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Mechanisms of selective attention in grasshopper choruses: who listens to whom?

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Abstract In many rhythmically signaling species of acoustic insects and anurans, males form choruses at typical population densities. Recent findings that females may prefer leading calls indicate that the timing of a male's signals relative to those of neighboring choruses is an important component of mate attraction. Within a chorus, however, males cannot time their calls such that they lead all neighbors. Hence, they are expected to show selective attention toward only a subset of the group. We used field playback experiments to determine the incidence of and mechanism(s) responsible for selective attention in choruses of the territorial grasshoppers *Ligurotettix coquilletti* and *L. planum*. Our data revealed significant selective attention in both species and are inconsistent with either fixed-threshold or fixed-number mechanisms. Rather, regulation of selective attention by a sliding-threshold mechanism is supported. We discuss these results in the context of the evolution of chorus structure.

Key words Selective attention · Sexual selection · Chorusing

Introduction

In many species of acoustic insects and anurans, male advertisement signals are most often produced under competitive circumstances. Subject to competition, as would occur under typical population densities, a male's advertisement signals should match or exceed those of neighbors to ensure territory retention and mating success (Gerhardt 1994; Greenfield 1994). Most studies of competitive signaling have investigated the influences of relative signal amplitude, length, rate, and frequency on territory ownership and attractiveness to females (Searcy and Andersson 1986; Andersson 1994). Recent findings, however, show that females may also be influenced strongly by the timing of a male's calls relative to those of his competitors: In various species, females orient preferentially toward the leading of two (or more) identical calls produced in close succession (Greenfield et al. 1997), and this preference persists even when the female must travel farther to the leading male (Snedden and Greenfield, in press). Such precedence effects have apparently selected for timing mechanisms by which males forego producing calls during a forbidden interval following a neighbor while increasing their incidence of leading calls (Greenfield and Roizen 1993; Greenfield et al. 1997). When all males in a local population adjust their call rhythms via such timing mechanisms, a synchronous or alternating chorus may emerge as a collective by-product (Greenfield and Roizen 1993; Greenfield et al. 1997).

Males may increase their production of leading calls via inhibitory-resetting, a timing mechanism whereby the central oscillator regulating call rhythm is inhibited and reset to its basal level upon hearing an acoustic stimulus such as a neighbor's call (Greenfield and Roizen 1993; Greenfield et al. 1997). When the neighbor's call ends, the oscillator is released from inhibition and ascends to its peak level, at which point a call is triggered to occur after a brief interval, the effector delay (see Fig. 1). Thus, the only following calls that an inhibitory-resetter will produce occur during the brief interval, equal in length to the effector delay, that begins at the onset of a neighbor's call: Such following calls would have already been triggered by the central oscillator when the neighbor's call began. Because the ascent of the oscillator to its peak level is faster after inhibition than during free-running activity, an inhibitory-resetter will produce more leading calls than a male who disregards his neighbor's signals: The inhibitory-resetter's oscillator is the first to reach peak level at the next call cycle.

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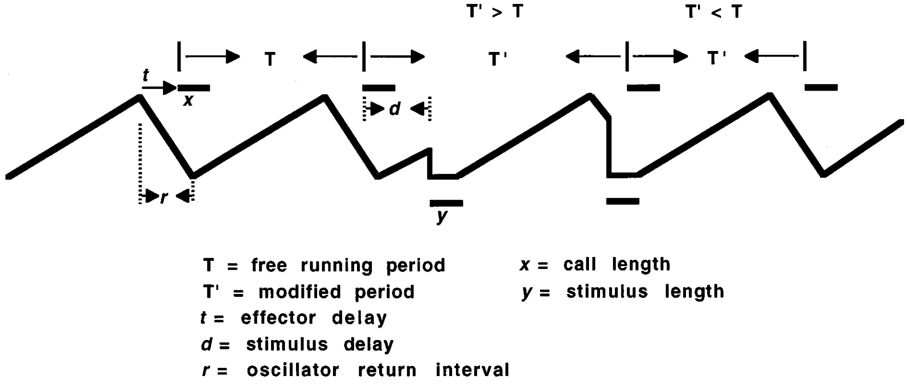

Fig. 1 Schematic representation of the model of inhibitory-resetting of a central nervous system rhythmic oscillator controlling signal production. When a male perceives a competitor's call (stimulus) during the rise-to-trigger of the oscillator, the oscillator is reset to the basal level, inhibited for the duration of the stimulus, and the subsequent (modified) call period is longer ($T' > T$) than the free-running period. When a competitor's call (stimulus) is perceived during the fall-to-basal of the oscillator, the oscillator is reset to the basal level, inhibited for the duration of the stimulus, and the subsequent (modified) call period is shorter ($T' < T$) than the free-running period. Inhibition lasts for one period only: Without further stimulation males return to the free-running period

Playback experiments show that inhibitory-resetting regulates male signal interactions in various acoustic insects and anurans, and computer simulations indicate that it is evolutionarily stable in pair-wise interactions as long as females prefer leading calls (Greenfield and Roizen 1993).

The above findings notwithstanding, males in natural populations normally interact with the signals of more than one neighbor, and the advantages of inhibitory-resetting then become problematic. Computer simulation indicates that inhibitory-resetting is not evolutionarily stable in multiple-male choruses unless it incorporates selective attention to only a subset of audible neighbors. Otherwise, an inhibitory-resetter would repeatedly reset his oscillator and seldom call. Thus, the prevalence of inhibitory-resetting among natural populations of acoustic insects and anurans suggests that some selective-attention modification must be present. That is, males should respond to (be reset by) only a subset of the signaling neighbors within their auditory range.

Selective attention appears to modify the responses of females to male calls in various acoustic species (Greenfield et al. 1997), and limited evidence for its regulation of male inhibitory-resetting has been found in the grasshopper *Ligurotettix planum* (Orthoptera: Acrididae: Gomphocerinae) (Minckley et al. 1995). In the present study, we investigate the possible regulation of inhibitory-resetting in *Ligurotettix* grasshoppers further and attempt to determine the specific mechanism(s) with which it may act. We initially propose that selective attention may act via one of the following rules (see Fig. 2): (1) a fixed-threshold mechanism, wherein a male responds to (is inhibited and reset by) only that subset of audible neighbors whose perceived call amplitudes exceed a fixed value, higher than its behavioral response threshold (BRT) when only one calling neighbor is present; (2) a fixed-number mechanism, wherein a male responds to only n of the neighbors whose perceived call amplitudes exceed the BRT; (3) a sliding-threshold mechanism, wherein a male responds to only those neighbors whose perceived call amplitudes are within x dB of the loudest neighbor(s) and above the BRT.

Here, we report a series of field playback experiments designed to discern which of the above possibilities operate in natural choruses.

Methods

General methods

Ligurotettix grasshoppers

Ligurotettix includes several species found in the deserts of southwestern North America. *L. coquilletti* occurs throughout the Sonoran and Mohave Deserts, where it feeds primarily on the foliage of creosote bushes (*Larrea tridentata*). *L. planum* occurs in the Chihuahuan Desert and feeds on the foliage of tarbushes (*Flourensia cernua*). In both species, males remain on and defend individual host shrubs as mating territories. The males produce rhythmic calls that function as territorial and sexual advertisement. Signal interactions between neighboring males entail the alternation of calls.

Populations studied

L. coquilletti were studied in a 35 × 67 m plot in Deep Canyon, California during July and August 1994. *L. planum* were studied in a 50 × 100 m plot in the San Simon Valley, Arizona, 10 km east of the hamlet of Portal, during June and July 1995. These sites are floristically and climatically representative of the Sonoran and Chihuahuan Deserts, respectively.

We marked all adult male *L. coquilletti* and *L. planum* in the study plots with unique combinations of enamel spots on the pronotum. Individual males were monitored daily, and we selected individuals with high site fidelity to a given host shrub for playback experiments. Such individuals are more likely to remain in a shrub throughout a playback trial and to continue interacting with the loudspeaker broadcasts.

We began our series of field playback experiments as male populations approached peak levels for the season. Playbacks were

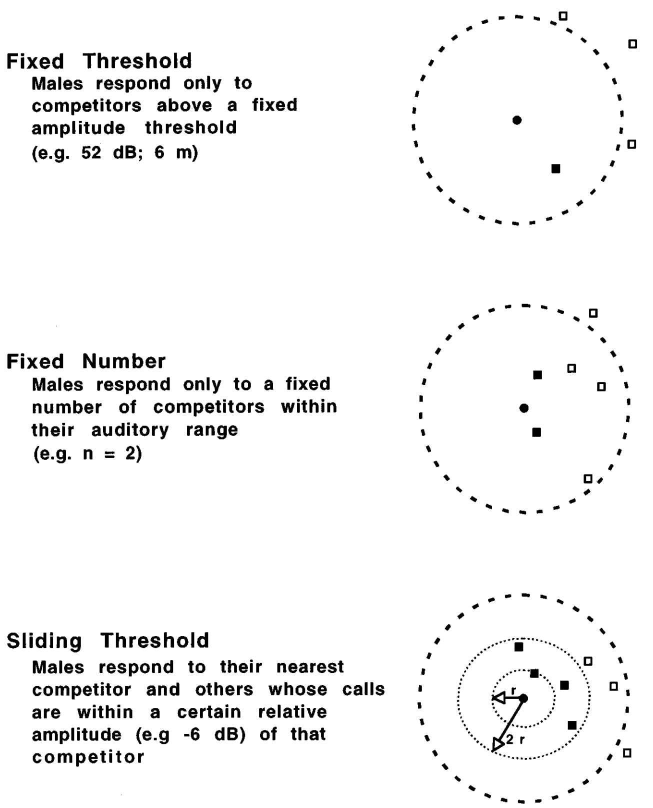

Fig. 2 Possible mechanisms of selective attention. *Filled circles* represent the focal male, *filled squares* represent males to which the focal male responds and *open squares* represent males whose call exceeds the behavioral response threshold (BRT, see text) but to which the focal male does not respond. All males are assumed to call at the same absolute amplitude, and sound attenuation over increasing distance is assumed to result only from spherical spreading. (1) *Fixed Threshold*. The focal male responds only to males whose perceived call amplitudes exceed a fixed value, greater than its threshold for behavioral response when only one calling neighbor is present. The *dashed line* circumscribes the area within which calling neighbors would elicit a response. (2) *Fixed Number*. The focal male responds only to n of the males (e.g., $n = 2$) whose perceived call amplitudes exceed some threshold value; i.e., if x males ($x > n$) exceed that value, the focal male only responds to the n loudest; if y males ($y < n$) exceed that value, the focal male responds to all y males. As in (1), the *dashed line* circumscribes the area within which perceived amplitudes of calling neighbors would exceed the threshold value. (3) *Sliding Threshold*. The focal male responds to the loudest male (at distance $= r$) and all those whose amplitudes exceed that of the loudest one, L, minus a threshold differential, df (e.g., df $= 6$ dB; distance $= 2r$), providing that each of these males, including the loudest one, exceed some threshold value. The focal male responds to all males situated between the two *concentric dotted lines*, the outer of which is within the threshold value [dashed line as in (1) and (2)]

conducted at times of day when signaling activity was maximum. These times were 20–50 min after sunset, the evening chorus, for *L. coquilletti* (Greenfield 1992) and a 4-h period from mid-morning to early afternoon for *L. planum* (Shelly and Greenfield 1989). The proportions of the male populations calling during these periods were highest, and the calling rhythms of individual males were faster and more regular than at other times. For *L. coquilletti*, testing during the evening chorus also minimized interference, because the insects were not easily disturbed by observers' movements in the receding twilight.

L. coquilletti advertisement calls are 20–30 ms clicks produced at 30–60 clicks min^{-1} (Bailey et al. 1993). Sound pressure levels (SPLs) of the clicks are approximately 63 dB (0 dB = 20 μPa) at 1 m, and their frequencies range from 4 to 35 kHz. *L. planum* advertisement calls are 300–400 ms rasps produced at 5–10 rasps min^{-1} (Minckley et al. 1995). SPLs of the rasps are also approximately 63 dB at 1 m, and their frequencies range from 3.5 to 9 kHz. Both *L. coquilletti* clicks (during the evening chorus) and *L. planum* rasps are produced by simultaneous stridulation of both hindlegs against the forewings.

L. coquilletti and *L. planum* both exhibit inhibitory-resetting responses to the calls of neighboring males. In *L. coquilletti*, this response is indicated by the absence of calls during a forbidden interval lasting from approximately 100 to 250 ms following a neighbor's call. In *L. planum*, this forbidden interval lasts from approximately 0.2 to 1.8 s following a neighbor's call (Minckley et al., 1995). These intervals correspond with delays, measured from the onsets of leading calls, of following calls that are avoided by females during phonotaxis (Minckley and Greenfield 1995; Greenfield 1997).

Playback experiments

General methods. For our playback experiments, we selected only males that were calling with a regular rhythm with rates exceeding 30 and 6 calls min^{-1} for *L. coquilletti* and *L. planum*, respectively. Three different experiments were conducted (only *L. planum* was tested in experiments 2, and 3), and individuals were tested once per experiment. An individual was never tested more than once per day. To enable clear interpretations of acoustic interactions between test males and playback broadcasts, we removed all singing neighbors within a 12-m radius of the test male prior to his trial. Removed males were held in a shaded, acoustically insulated box during the trial and returned to their respective shrubs afterward.

We broadcast playback signals to the test male from two to four surrounding loudspeakers [Radio Shack model 40-1377; flat response (± 2 dB) from 4–50 kHz] oriented vertically upward, with the same face of the speaker box always oriented toward the animal; the male's calling was simultaneously recorded with a microphone (Shure model BG 4.0 condenser microphone, flat response from 4 to 18 kHz) positioned adjacent to him. Speakers positioned in this manner produce approximately equivalent (± 2.5 dB) SPLs in all horizontal directions. Although our playbacks did not reproduce the entire frequency spectrum of *L. coquilletti* calls, these signals elicit responses from both males (data herein) and females (data in Greenfield 1997) that are indistinguishable from responses to calls of live males. For experiments that used only two loudspeakers, signals were played back with a stereo digital tape recorder (Casio model DA-7; sampling frequency 48 kHz), the playback tape recorder. The male's calls were recorded on a second stereo cassette recorder (Marantz model PMD-430), the recording tape recorder. We sent the output of each channel of the playback tape recorder to a separate loudspeaker. The output cable from one of the channels, the marker, was split such that its signal was sent to both a loudspeaker and the left channel of the recording tape recorder. The right channel of the recording tape recorder received input from the microphone adjacent to the test male. Thus, the recording tape recorder captured the relative timing of the playback broadcasts (marker signals) and the male's calls.

For experiments (with *L. planum*) in which three or four loudspeakers were used, the playback tape recorder was replaced by a computer with an 8-channel digital:analog (D:A) output board (see Minckley et al. 1995). As before, we split one channel (the marker) and sent its signal to both a loudspeaker and the recording tape recorder.

Using a SPL meter (General Radio model 1982), we measured peak SPLs of the loudspeaker broadcasts of playback signals and adjusted the loudspeakers to 63 dB at 1 m for both *L. coquilletti* and *L. planum*. The one-octave bandwidth filter on the SPL meter was centered at 16 kHz for *L. coquilletti* calls and at 4 kHz for *L. planum* calls. SPLs were measured at a distance of 1 m from the loudspeaker along a horizontal line between the loudspeaker and the test male, as measuring SPL at the position of the focal male would have disturbed the subject. Owing to the sparse vegetation at the field sites, we were always able to position the loudspeakers such that foliage did not intervene between them and the subjects. Occasional checks of SPL at the subject's location confirmed that the perceived broadcasts of the nearby loudspeakers remained louder than those of the more distant ones and that sound largely attenuated in accordance with the inverse-square law. Thus, in all experiments, we assume sound attenuation due only to spherical spreading.

Evaluation of our SPL meter (see Prestwich et al. 1989) indicated that peak SPLs of very brief signals were underestimated (by 3 and 1 dB for *L. coquilletti* and *L. planum* calls, respectively). All SPLs of male calls and playback signals reported here are corrected to the true values.

Signal preparation. All playback signals were derived from tape recordings (Casio model DA-7 recorder; Shure model BG 4.0 condenser microphone, flat response from 40 to 18,000 Hz) of *L. coquilletti* or *L. planum* male advertisement calls. Recordings were digitized (sampling frequency of 60 kHz) and filtered (high-pass digital filter; cutoff frequency 3 kHz), and a representative call was then copied to a second channel. Using an editing program, we delayed the signal on the second channel by a specific time interval and created a 6-min repetition which was transferred to a playback tape recorder. Thus, we prepared playback stimuli in which identical calls were repeated periodically on two channels, with a specific delay separating calls on the left and right channels.

For experiments in which three or four loudspeakers were used, multi-channel files were prepared via custom software (see Minckley et al. 1995). These files were continuously looped, and the signals were played directly to the loudspeakers via the computer.

Analysis of recordings. Recordings were digitized (see Minckley et al. 1995), and the onset times (±0.5 ms) of all marker signals and test male calls were determined with a signal analysis program. Because each loudspeaker's signals occurred at a specific time relative to the marker signal, we could compute the delay between the test male's calls and the previous signal from each of the broadcasting loudspeakers. Thus, a complete transcription of the interactions between the test male and the surrounding loudspeakers was achieved.

Experiment 1: does selective attention occur and does it rely on a fixed-threshold mechanism? (two-loudspeaker playback)

Our initial playback experiment tested whether *L. coquilletti* and *L. planum* males interacted with all calling neighbors whose perceived SPLs exceeded hearing thresholds or with only a subset of such neighbors. We relied on previous neurophysiological determinations of hearing thresholds and deployed two loudspeakers on opposite sides of the test male, both broadcasting playback stimuli above the test male's hearing threshold but one twice as distant and therefore 6 dB lower in perceived SPL. Stimuli from the two loudspeakers were broadcast 180° out-of-phase (i.e., alternating; see Fig. 3) during the first half of each playback trial. The loudspeaker nearer the test male was then turned off during the second half of the trial, and only the more distant loudspeaker continued broadcasting.

We evaluated interaction between a test male and a surrounding loudspeaker by noting whether the male exhibited an inhibitory-resetting response to the loudspeaker; i.e., refrained from calling during a specific interval following the loudspeaker broadcasts. Responses to only the nearer loudspeaker and ignoring the distant loudspeaker during the first half of a playback trial would be construed as evidence for selective attention. Responses to the distant loudspeaker during the second half of a playback trial would confirm that these broadcasts were above hearing threshold and provide additional support for selective attention. The latter responses would also indicate that selective attention does not rely on a fixed-threshold mechanism in which a male interacts with all stimuli above a given SPL set at some value greater than its behavioral hearing threshold.

We tested nine *L. coquilletti* males in 2-min trials, positioning the two loudspeakers 1 and 2 m from the test male. Thus, SPLs perceived by the test male were 63 and 57 dB, well above the neurophysiological and behavioral hearing threshold (45–48 dB SPL; see Bailey et al. 1993). Each loudspeaker broadcast a recorded male click every 1.2 s. Thus, stimulus clicks occurred every 0.6 s during the first half of a playback trial (Fig. 3). Interactions between the test male and a loudspeaker were judged by an absence of calls initiated during a 150-ms forbidden interval (see Fig. 3) beginning 100 ms following the onset of a stimulus click.

For *L. planum*, we tested 15 males in 6-min trials, positioning the two loudspeakers 3 and 6 m from the test male. Thus, SPLs perceived by the test male were 53.5 and 47.5 dB; we assumed that

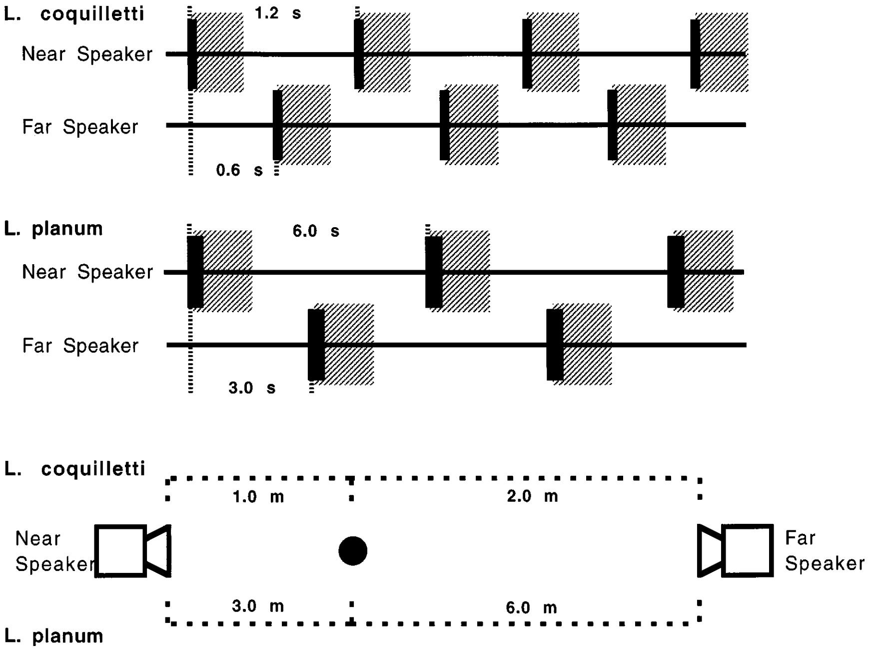

Fig. 3 Schematic representation of the loudspeaker arrangement and playback sequence for experiment 1 (two-loudspeaker playback). Stimulus signals were offset in a leader-follower relationship by 0.6 s for *Ligurotettix coquilletti* and by 3.0 s for *L. planum*. *Hatched areas* indicate the forbidden interval following the onset of a call during which the calls of another male are discriminated against by females. The duration of the forbidden intervals are 150 ms (beginning 100 ms following call onset) for *L. coquilletti*, and 1.6 s (beginning 0.2 s following call onset) for *L. planum*. The figure is not drawn to scale

the neurophysiological hearing threshold was comparable to that determined for *L. coquilletti*. Each loudspeaker broadcast a recorded male rasp every 6.0 s. Thus, stimulus rasps occurred every 3.0 s during the first half of a playback trial (Fig. 3). Interactions between the test male and a loudspeaker were judged by an absence of calls initiated during a 1.6-s forbidden interval (see Fig. 3) beginning 0.2 s following the onset of a stimulus rasp.

Experiment 2: does selective attention rely on a fixed-number mechanism? (four-loudspeaker playback)

We tested for the occurrence of a fixed-number mechanism in an experiment deploying four loudspeakers. Here, the number of loudspeakers surrounding the test male was successively increased from two to three and from three to four during a trial. An increase in the number of loudspeakers that he responded to, e.g., from one of two to two of three, or from two of three to three of four, would provide evidence that a fixed-number mechanism does not occur.

We tested 19 *L. planum* males in 6-min trials. During the initial 2 min of each trial, the test male was surrounded by two broadcasting loudspeakers positioned 3.0 and 4.5 m distant. A third loudspeaker at 6.0 m began broadcasting during the next 2 min, and a fourth at 7.5 m began during the final 2 min. The four loudspeakers were arranged such that adjacent ones were separated in azimuth by 90°. Each loudspeaker broadcast a stimulus rasp once per 6.0-s period. The broadcasts were delivered in a regular sequence beginning with the nearest and ending with the farthest loudspeaker. A 1.0-s delay separated the broadcasts of successive loudspeakers, thus leaving a 3.0-s silent interval during each 6.0-s period (following the 7.5 m loudspeaker).

Experiment 3: does selective attention rely on a sliding-threshold mechanism? (four-loudspeaker playback)

We next asked whether the subset of calling neighbors that a male interacts with is determined by the perceived SPLs of the loudest neighbors. That is, do males only respond to those neighbors whose calls are within x dB of the loudest (= nearest) one(s)? We used a four-loudspeaker experiment, deploying the loudspeakers surrounding the test male in either a close or a dispersed array (see Fig. 4). Responses to a loudspeaker positioned at a given distance in the dispersed array but not in the close array would indicate that a sliding-threshold is used.

We tested 26 *L. planum* males in 10-min trials. In half of the trials the four loudspeakers were arranged in the close array during the first 5 min and in the dispersed array during the latter 5 min. This sequence was reversed in the remaining half of the trials. Loudspeakers were positioned 3.0, 4.5, 6.0, and 7.5 m distant from the test male in the close array, and 3.0, 6.0, 7.5, and 8.5 m distant in the dispersed array. In both arrays, adjacent loudspeakers were separated by 90° azimuth angles (see Fig. 4). A stimulus signal was broadcast from one of the speakers every 1.5 s. Within each successive 6.0-s period measured from the start of the playback, the broadcast sequence of the four loudspeakers was randomized (see Fig. 4), preventing the test male from possibly entraining his responses to a particular loudspeaker(s) based on its anticipated broadcast time in the four-loudspeaker sequence.

Results

Experiment 1: does selective attention occur and does it rely on a fixed-threshold mechanism?

We found evidence that selective attention regulates inhibitory-resetting in both *L. coquilletti* and *L. planum*, but a fixed-threshold mechanism was indicated in neither species. *L. coquilletti* males called less during the 150-ms forbidden interval (0.1–0.25 s) following broadcasts from the nearby loudspeaker than during the 150-ms interval following the far loudspeaker in the first half of the trials (binomial test, $P < 0.05$, Fig. 5). When the nearby loudspeaker ceased broadcasting, in the second half of a trial, males again called less than expected by chance (binomial test, $P < 0.05$) following the distant loudspeaker and also gave fewer calls than during the same forbidden interval when both loudspeakers were broadcasting (binomial test, $P < 0.05$, Fig. 5). These findings imply that *L. coquilletti* males who hear both nearby (1 m) and distant (2 m) neighbors would only pay attention to the nearby one. However, their threshold for selective attention would move outward (and decrease to a lower SPL) and include the distant neighbor if it is the only one calling.

Results from *L. planum* males were less clear, but a similar pattern was revealed. In the first half of the trials, when both loudspeakers were broadcasting, males called less than expected during the 1.6-s forbidden interval (0.2–1.8 s) following the nearby loudspeaker (binomial

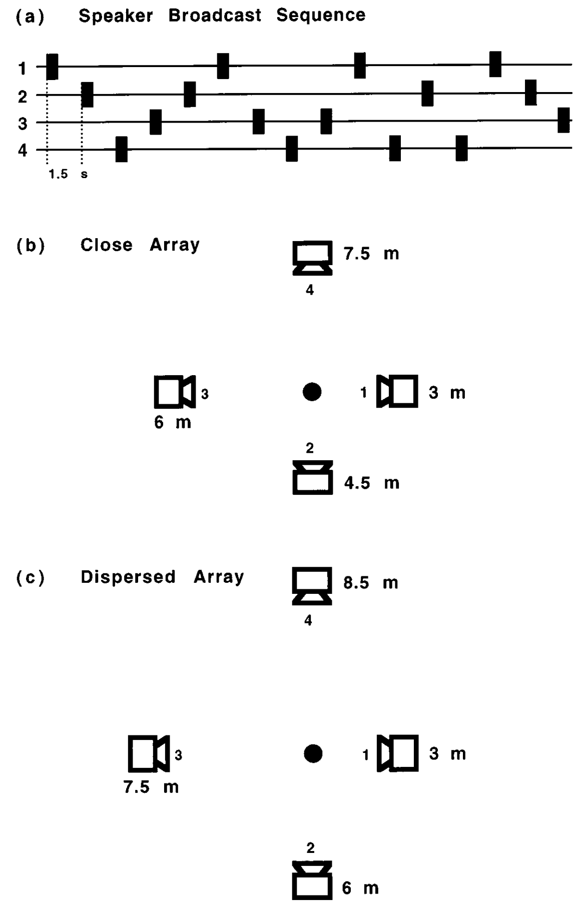

Fig. 4 Schematic representation of the loudspeaker arrangement and stimulus sequence used in experiment 3 to test whether males use a sliding-threshold rule. Stimuli were presented every 1.5 s from one of four loudspeakers in either a close (**b**) or dispersed (**c**) array. Within each successive 6-s period, measured from the start of the playback, the order of loudspeaker broadcasts was randomized. The figure is not drawn to scale

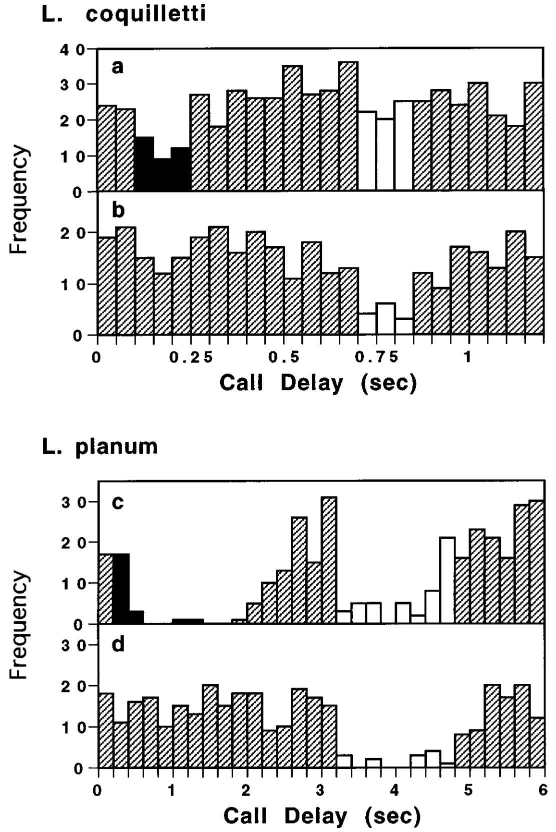

Fig. 5 Call delay histograms for experiment 1 (two-loudspeaker playback) showing that males do not follow a fixed-threshold rule. *Solid bars* represent calls given during the forbidden interval (*L. coquilletti* = 0.1–0.25 s, *L. planum* = 0.2–1.8 s; see Introduction) following the stimulus broadcast from the nearby loudspeaker, *open bars* represent calls given during the forbidden interval following the stimulus broadcast from the far loudspeaker. Both loudspeakers broadcasting in (*a*) and (*c*); only the far speaker broadcasting in (*b*) and (*d*). Data for *L. coquilletti* are from 9 males, and for *L. planum* from 15 males

test, $P < 0.05$), but they also called less than expected following the distant loudspeaker (binomial test, $P < 0.05$, Fig. 5). Five of 15 males tested responded to both loudspeakers. But of the 10 that responded to only one of the loudspeakers, 9 responded to only the nearby loudspeaker, indicating that males pay significantly more attention to the nearby loudspeaker than the far one (binomial test, $P < 0.05$). When the nearby loudspeaker ceased broadcasting, in the second half of a trial, males produced fewer calls during the forbidden interval following the distant loudspeaker than expected by chance (binomial test, $P < 0.05$, Fig. 5) and fewer calls than during the same forbidden interval when both speakers were broadcasting (binomial test, $P < 0.05$). These findings imply that *L. planum* males who hear both nearby (3 m) and distant (6 m) neighbors would pay more attention to the nearby one. As in *L. coquilletti*, their attention to the distant neighbor would increase if it is the only one calling.

No *L. coquilletti* males responded to both loudspeakers during the first half of the trials; however, 5 of 15 *L. planum* did respond to both loudspeakers. That these males responded to both loudspeakers during the first half of the trial may be a result of our having placed the far loudspeaker too close to them (i.e., well above the BRT).

Experiment 2: does selective attention rely on a fixed-number mechanism?

We found no evidence indicating that *L. planum* relies on a fixed-number mechanism for selective attention. As the number of broadcasting loudspeakers was increased from two to three, test males continued to call less than expected by chance following only the nearest two loudspeakers (Fig. 6b). However, as the number of broadcasting loudspeakers was increased from three to four (Fig. 6c), test males increased the number of loudspeakers following which they called less than expected to three. We compared the number of male calls given during a 1-s interval (2.8–3.8 s) when three and four loudspeakers were broadcasting and found that males produced significantly fewer calls during this period when four loudspeakers were broadcasting (McNemar's test, chi-square$_{\text{cont}}$ = 4.0832, $v = 1$, $P < 0.05$). These findings imply that *L. planum* pay attention to varying numbers of calling neighbors depending on the number of calling neighbors present.

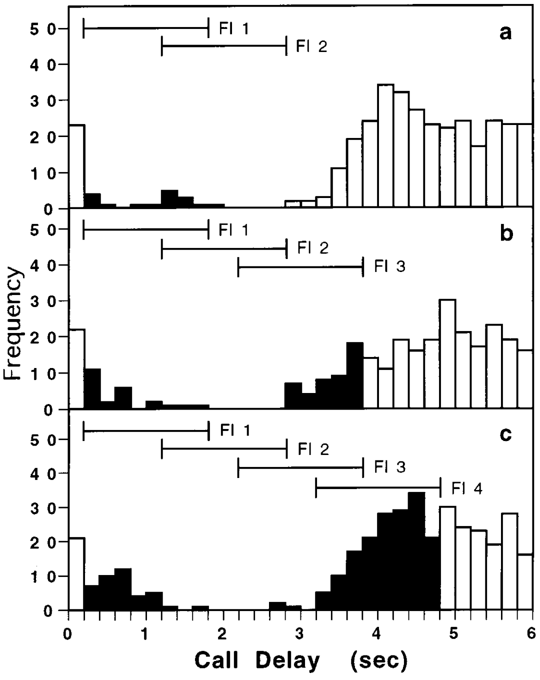

Fig. 6a–c Call delay histograms for experiment 2 (four-loudspeaker playback) showing that males do not respond to a fixed number of competitors. *Solid bars* represent calls given during the 1.6-s forbidden interval following the stimuli broadcast from two loudspeakers (3.0 and 4.5 m) (**a**), three loudspeakers (3.0, 4.5, 6.0 m) (**b**), and four loudspeakers (3.0, 4.5, 6.0, and 7.5 m) (**c**). *Horizontal lines* indicate the forbidden interval (*FI*) following the onset of each stimulus. Data are from 19 *L. planum* males

Experiment 3: does selective attention rely on a sliding-threshold mechanism?

We found evidence indicating that selective attention in *L. planum* is regulated by a sliding-threshold mechanism. When the four loudspeakers were arranged in the close array, males called less than expected following the loudspeakers 3.0, 4.5, and 6.0 m distant and all males ignored broadcasts from the loudspeaker at 7.5 m (Fig. 7a). However, when presented with the dispersed-loudspeaker array, 19 of 26 males did respond to the loudspeaker at 7.5 m (McNemar's test, chi-square$_{\mathrm{cont}}$ = 17.053, $v = 1$, $P < 0.001$). All males ignored the loudspeaker at 8.5 m (Fig. 7b). These findings imply that whether or not a *L. planum* male pays attention to a given calling neighbor depends on the distances to (SPLs of) the nearer neighbors. But in both our close and dispersed arrays, the nearest neighbor was 3.0 m distant, suggesting that the sliding-threshold for response depends not only on the nearest neighbor but on the entire neighborhood of nearby males.

Our data, though consistent with a sliding-threshold mechanism, are also consistent with "respond to up to three competitors" or "respond to *n*–1" (where *n* is the number of competitors) rules. We suggest that the sliding-threshold mechanism is more parsimonious, and likely, as it requires only an auditory threshold and not that males can (also) count. A sliding-threshold mechanism would also more effectively allow males to monitor and respond to changing numbers and densities of competitors within a dynamic chorus structure. Playback experiments employing more than four speakers will be required to differentiate between these possible mechanisms.

Discussion

Acoustic signals, whether they serve to attract mates and/or deter rivals, can only be an effective means of communication if they are readily discernible in a complex acoustic environment. Many biotic and abiotic sources of noise and interference can influence the effectiveness of both signal transmission and perception (Marten and Marler 1977; Marten et al. 1977; Gerhardt 1994). For females, generally the phonotactic sex, the problem is one of determining the correct species, the "best" male from among a group of conspecifics, and that male's spatial location within the group, all when faced with a noisy environment. Various signal attributes, such as amplitude and frequency, may allow some males to stand out from the crowd and background noise and can be used, in part, by females in discrimination between potential mates (Gerhardt 1994). Recently, the timing of a male's signals relative to those of his competitors has also been shown to be important in the attraction of females (Greenfield et al., 1997; Snedden and Greenfield, in press). The problem for a male is then not only to ensure that his signals are perceived above the biotic and abiotic background noise, but also to ensure that his signals are perceived at a critical time relative to those of his neighbors. Males of several species of frogs and insects appear to have evolved a specialized inhibitory-resetting mechanism to cope with the problem of relative signal timing (Greenfield and Roizen 1993; Greenfield et al. 1997). However, computer simulations suggest that this mechanism can be stable only when males exhibit selective attention whereby they re-

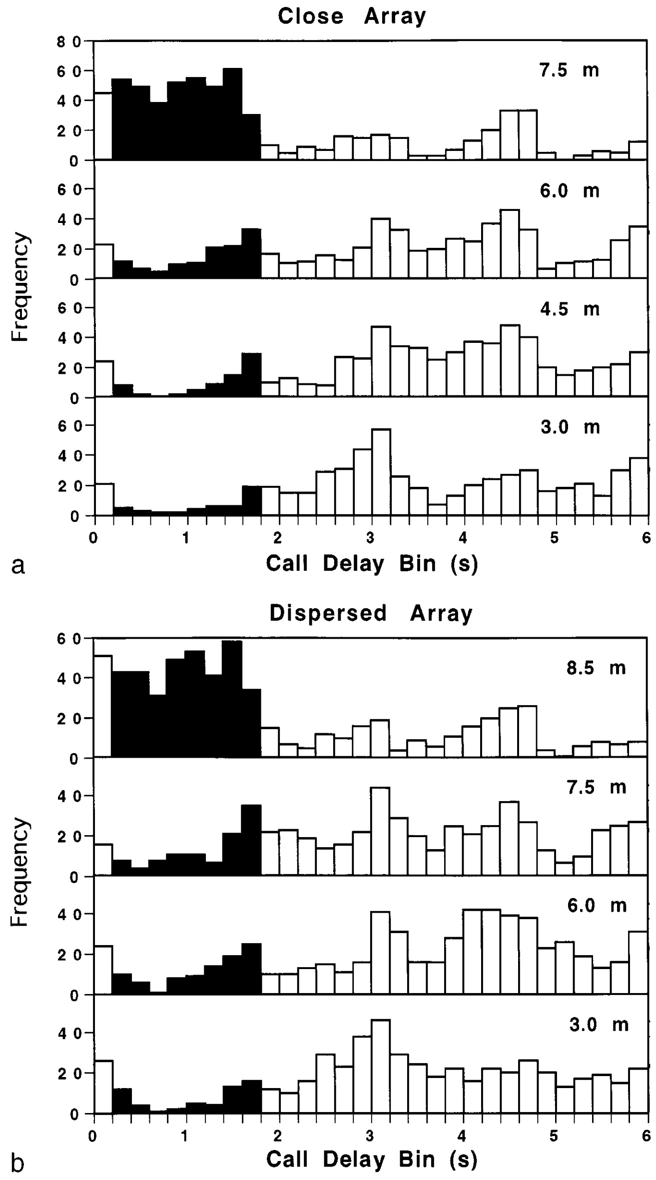

Fig. 7 Call delay histograms from experiment 3 (four-loudspeaker playback): close array (**a**), and dispersed array (**b**). *Solid bars* represent calls given during the 1.6-s forbidden intervals following stimulus broadcast. When presented with the close array, males responded to the loudspeakers at 3.0, 4.5, and 6.0 m but not to the loudspeaker at 7.5 m. When presented with the dispersed array, however, males responded to the loudspeakers at 3.0, 6.0, and 7.5 m but not the loudspeaker at 8.5 m, suggesting that they follow a sliding-threshold rule. Data are from 26 *L. planum* males

spond to but a subset of the signaling competitors within their auditory range (Greenfield et al. 1997).

The results of the experiments reported here show that male *L. coquilletti* and *L. planum* grasshoppers do exhibit selective attention toward only a subset of their competitors. Further, our results suggest that this selective attention is regulated by a sliding-threshold mechanism whereby males respond to their nearest competitor and also those males within a certain relative amplitude (distance) of that competitor. However, natural choruses are likely to represent a much more dynamic competitive arena than even our four-loudspeaker playback protocol.

Males may often space themselves much closer to their neighbors than the maximum distance over which they can perceive, and respond to, conspecific signals (Römer and Bailey 1986; Gerhardt et al. 1989). Further, the movement of males in and out of, as well as within, an area will alter both local density and nearest-neighbor distances. The alternative fixed-threshold and fixed-number mechanisms tested here, although possibly effective at low density and in situations where males remain spatially fixed, might not allow males to adjust their signaling readily to changes in the number and spatial location of their competitors. Once a sliding-threshold mechanism arises, the dynamics of competition might be, at least in part, responsible for its maintenance in the context of signal interactions.

The selection pressures favoring the evolution of selective attention per se are probably common to both males and females and likely derive from a necessity to discriminate point-source sounds in a noisy environment. This cocktail party effect (Cherry 1953; Schwartz and Gerhardt 1989) may be a consequence of the neural architecture responsible for directional hearing (Pollack 1988). Pollack (1988) suggests that the louder of two stimuli, both of which are suprathreshold, may elicit a strong post-response hyperpolarization of the auditory neuron, thus dampening response to the weaker stimulus. Alternatively (or additionally), stimulation at the ipsilateral ear may cause peripheral inhibition at the contralateral ear such that subsequent stimuli are rendered subthreshold (Römer 1993; Römer et al. 1997). Hierarchical discrimination of signals is also likely accomplished at higher processing levels in the brain.

Irrespective of the neural mechanism(s) involved or their selective origin, selective attention is a necessary precursor to the evolution of an inhibitory-resetting mechanism regulating male signaling (see Greenfield et al. 1997) and, consequently, chorus structure. Thus, a thorough understanding of chorus dynamics must include careful study of the selective-attention phenomenon.

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References

Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ

Bailey WJ, Greenfield MD, Shelly TE (1993) Transmission and perception of acoustic signals in the desert clicker, *Ligurotettix coquilletti* (Orthoptera: Acrididae). J Insect Behav 6:141–154

Cherry EC (1953) Some experiments on the recognition of speech, with one and with two ears. J Acoust Soc Am 25:975–979

Gerhardt HC (1994) The evolution of vocalization in frogs and toads. Annu Rev Ecol Syst 25:293–324

Gerhardt HC, Diekamp B, Ptacek M (1989) Inter-male spacing in choruses of the spring peeper, *Pseudacris crucifer*. Anim Behav 38:1012–1024

Greenfield MD (1992) The evening chorus of the desert clicker, *Ligurotettix coquilletti* (Orthoptera: Acrididae): mating investment with delayed returns. Ethology 91:265–278

Greenfield MD (1994) Cooperation and conflict in the evolution of signal interactions. Annu Rev Ecol Syst 25:97–126

Greenfield MD (1997) Sexual selection and the evolution of advertisement signals. Perspect Ethol 12:145–177

Greenfield MD, Roizen I (1993) Katydid synchronous chorusing is an evolutionary stable outcome of female choice. Nature 364:618–620

Greenfield MD, Tourtellot MK, Snedden WA (1997) Precedence effects and the evolution of chorusing. Proc R Soc Lond B 264:1355–1361

Marten K, Marler P (1977) Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behav Ecol Sociobiol 2:271–290

Marten K, Quine D, Marler P (1977) Sound transmission and its significance for animal vocalization. II. Tropical forest habitats. Behav Ecol Sociobiol 2:291–302

Minckley RL, Greenfield MD (1995) Psychoacoustics of female phonotaxis and the evolution of male signal interactions. Ethol Ecol Evol 7:235–243

Minckley RL, Greenfield MD, Tourtellot MK (1995) Chorus structure in tarbush grasshoppers: inhibition, selective phonoresponse, and signal competition. Anim Behav 50:579–594

Pollack GS (1988) Selective attention in an insect auditory neuron. J Neurosci 8:2635–2639

Prestwich KN, Brugger KE, Topping M (1989) Energy and communication in three species of hylid frogs: power input, power output and efficiency. J Exp Biol 144:53–80

Römer H (1993) Environmental and biological constraints for the evolution of long-range signaling and hearing in acoustic insects. Phil Trans R Soc Lond B 340:179–185

Römer H, Bailey WJ (1986) Insect hearing in the field: II. Male spacing behavior and correlated acoustic cues in the bushcricket *Mygalopsis marki*. J Comp Physiol A 159:627–638

Römer H, Hedwig B, Ott S (1997) Proximate mechanism of female preference for the leader male in synchronizing bushcrickets (*Mecopoda elongata*). In: Elsner N, Waessle H (eds) Proceedings of the 25th Göttingen Neurobiology Conference. Thieme, Stuttgart, p 322

Schwartz JJ, Gerhardt HC (1989) Spatially mediated release from auditory masking in an anuran amphibian. J Comp Physiol A 166:37–41

Searcy WA, Andersson M (1986) Sexual selection and the evolution of song. Annu Rev Ecol Syst 17:507–533

Shelly TE, Greenfield MD (1989) Satellites and transients: ecological constraints on alternative mating tactics in male grasshoppers. Behaviour 109:200–221

Snedden WA, Greenfield MD (in press) Females prefer leading males: relative call timing and sexual selection in katydid choruses. Anim Behav

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