly reset to its basal level before triggering its chirps. Occasionally, even matched males would interrupt their regular synchrony with brief bouts of alternation or solo calling when chirp periods simply fluctuate.

Natural recordings and playback tests with other synchronizing acoustic insects suggest that control by inhibitory resetting mecha-

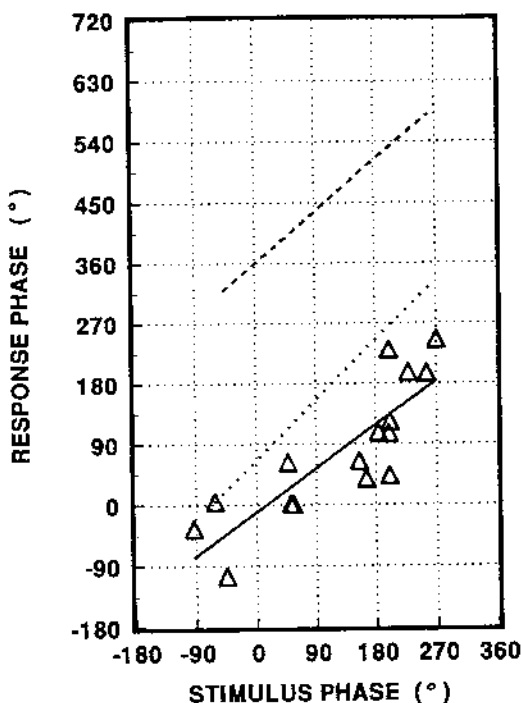


FIG. 4. Phase response curves (PRC) showing regression of response phase against stimulus phase (see text) for *Sphyrometopa femorata*. Solid line is PRC obtained from a normal 200-ms stimulus; dotted and dashed lines indicate PRCs obtained from stimuli artificially lengthened to 400 and 800 ms, respectively. Triangles indicate data from 16 different males tested with the 200-ms stimulus.

nisms is widespread. The Neotropical agraeiine katydid *Sphyrometopa femorata* produces 220-ms calls, comprised of paired chirps, at $1.7\text{--}2.1 \text{ s}^{-1}$ ($T = 480\text{--}590 \text{ ms}$) and synchronizes its calls with a degree of precision comparable to that in *N. spiza* (Greenfield, unpublished data; *e.g.*, see Fig. 1b). Playback tests using normal stimulus calls indicated a PRC for *S. femorata* with a slope ≈ 0.7 and a transition phase $\approx 270^\circ$ (Fig. 4). Artificially lengthened stimulus calls yielded parallel PRCs elevated by $\approx (l/T) \cdot 360^\circ$ above the fundamental one, and series of stimulus calls delivered at rates slower than T^{-1} resulted in phase-locked responses that alternated with the stimuli. Walker (1969) studied synchrony in the snowy tree cricket, *Oecanthus fultoni* (Orthoptera: Gryllidae: Oecanthinae), and reported a PRC with a slope slightly less than 1 and a transition phase $\approx 220^\circ$. Unlike either of

the tettigoniids discussed above, uninterrupted runs of synchrony several hundred periods in length occur regularly in *O. fultoni*. Highly regular synchrony originates from the low transition phase, which prevents resetting prior to chirping, and relatively small spontaneous fluctuations in the chirp period. Neither *S. femorata* nor *O. fultoni* completely overlap their calls, and in both species chorusing males regularly exchange the leading role over successive periods.

FUNCTIONS OF SYNCHRONOUS CHORUSING

An incidental by-product of competitive signal jamming

Tests of female choice in *N. spiza* provide compelling evidence that the inhibitory resetting mechanism in this species is a means of signal jamming and that the synchronous chorusing is merely an incidental by-product of this mechanism (Greenfield and Roizen, 1993). These tests consisted of playback trials conducted in an acoustically insulated laboratory arena in which centrally released females were presented with a choice of calls from two loudspeakers spatially separated by 180°. Responses were scored by phonotaxis toward one of the loudspeakers. When females were presented with a choice of normal 55-ms stimulus chirps versus shortened 27.5-ms chirps, each delivered at 2.5 s⁻¹ and temporally separated by a phase angle of 180°, preference was strongly biased toward the longer chirps. Given the tendency for female choice of signals in acoustic animals to be influenced by "non-arbitrary criteria" reflecting energy (e.g., Klump and Gerhardt, 1987), selection of the stimulus with higher acoustic power was expected.

In further trials in which the phase angle was adjusted to values other than 180°, females continued to prefer the longer chirps—except when short chirps were broadcast immediately prior to the long ones (phase angles of -42° or -12°). Here, female preference was reversed, and the short, leading chirps were chosen. Such selection of leading stimuli is a "precedence effect" (*sensu* Wytenbach and Hoy, 1993), examples of which are known among female preferences in several acoustic insects (e.g., Stiedl

et al., 1994; Minckley, unpublished data) and anurans (e.g., Whitney and Krebs, 1975; Dyson and Passmore, 1988a; Klump and Gerhardt, 1992). In *N. spiza* and one of the anuran species tested (see Dyson and Passmore, 1988b), the preference for leading calls is strong enough to override other non-arbitrary call attributes such as length or SPL. Female *N. spiza* apparently choose leading chirps solely based on their sudden onsets of sound rather than because pulses at the beginning of a chirp are more critical and remain unmasked in leading chirps. A playback test in which a normal 55-ms chirp was bisected into beginning and ending halves, which were then broadcast in alternation from two loudspeakers, revealed no female preference for beginning halves.

Evolutionary stability of inhibitory resetting

The precedence effect in *N. spiza* would impose strong selection pressure on males to adopt a mechanism that (a) averts calling shortly after a neighbor and (b) relegates the neighbor to this following role (Greenfield and Roizen, 1993). Resetting with a rapid rebound following inhibition (PRC slope < 1) meets these criteria for signal jamming, and it is evolutionarily stable (ES) in a limited sense. A two-player game was modelled in which males producing identical chirps at equal rates could (1) time their calls regardless of their neighbor or (2) adhere to the rules of inhibitory resetting. Computer simulation showed that inhibitory resetters always lured more females than regardless males did, as long as leading calls were more attractive than following ones and females were influenced by the summation of sequential stimuli. Both stipulations occur in *N. spiza*. The game model assumes that male calling is limited by energy and that equally vigorous males will call at the same maximum rates. Future modeling should relax some of these assumptions and investigate ES outcomes in the following settings: (1) *n*-player (*n* > 2) games, (2) situations where options other than regardless and basic inhibitory resetting strategies are available (e.g., the ability to increase chirp rate above the maximum for several successive periods, while compensating later

with a slower rate), and (3) cases where the males have unequal energy reserves.

Precedence effects in the psychoacoustics of female choice

Whereas the link between female preference for leading calls and synchronous chorusing by males seems clear, the origin of the precedence effect itself is enigmatic. Such psychoacoustic features may reflect various categories of indirect female choice (Kirkpatrick and Ryan, 1991). If certain males who possess greater overall "vigor" are consistent leaders because they can rebound quickly from resetting, "good genes" selection may account for the female preference. Alternatively, preference for leading chirps may be a form of "arbitrary" (Fisherian) selection and may be driven by a "sensory bias" (see Ryan *et al.*, 1990). The latter is suggested by the occurrence of precedence effects in a variety of taxa, including man, and in situations outside the realm of female choice (see Wyttenbach and Hoy, 1993).

Cooperative functions

Perhaps owing to a perceived incompatibility of synchrony and competition, traditional explanations for synchronous chorusing have stressed cooperation. These hypotheses propose that synchronous choristers benefit from (1) preserving a species-specific rhythm that females must hear issuing from or within a local group of callers before approaching any one male (Walker, 1969; Lloyd, 1973), (2) perceptually confusing phonotactic natural enemies who would be unable to localize any one source of sound if calls radiate from all directions at once (Otte, 1977), or (3) maximizing the peak signal amplitude of a local group of males (see Buck and Buck, 1978). The first two hypotheses are based on the argument that males who do not synchronize would be committing spiteful acts, behavior not expected in most conditions because of evolutionary instability (Knowlton and Parker, 1979). The last hypothesis supposes that groups of males compete for distant females who evaluate calls based on peak, as opposed to time-averaged, SPL values. Males in synchronizing groups would therefore enjoy

higher female encounter rates on a per individual basis than males in nonsynchronizing groups. Such males would, of course, also be expected to compete within their group for females who do arrive at the site.

Assessment of chorusing function suffers largely from a paucity of appropriate testing, and none of the several functional studies of rhythmic synchrony have supported any of the cooperative hypotheses. In fact, only one signal interaction case has been demonstrated to be cooperative: synchrony of the sporadic calls produced by the hylid frog *Smilisca sila* (Tuttle and Ryan, 1982). Temporally concentrated calls appear to invite predatory bats less than dispersed ones do. *N. spiza* calls, however, do not attract any phonotactic natural enemies, and playback trials in the arena showed that females could localize synchronized calls as readily as alternated ones. Furthermore, no evidence suggested that males were spatially distributed in dense aggregations that might compete on an inter-group level. Consequently, the competitive hypothesis for inhibitory resetting and epiphenomenon status for synchrony are favored as likely explanations in *N. spiza*. Comparable investigations on other rhythmic synchronizers are urged.

ALTERNATION YIELDED BY PHASE DELAY MECHANISMS

Inhibitory resetting with a rapid rebound

An observer perceives signal alternation as an event fundamentally different from synchrony and may suppose that very different mechanisms are responsible for it. Several workers (*e.g.*, Jones, 1966; Loftus-Hills, 1974), however, have noted that regular alternation in insects and anurans tends to be interrupted by occasional synchrony and have suggested that both formats of interaction share similar mechanisms. Alternation in the North American grasshopper *Ligurotettix planum* (Orthoptera: Acrididae: Gomphocerinae) provides an excellent example (Minckley *et al.*, 1995). *L. planum* males produce 350-ms "rasp" calls at rates ranging from 4–12 min⁻¹, and neighbors seem to avoid overlapping one another's calls. Further analysis reveals that

the situation is more complicated, however, since neighbors do completely overlap calls on occasion.

Recordings of natural chorusing and playback experiments similar to those conducted on *N. spiza* showed that *L. planum* males timed their calls interactively via an inhibitory resetting mechanism (Minckley *et al.*, 1995). This mechanism could be characterized by a sawtooth pacemaker model with a steep ascent to the trigger level following inhibition and by a PRC with a slope ≈ 0.6 . Such features imply that a male *L. planum* can rebound from inhibition in an interval much shorter (≈ 1.45 s) than its typical call period (≈ 10 s) if the stimulus occurs late in the call period. Consequently, two individuals who sustain equivalent calling rates would alternate except during occasions when stochastic fluctuations in period length, aided by a 200-ms effector delay, allow calls to overlap or when both happen to produce their first calls at the same time (see Sismondo, 1990). As in synchrony, there were no indications that males adjusted their calling rates to "accommodate" a slower neighbor and maintain regular alternation. Reinterpretations of data on phonoresponses in alternating gryllids (*e.g.*, Cade and Otte, 1982) and tettigoniids (*e.g.*, Shaw 1968) suggest that this modified phase delay mechanism accounts for alternation in a variety of acoustic insects.

Signal jamming in slow callers

Playback experiments in a 9-m diam. outdoor arena showed that female choice in *L. planum* was influenced strongly by a precedence effect similar to that found in *N. spiza*: Female *L. planum* oriented toward the leading of two calls if the phase angle was $< 90^\circ$ (Minckley, unpublished data). Thus, *L. planum* males too would be under strong selection pressure to adopt a mechanism preventing calling shortly after a neighbor's calls. That the mechanism used by *L. planum* yields collective alternation rather than synchrony may be a simple artefact of the insect's long call period and general constraints on rebound intervals (τ) in pacemakers (Greenfield 1994). If lower bounds for τ do exist, as T declines (*e.g.*, *N. spiza*, *O. fultoni*, *S. femorata*), the $\tau:T$ ratio

would increase and approach 1, thereby making synchrony inevitable. A review of rhythmic chorusing in insects shows that synchrony is generally restricted to species with calling rates faster than 1 s^{-1} . This rule seems to transcend phylogenetic factors, as both synchrony and alternation occur not only within the same families but even within the same genus (*e.g.*, *Platyceles* (Tettigoniidae: Decticinae); see Samways, 1976). Moreover, rhythmic chorusing in anurans upholds this interpretation. Most anurans call at rates slower than 1 s^{-1} , and chorusing interactions are typically alternating in format (Tuttle and Ryan, 1982).

Perceptual constraints and alternation

Additional playback experiments suggest, however, that alternation in *L. planum* may not be entirely artefactual. Unlike *N. spiza*, female *L. planum* do experience difficulty localizing sources of sound that are synchronized (or just overlapping); *i.e.*, little phonotaxis toward leading or following calls occurred when phase angles were $< 15^\circ$ (Minckley, unpublished data). This may reflect neurophysiological differences between ensiferan (Gryllidae, Tettigoniidae, etc.) and caeliferan (Acrididae, etc.) Orthoptera: While the former are known to have the central capacity to separate acoustic stimuli broadcast simultaneously from different directions (*e.g.*, Pollack, 1986), the latter may not (*e.g.*, von Helversen, 1984). Because of this limitation in neural processing, male *L. planum* may be selected to cooperate by avoiding call overlap as well as to compete by evading jamming effects of a neighbor's signals. A phase delay mechanism that generates alternation would satisfy both demands.

Alternation may be specifically selected for by another perceptual constraint. A growing body of evidence indicates that the hearing of many acoustic insects and anurans is handicapped during calling. This may originate in simple masking (Hedwig, 1990) or in neural (Wolf and von Helversen, 1986) or biomechanical (Narins, 1992a) devices designed to protect the ears and prevent self-stimulation. However, in many insect and anuran species males space themselves regularly and maintain territories by monitor-

ing the calls of neighbors, and reduced hearing during calling would be a hindrance. Interactive mechanisms that reduce call overlap would circumvent this potential difficulty. The territorial behavior of male *L. planum* and behavioral evidence that hearing is impaired during calling (Greenfield and Minckley, 1993) suggest that this factor too may have selected for a phase delay mechanism yielding alternation.

Alternation in dense choruses

If production of following and overlapping calls is specifically avoided in alternators, these species would experience difficulties in high population density that do not beset synchronizers. As the number of calling neighbors increases, a focal male must either reduce his calling rate drastically or forgo adherence to the rules of chorusing. Recent experiments with several insect (*e.g.*, Minckley *et al.*, 1995) and anuran (*e.g.*, Brush and Narins, 1989; Narins, 1992*b*; Schwartz, 1993, 1994) alternators show that they typically solve this dilemma by modifying the rules: All but the nearest (loudest?) neighbors are ignored during adjustment of fine-scale call timing. Thus, some anomalous cases in which synchrony and alternation appear to occur simultaneously within a chorus (*e.g.*, Moore *et al.*, 1989) may be explained. Such facultative application of phase delay mechanisms would be adaptive if females too ignore more distant callers when evaluating leading/following roles or other signaling attributes of chorusing males. Evidence from a tettigoniid (Römer, 1993) and a hylid frog (Gerhardt and Klump, 1988) suggests that females may be selectively attentive in this fashion.

Selective attention to nearby neighbors is enhanced in some alternating anuran species by the ability to rebound from inhibition in an extremely short interval (see Zelik and Narins, 1985; Moore *et al.*, 1989). After a male calls, he first enters a "refractory period" (see Narins, 1982) during which stimuli have no effect on the timing of his subsequent call, but following this period he can call very quickly after the end of a stimulus. This modified phase delay mechanism, which may also occur to a limited

degree in some insects, represents a means of inserting one's call into a short, unpredictable gap, a valuable ability in dense choruses.

CONCLUSION

Some cases of rhythmic chorusing in insects involve alterations in the free-running rhythm (*e.g.*, Sismondo, 1990) or rapid phonoresponses (*e.g.*, Alexander and Moore, 1958) that yield synchrony with the concurrent signal. These events clearly differ mechanistically from the phenomena discussed here. However, the vast majority of insect and anuran choruses that have been studied are regulated by some version of the basic phase delay interactive algorithm. These studies demonstrate how a fundamental neuroethological feature may be modified to function in a great variety of behavioral situations and may generate an assortment of observable phenomena. Moreover, they indicate the possibility that some collective displays can merely be epiphenomena, and they reveal critical aspects of sexual communication and sexual selection that most certainly would have passed unnoticed in non-interactive studies.

ACKNOWLEDGMENTS

I thank Robert Minckley and Joshua Schwartz for comments on the manuscript, Cindy Lin for field assistance with *Sphyrometopa femorata* choruses, and the U.S. National Science Foundation (grant # BNS 91-96177) for financial support.

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