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Frogs Have Rules: Selective Attention Algorithms Regulate Chorusing in *Physalaemus pustulosus* (Leptodactylidae)

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Abstract

In various acoustic insects and frogs, females preferentially orient towards the leading of two or more males' advertisement signals that occur closely in time. Such preferences in receivers have apparently selected for timing mechanisms whereby male signallers actively refrain from calling immediately following the onset of a neighbour's call and thereby increase their production of leading calls. However, indiscriminate application of this inhibitory mechanism to all neighbours might severely reduce a male's calling rate, particularly in high density. Consequently, mechanisms of selective attention to only a subset of signalling neighbours are expected.

Female Túngara frogs (*Physalaemus pustulosus*) exhibit strong preferences for leading male calls, and males refrain from calling immediately following a neighbour. Four-loudspeaker playback experiments demonstrated that males do selectively apply this inhibitory mechanism to only a subset of close signalling neighbours. Selective attention is regulated by a combination of sliding threshold and fixed number rules: (i) Attend to the loudest (nearest) conspecific neighbour and those additional ones whose calls are within 6–8 dB of the loudest one; (ii) attend to only two neighbours in total when the calls are weak or the second one is much farther than the first; (iii) attend to three neighbours when the calls are loud or all neighbours are approximately equidistant. The means by which such plasticity may be achieved and its potential adaptiveness are discussed.

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Introduction

It is becoming increasingly evident that the relative timing of a male's advertisement signals within the social environment can represent a critical aspect of

his sexual attractiveness. In various species of chorusing anurans and insects, localization and preference of male signals by females is influenced by a psychoacoustic 'precedence effect' (sensu Zurek 1987): Females attend and orient to the leading of two or more spatially separated signals that occur closely in time (Dyson & Passmore 1988; Stiedl 1991; Greenfield & Roizen 1993; Howard & Palmer 1995; Minckley & Greenfield 1995; Galliard & Shaw 1996; Grafe 1996; see also Backwell et al. 1998 and Vencl & Carlson 1998 for similar phenomena in visual signals). While the evolution of neurophysiological mechanisms, e.g. forward masking, responsible for precedence effects among receivers remains unclear (see Wytenbach & Hoy 1993; Römer et al. 1997; Snedden & Greenfield 1998), these effects have apparently selected for signal timing mechanisms that reduce the incidence of ineffective following calls (Greenfield 1994a). Among species that call rhythmically, a signaller may employ 'inhibitory-resetting', a sensorimotor mechanism wherein the central generator controlling his signalling descends to its basal level when a conspecific neighbour's signal is heard (Greenfield et al. 1997). The generator remains inhibited at this level until that signal terminates, at which time the generator is reset and rebounds to its trigger level and the subsequent production of a call. Thus, a signaller avoids calling immediately following its neighbour and increases its incidence of leading calls (Greenfield 1994a; see also Buck 1988 and Aizawa 1998 for discussion of mechanisms among visual signallers). But, in a dense chorus a signaller applying inhibitory-resetting indiscriminately to all signalling neighbours he perceived, might call so infrequently as to render the measure counterproductive. Consequently, some sensory modification of this mechanism in which signallers attend to only a subset of their signalling neighbours is predicted (Brush & Narins 1989; Greenfield et al. 1997).

Preliminary work on several chorusing insects confirms the above expectation: Signalling males apply the inhibitory-resetting mechanism to only a subset of those neighbours whose calls exceed their behavioural hearing threshold (Minckley et al. 1995; Snedden et al. 1998). In one species, playback experiments suggest that the subset may be defined, at least in part, by a sliding threshold: Attend to the loudest neighbour, calling at L dB, and to all those whose perceived calls are within df dB, a threshold differential, of that neighbour, provided that $L-df$ exceeds the behavioral response threshold (see Pollack 1988 and Römer 1993 on potential neural mechanisms). Presumably, this subset includes those neighbours who are the focal male's strongest competitors for females (Snedden et al. 1998). Nonetheless, other potential mechanisms could not be ruled out. Here, we pursue this basic problem further in a chorusing anuran, *Physalaemus pustulosus*, for which the dilemma of calling indiscriminately vs. applying an inhibitory-resetting mechanism is particularly acute. *P. pustulosus* males may form dense clusters nightly at temporary pools, where they advertise to receptive females. Advertisement consists of 'whines' or 'whines + chucks' delivered rhythmically at approximately 0.5 calls s^{-1} (Ryan 1985). Playback experiments indicate that female orientation is influenced by a strong precedence effect and that males do not call during a 600-ms interval beginning shortly after the onset of a conspecific call (Snedden & Rand, unpubl. data). But, in the field males often call regularly amidst four or more calling

neighbours within a 2-m radius (Ryan 1985; Snedden & Rand, unpubl. data). We therefore carried out a series of 4-loudspeaker playback experiments to determine how *P. pustulosus* males modify their basic inhibitory-resetting mechanism in the social situations normally experienced. We found that while *P. pustulosus* apply a sliding threshold modification as described above, under certain circumstances they restrict their attention to only particular neighbours from among the subset whose calls exceed the threshold. Additionally, they also lower the threshold under other circumstances. Such selective attention rules may be necessitated by the chorus densities in this species.

Methods and Materials

Physalaemus pustulosus Natural History and Acoustic Behaviour

Physalaemus pustulosus are leptodactylid frogs common throughout the lowlands of Central America and northern South America. Choruses of advertising males assemble nightly at temporary pools during the rainy season (May–Nov.). Calling begins at dusk and continues for several hours in the form of repeated ‘unison bouts’ (see Ryan 1985). Individual calls consist of a 300–400 ms ‘whine’ followed by one or more shorter ‘chucks.’ Whines and chucks include frequencies ranging from 400 to 3600 Hz; most energy in whines is below 900 Hz (Ryan 1985; Ryan et al. 1990).

Assemblages of two or three males may call in a regularly alternating fashion, with the calling rhythms of each male separated by $\approx 180^\circ$ or 120° phase angles, respectively (Snedden & Rand, unpubl. data). When larger choruses assemble, the sequence does not adhere to a recognizable temporal pattern. Call rates of individuals in choruses are slightly slower than the 0.5 s^{-1} seen in solo calling. Some individuals call throughout a unison bout, which may last from 30 s to over 5 min, whereas others start and stop calling during the bout (Snedden & Rand, unpubl. data). Individuals may change positions within the chorus between bouts.

Female *P. pustulosus* presented with male calls broadcast from two loudspeakers orient preferentially toward those calls whose onsets lead others by 10–350 ms (Snedden & Rand, unpubl. data). Males exhibit a commensurate inhibitory-resetting mechanism whereby they do not initiate calls during an interval from 50 to 600 ms following the onset of a neighbour’s call (Greenfield et al. 1997; Snedden & Rand, unpubl. data; see also Moore et al. 1989). Presumably, calls that are given during the initial 50 ms following a neighbour have already been triggered by the focal male’s call generator, indicating a ‘motor delay’ of 50-ms duration (see Loftus-Hills 1974; Greenfield 1994a, b).

Playback Experiments

We studied how male *P. pustulosus* apply inhibitory-resetting to signalling neighbours via a series of playback experiments conducted on frogs collected in the vicinity of Gamboa, Panama, during May and June 1998. Male frogs found calling were collected during evening hours, toe-clipped (to preclude recapture),

and placed in 10-l translucent polyethylene bags containing 2–3 cm of rainwater and a Styrofoam float. The bags were inflated, closed, and kept in a room subject to outdoor temperature and photoperiod. On the following afternoon we moved the bags to an adjoining acoustic laboratory kept at 26°C and shaded them from light. Bags with frogs that began to call were then transferred singly to the centre of a darkened, soundproof chamber (2.7 × 1.8 × 1.8 m; l × w × h; Acoustic Systems, Austin, Texas; sound reduction 44–60 dB from 500 to 4000 Hz) within the laboratory. Here, the frog was subjected to a series of trials of various playback categories in which synthetic *P. pustulosus* calls were broadcast from four equidistant, surrounding loudspeakers (Fig. 1). Each calling male was tested in one series of trials only, removed from the chamber, and later returned to the field. A total of 32 frogs were tested in this fashion over a 17-d period.

The polyethylene bags served to retain the test male at a designated (central) location in the soundproof chamber. Acoustic measurements (see below) showed that the plastic bags were acoustically transparent for transmission of male call broadcasts: Sound pressure levels (SPLs) of loudspeaker broadcasts measured inside and immediately outside the bag differed by less than 0.5 dB, and there were no detectable influences on call frequency or temporal structure (Fig. 2).

Stimulus Design and Presentation

Calls used in all trials were identical and generated via a digital signal processing program (Signal; see Fig. 2). This call included a 350-ms whine followed by one 90-ms chuck and was designed to bear temporal envelope and spectral features typical for the Gamboa *P. pustulosus* population. We copied the call onto four channels of a multichannel digital signal processing program (DACQ12B; Sili-

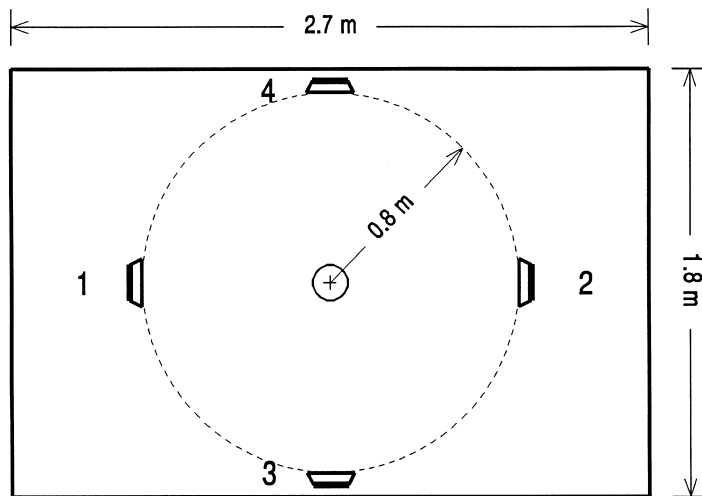


Fig. 1. Positions of 4 loudspeakers (trapezoids 1–4) surrounding test male (circle) in soundproof chamber

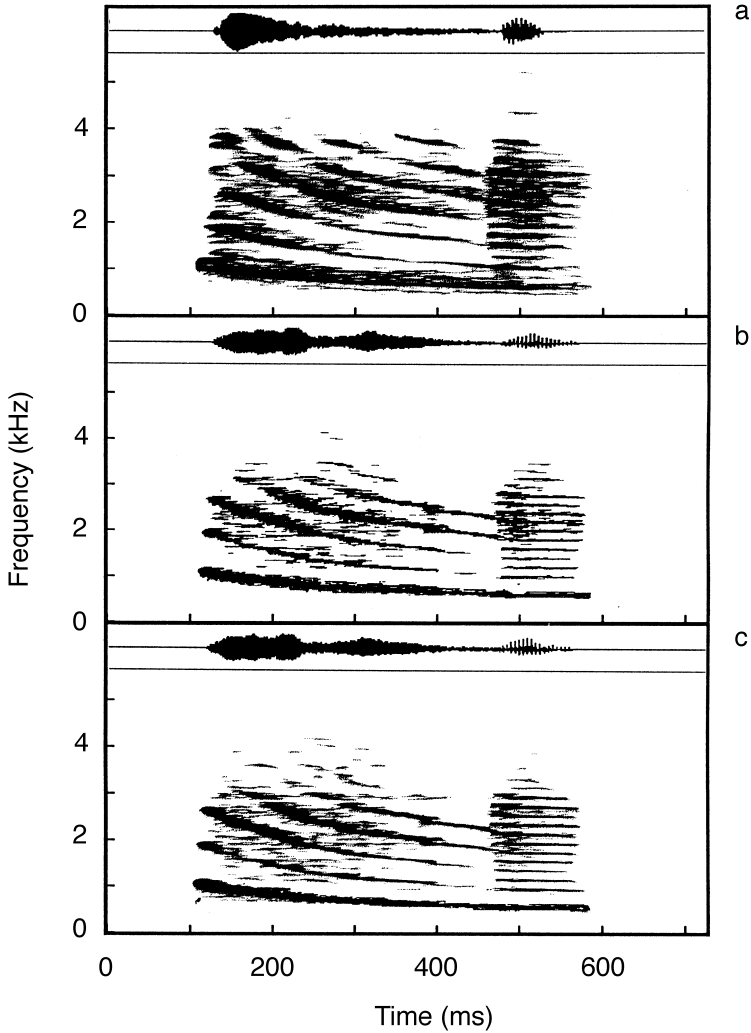


Fig. 2: Oscillograms and sonagrams of a *P. pustulosus* male call and of synthetic calls broadcast in all playback trials. (a) Call recorded from a male in Gamboa, Panama in Jun. 1998. (b) Broadcast of synthetic call as recorded within polyethylene bag holding test male. (c) Broadcast of synthetic call as recorded immediately outside bag. Bag and loudspeaker broadcasting call were positioned as in Fig. 1; see text for details of recording

conSoft; San Jose, CA) stored on a notebook computer. During a trial, outputs from these channels were sent to each of the four loudspeakers (Radio Shack model 1325 Tandy Corp., Fort Worth, TX; frequency response ± 2 dB SPL from 70 to 10 000 Hz) via a multichannel digital: analog I/O device (DACQPOD 12B80; SiliconSoft). Gain of each loudspeaker was controlled separately with a 1-W

amplifier (model TA-001, Mark V Electronics, Montebello, CA) in its circuit. We monitored the calling of the test male and the loudspeaker broadcasts with an omnidirectional tieclip microphone (Radio Shack model 33-3003; frequency response from 70 to 16 000 Hz) attached to the top of the polyethylene bag. Output from the microphone was sent to one channel of a stereo cassette tape recorder (Marantz model PMD 430). The other tape recorder channel received output split from the computer channel leading to loudspeaker number 1, the 'marker' loudspeaker (see Snedden et al. 1998). Thus, we could transcribe the tape recording of a trial and accurately compare the timing (± 0.5 ms) of the test male's calls with the loudspeaker broadcasts. Both computer and tape recorder were kept outside of the soundproof chamber.

Each playback trial used the same pseudorandom sequence of broadcasts from the four loudspeakers. In this sequence a call was broadcast every 450 ms from a different loudspeaker randomly selected without replacement until all four loudspeakers were used. A novel, random order of broadcasts from the four loudspeakers then followed immediately (Fig. 3a, b; see also Snedden et al. 1998). This process was repeated 10 times for a total of 40 calls, 10 per loudspeaker; the entire 40-call sequence, 18 s in length, was itself repeated 10 times for a 3-min trial. In one category (1) of trials, though, calls were broadcast every 600 ms, with the 40-call sequence, 24 s in length, repeated only 7.5 times (Fig. 3c), and in another category (12), playback continued for 6 min. The pseudorandom sequence prevented males from entraining their call rhythm to a periodic broadcast from any one loudspeaker.

In playback categories 2-11 (see Table 1), calling was present during > 95% of the time (Fig. 3b). This nearly continuous production of sound is typically found in *P. pustulosus* choruses including four or more males (Snedden & Rand, unpubl. data). Unlike our four-loudspeaker playback, males in natural choruses interact with one another and are unlikely to produce an even timing of calls because their free-running rhythms and the parameters of their inhibitory-resetting mechanisms are probably not identical. We did not include this aspect of chorus structure as a factor in our playback categories in order to test specifically the influence of neighbour spacing on a calling male's attention.

Males were tested with a series of up to 12 playback trials, each trial using a different playback category. Approximately 1 min elapsed between consecutive trials. A randomized block design was employed to order the sequence of playback categories presented to a male. Approximately 50% of the males tested ceased calling before half of all 12 trials were completed. Thus, the males tested were not all subjected to an identical set of stimuli (playback categories), and only a few were tested with all 12. This problem was an inevitable consequence of the normal calling of *P. pustulosus* in bouts.

The stimuli presented in the 12 categories of playback trials are listed in Table 1. SPLs used were chosen in consideration of the average loudness of a male *P. pustulosus* (90 dB SPL (re 20 μ Pa) at 0.5 m) and the typical spacing of advertising males. At the beginning of each night, SPLs of each loudspeaker's broadcasts were measured at the position of the test male using a General Radio model 1981

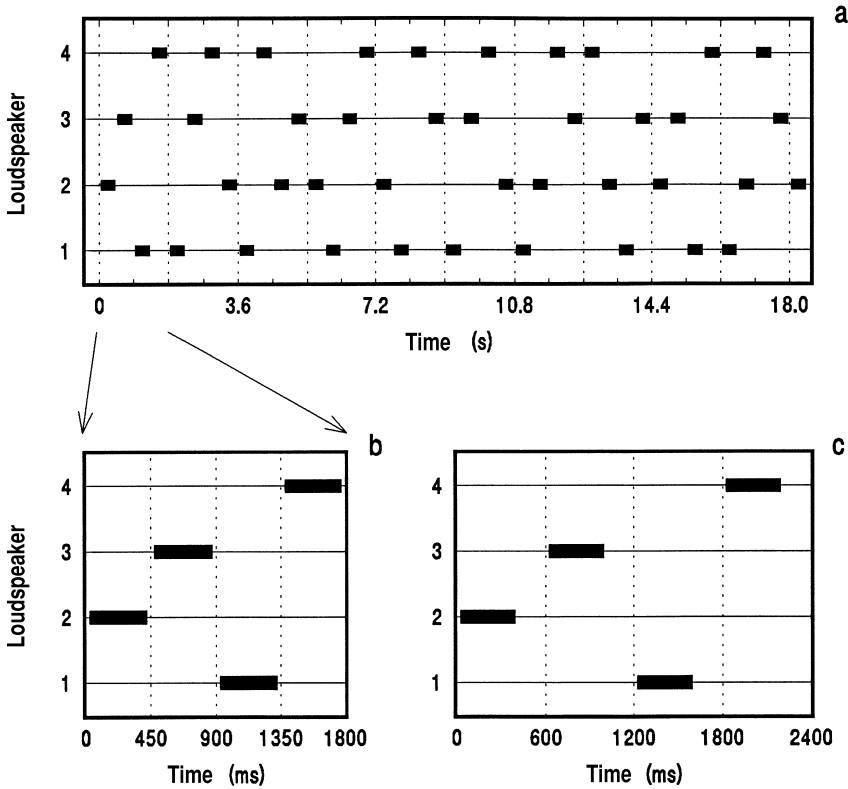


Fig. 3: Pseudorandom sequence of calls broadcast from four loudspeakers in playback trials. (a) 18-s sequence used in playback categories 2–12 (see Table 1); sequence was repeated 10 times for a 3-min trial and 20 times for the 6-min trials in Category 12. (b) The 18-s sequence consists of 10 successive 1800-ms sequences, each including four broadcasts of a 440-ms call from a different one of the four loudspeakers, chosen randomly without replacement, every 450 ms. This randomization process was repeated for each of the 10 successive 1800-ms sequences. (c) 2400-ms sequence, with calls, chosen randomly without replacement as above, every 600 ms. This randomization process was repeated for each of 10 successive 2400-ms sequences; the resulting 24-s sequence was repeated 7.5 times for the 3-min trials in Category 1

sound pressure level meter (peak setting). We adjusted the amplifier gains on each loudspeaker such that all broadcasts were equalized (± 1 dB) at 90 dB SPL. During the playback trials, we used a function in the computer’s signal processing program to attenuate differentially the SPLs broadcast from each loudspeaker and achieve the array of stimuli shown in Table 1. We later confirmed these attenuated SPLs by comparing digitized transcriptions of the trial’s tape recording with digitized recordings of continuous signals that had also been measured with the SPL meter. For a given playback category, we used a randomized-block design to select which loudspeakers broadcast the various SPLs to a given male.

The specific SPLs broadcast by the four loudspeakers in a playback category

Table 1: Arrays of loudspeaker stimuli presented to males in playback trials

Playback category	SPLs (dB) ^a	Period ^b	Trial length	n
1	90 86 82 78	600 ms	3 min	13
2	90 86 82 78	450 ms	3 min	19
3	84 80 76 72			19
4	81 77 73 69			7
5	78 74 70 66			17
6	90 86 86 78	450 ms	3 min	11
7	86 86 86 78			17
8	90 82 82 82	450 ms	3 min	7
9	90 82 82 78			7
10	90 78 78 78			10
11	86 78 78 78			6
12 ^c	90 86 82 78	450 ms	6 min	14

^a Peak amplitudes, as measured at the location of the test male, of male *P. pustulosus* calls broadcast from the four loudspeakers during a trial. Each loudspeaker (see Fig. 1) broadcast a given SPL throughout a trial except in Category 12.

^b Length of time elapsing between onsets of successive loudspeaker broadcasts (see Fig. 2b, c).

^c Loudspeakers broadcasting 90 and 78-dB calls were switched every 90 s during a 6-min trial, as were loudspeakers broadcasting 86 and 82-dB calls.

were considered as representative of neighbours, each calling with the same absolute SPL (as measured at a fixed distance), situated at various distances from the focal male. We constructed the array of playback categories to determine how a male would call in the various situations expected in natural choruses. From male calling responses in the different playback categories tested, we then elucidated the rules controlling chorusing behaviour in *P. pustulosus*.

Analysis of Responses

A male's response to a loudspeaker's broadcasts was assessed by comparing the number of calls he initiated in a 'critical interval' following the onset of those broadcasts with the number expected in those intervals were he calling randomly over time (see Fig. 4). We used a critical interval extending from 50 to 350 ms following the onset of the loudspeaker broadcast: Calls initiated before the 50-ms mark were probably triggered prior to the onset of the broadcast, and the female rejection of following calls held for calls made as much as 350 ms after a leading call. Thus, in a natural chorus, calls beginning during this critical interval would be relatively unattractive to nearby females. We considered a male to be responding to a given loudspeaker during a trial if he initiated significantly fewer calls than

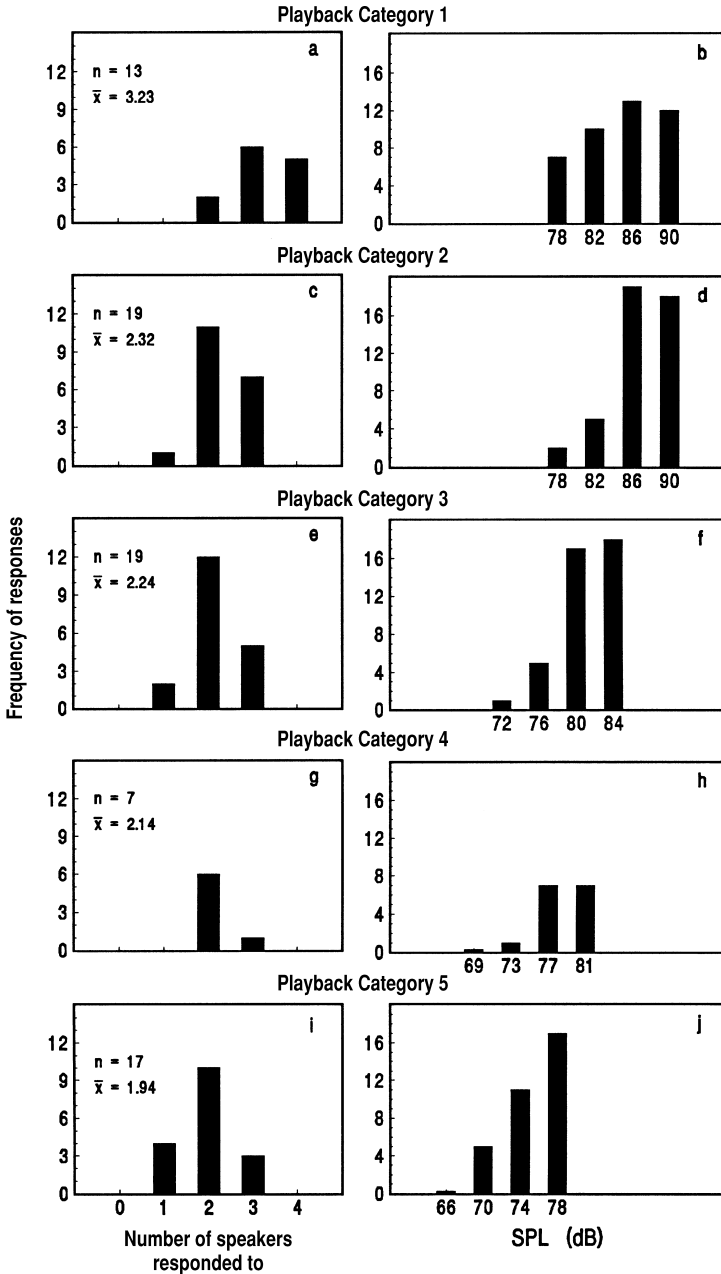


Fig. 4: Responses of test males to playback categories 1–5. (a, c, e, g, i) Frequencies of males responding to various numbers of loudspeakers during a 3-min trial of a given playback category. Total number of males tested (n) and mean number of loudspeakers responded to (\bar{x}) are shown. (b, d, f, h, j) Frequencies of males responding to each of the four different SPLs broadcast in a given playback category. See Table 1 for additional details on playback categories. A male was considered to have responded to a loudspeaker if the proportion of his calls that followed its broadcasts (begin 50–350 ms following onset of loudspeaker broadcast) was lower than the random expectation ($= 0.1250$ for Category 1, 0.1667 for categories 2–5; $p \leq 0.05$, Binomial test)

expected during that loudspeaker's critical interval (see Fig. 4). That is, response as used here actually refers to inhibition and suppression of calling.

Results

Do *P. pustulosus* Respond Selectively to Neighbours' Calls?

Approximately 40% of the males tested refrained from calling during the critical intervals following all four loudspeakers (90, 86, 82, and 78 dB SPL) in Category 1 trials, wherein loudspeaker broadcasts were delivered every 600 ms (Figs 3c, 4a, b). All males except one responded to (i.e. refrained from calling following) either the 82 or 78-dB SPL loudspeaker. Therefore, we assume that the behavioural response threshold (BRT) is ≤ 78 dB SPL at this condition for most individuals. We infer that when lengthy silent gaps (160 ms; see Fig. 3c) exist between succeeding stimuli, males respond to most stimuli (≥ 78 dB SPL) and place their calls within the gaps.

In Category 2 trials, wherein the same SPLs were used but loudspeaker broadcasts were delivered every 450 ms (Fig. 3b), nearly all males called during the critical intervals following the 78-dB loudspeaker, and many called following the 82-dB loudspeaker as well (Fig. 4c, d). A significantly lower proportion (3 of 12) responded to 3 or 4 loudspeakers in Category 2 trials than in Category 1 trials (7 of 8; $p = 0.02$; G-test, with Yates correction for continuity; to preserve independence, analysis was restricted to males tested in only one of these two playback categories). Because 78 dB exceeds the BRT of most males, we infer that in the absence of lengthy silent gaps between succeeding stimuli, males respond selectively to the louder ones only.

Do *P. pustulosus* Employ a Sliding Threshold in their Selective Responses?

Male responses in Category 2–5 trials are consistent with the operation of a sliding threshold whose threshold differential (df) $\cong 6$ dB (Fig. 4). Most males responded to the loudest loudspeaker and ignored the weakest regardless of their absolute SPLs (Fig. 4d, f, h, j). All nine males tested with both playback Categories 2 and 5 responded to 78 dB in Category 5 trials, wherein these broadcasts were the loudest ones, but did not respond to 78 dB in Category 2 trials ($p = 0.004$; Sign test, 2-tailed). But, these results are also consistent with 'fixed number' rules: For example, males may be responding to the two loudest loudspeakers and/or ignoring the two weakest ones. On the other hand, we found a downward trend, albeit nonsignificant (Friedman's test, $p > 0.05$), in the mean number of loudspeakers to which a male responded as the SPL of the loudest loudspeaker (L) declined from 90 (playback Category 2; $\bar{x} = 2.32$ loudspeakers) to 78 (playback Category 5; $\bar{x} = 1.94$ loudspeakers; Fig. 4). To the extent that a sliding threshold rule is used, df may be reduced at lower L s.

Do Fixed Number Rules Explain Selective Responses?

Responses to playback Categories 6–11 help clarify the contributions of sliding threshold and fixed number rules to *P. pustulosus* chorusing. By testing playbacks

in which two or three of the louder (categories 6–7) or weaker (categories 8–11) loudspeaker broadcasts were equivalent in SPL, we inferred that selective responses were not attributable to a sliding threshold rule alone. For five of these six playback categories, the majority of males did not respond to all of the loudspeakers broadcasting equivalent SPLs (Fig. 5). Rather, they responded to only one of two, or to one or two of three, of these loudspeakers.

The proportions of a male's calls produced following loudspeakers of equivalent SPL in a trial were averaged, and the proportions produced following each of the individual loudspeakers were then compared with this average expectation. These comparisons indicated that in approximately 50% of all cases a male produced a significantly different ($p \leq 0.05$; Binomial test, 2-tailed) proportion of calls following a given loudspeaker than expected. Were a sliding threshold the sole rule, males would have accorded an equal level of response to each loudspeaker broadcasting a given SPL.

The above findings should not be construed as evidence for an unmodified fixed-number rule, though. Males clearly responded to different numbers of loudspeakers depending on the SPLs broadcast in a playback category. Among playback categories in which the period = 450 ms and the loudest and weakest loudspeakers broadcast 90 and 78 dB, respectively, the mean number of loudspeakers that males responded to ranged from 2.55 (Category 6) to 1.90 (Category 10) (Fig. 5). Males responded to fewer loudspeakers in Category 10 trials than in Category 6 trials ($p = 0.03$; Sign test, 2-tailed; $n = 8$). This difference reflects a higher level of response to 86-dB loudspeakers in playback Category 6 than to 78-dB loudspeakers in playback Category 10.

How Do *P. pustulosus* Select Attended Stimuli?

When presented with two or three loudspeakers broadcasting at equivalent SPL, *P. pustulosus* are somehow stimulated to respond to some and to ignore others. This selectivity could not be associated with any measured characteristic of the loudspeakers. Digitized transcriptions of tape recordings of the playback trials indicated small discrepancies (± 1 dB) between the SPLs of loudspeaker broadcasts and their intended values. Nonetheless, we found no evidence that males responded to the louder/loudest loudspeaker of an equivalent set (Table 2). Likewise, we did not find that males favoured particular loudspeakers (or loudspeaker positions) (Table 2). When males responded to one or two of three equivalent loudspeakers, they showed no overall tendency to ignore or to respond to two adjacent or two opposite loudspeakers (Table 2).

How Do *P. pustulosus* Respond to Chorus Dynamics?

In a natural chorus a male's neighbours may move, and they may also start and stop calling during a bout. We simulated such changes in playback Category 12 trials and tested how well males redirected their attention when the loudspeakers broadcasting the louder and weaker stimuli were switched every 90 s over a 6-min interval (Table 1). The majority of males redirected their attention to the new

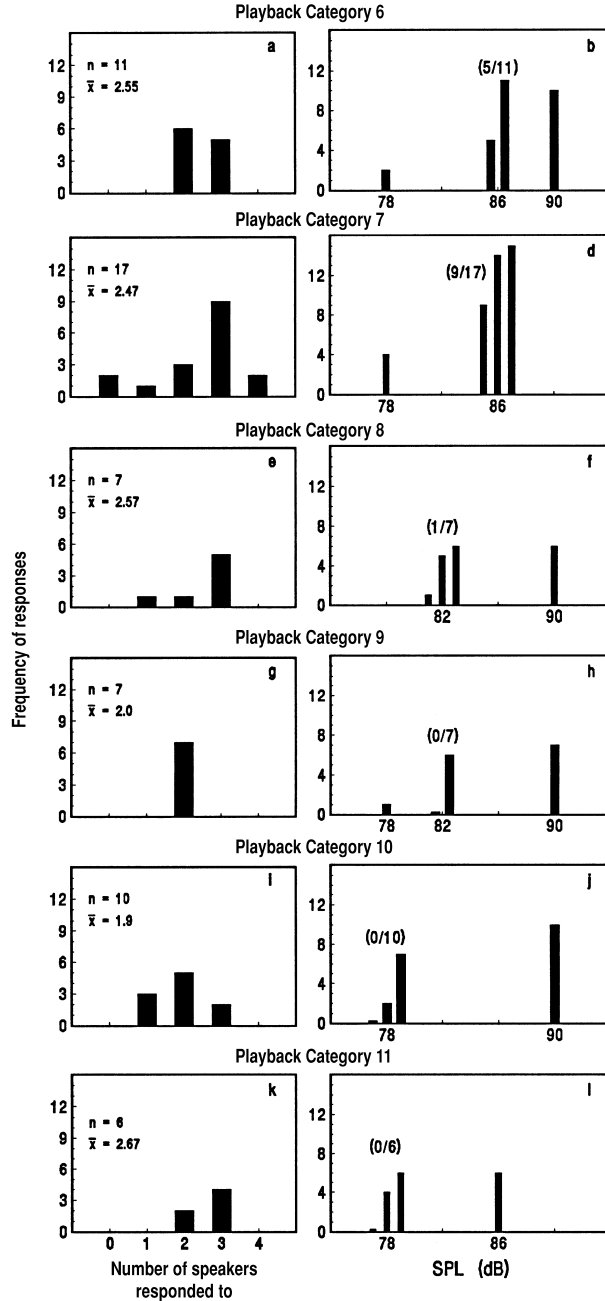


Fig. 5: Responses of test males to playback categories 6–11. (a, c, e, g, i, k) Frequencies of males responding to various numbers of loudspeakers during a 3-min trial of a given playback category. Total number of males tested (n) and mean number of loudspeakers responded to (\bar{x}) are shown. (b, d, f, h, j, l) Frequencies of males responding to each of the SPLs broadcast in a given playback category; note that in each category two or three of the four loudspeakers broadcast equivalent SPLs. Parenthetical values are proportions of males tested that responded to all of the loudspeakers broadcasting an equivalent SPL. See Table 1 for additional details on playback categories. See Fig. 4 for response criterion

Table 2: Responses to loudspeakers broadcasting equivalent SPLs

Louder/loudest loudspeaker responded to ^a :	Yes	No		
	19	16		
	Loudspeaker			
	1	2	3	4
Frequency of responses to loudspeaker ^b :	10	9	20	14
Opposite loudspeakers both responded to or both ignored ^c :	Yes	No		
	14	14		

^a Peak amplitudes of loudspeakers broadcasting equivalent SPLs in playback categories 6–11 always differed by ± 1 dB. For all trials in categories 6–11 in which a male responded to only one of two, or to only one or two of three, of the loudspeakers broadcasting equivalent SPLs, the number of trials in which the male responded to the louder(est) loudspeaker are shown.

^b For all responses to loudspeakers broadcasting two or three equivalent SPLs in all trials in categories 6–11, the number of trials in which a male responded to the listed loudspeaker (position) are shown.

^c For all trials in categories 7, 8, 10, and 11 in which a male responded to only one or two of the three loudspeakers broadcasting equivalent SPLs, the number of trials in which the male responded to (or ignored) two opposite loudspeakers (1 and 2, or 3 and 4; see Fig. 1) are shown.

louder loudspeakers and began ignoring the new weaker loudspeakers almost immediately following a switch. We assessed a male's redirection ability by comparing the incidence of his calls that followed the louder (90 and 86 dB) loudspeakers during the initial 20 s after a switch with that incidence during the 20 s preceding the switch (Fig. 6). Overall, the males tested were not more likely to produce calls following 90 and 86-dB loudspeakers after a switch than before ($p > 0.25$; McNemar's test).

We obtained an additional assessment of redirection ability by reexamining results from playback Categories 2–5. As above, we compared the incidence of a male's calls that followed the two louder loudspeakers during the initial 20 s (or initial 10 calls) of a trial with that incidence during the remaining 160 s (or next 30 calls). Again, the males tested were not more likely to produce calls following 90 and 86-dB loudspeakers at the beginning of a trial ($p > 0.25$; McNemar's test).

Discussion

Selective Attention Algorithms

Results from our playback experiments indicate that when lengthy silent gaps do not regularly occur in a chorus, *P. pustulosus* would respond to some neighbours whose calls exceed a specific behavioural response threshold (BRT) but ignore others. The mechanisms leading to this selectivity are apparently a sliding threshold

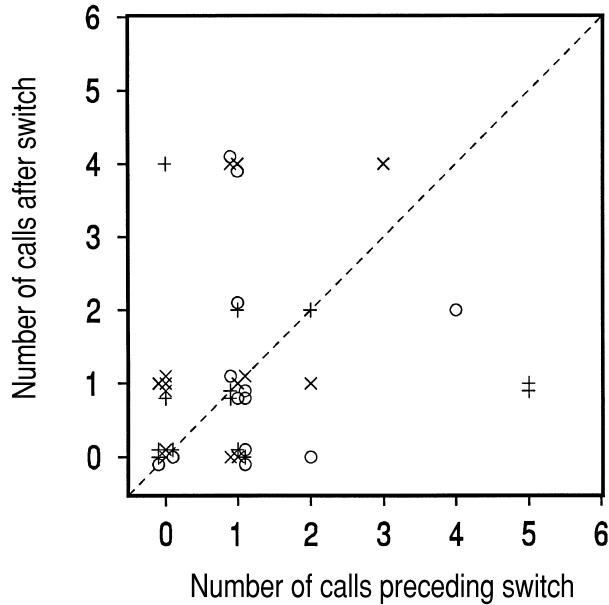


Fig. 6: Numbers of calls produced by test males during the critical intervals following the two loudest (86 and 90 dB SPL) loudspeakers in playback Category 12 trials. Symbols indicate the numbers of such calls that each male produced during the 20 s immediately preceding a switch in loudspeaker amplitudes and during the 20 s immediately after a switch. \times : calls preceding and after switch at 90 s, $n = 14$; $+$: at 180 s, $n = 13$; \circ : at 270 s, $n = 13$. See Table 1 and text for description of playback Category 12

and a fixed number rule. Males ignore calls that are more than 6–8 dB below the loudest one perceived, with the magnitude (df) of this sliding threshold declining slightly when the SPL of the loudest one (L) is low. But, when three calls (including the loudest) are within the sliding threshold, many males respond to two only and ignore the third (Fig. 5b, d). Conversely, when no calls (other than the loudest) are within the sliding threshold, most males do respond to one of the weak, sub-threshold calls as well as to the loudest one (Fig. 5f, h, j, l). These findings could be modelled by various algorithms, including the following two: (1) Respond to all call sources whose SPL exceeds $L - df$, provided that the number of such sources = 2; ignore all but two (or three) sources if the number of sources exceeding $L - df$ is > 2 , and respond to one of the subthreshold sources if the only source exceeding $L - df$ is the loudest one. (2) Respond to two (or three) among the loudest call sources; respond to three sources if L is high or if the SPLs of several sources are close to L (exceed $L - df$). Our current experiments do not permit distinction of these two algorithms, one based on modification of a sliding threshold by a fixed number rule and the other based on modification of a fixed number rule by a sliding threshold. Moreover, individual males may follow different combinations or hierarchies of these rules, and such differences may depend upon the individual's

experience in the field prior to testing. We cannot evaluate these possibilities based on our current data.

The algorithms combining sliding threshold and fixed number rules assume that the angular separations of call sources are high (90° in our experiments) and that a sufficient number of neighbours are calling regularly so as to make the chorus perceived by a focal male nearly continuous. At present, we do not know how a male would respond to call sources whose angular separation is small or to the extreme case in which nearby and distant call sources are situated in the same direction. When fewer calling neighbours are present or their call rates are slower, though, our data (Fig. 4a, b) show that males would ignore these rules and respond to most neighbours whose perceived calls exceed the BRT. Thus, the rules seem to be an adaptation to the high densities and loud calls in *P. pustulosus*, and they effectively reconcile the conflicting pressures to call regularly and to avoid calling as a follower. Males may be unable to escape from this quandary in space or time: Their breeding biology requires that they be present at certain temporary pools, and signal competition with neighbours may demand that they call in unison bouts; that is, a male may not gain by calling between the bouts of neighbours (see Schwartz 1991; Greenfield 1994a). Ultimately, the rules appear to be driven by the precedence effect in receivers, which is quite strong in this species (Snedden & Rand, unpubl. data).

Decisions in the Attention Process

The specific nature of selective responses in *P. pustulosus* highlights critical issues in decision-making. Is a modification of a sliding threshold rule by a fixed number rule, or vice-versa, an advantage over either rule singly? By using either rule alone, a male might respond to too many neighbours or neighbours that are too distant. Given that males often respond to call sources that we cannot physically distinguish from ignored ones (see Posner & Dehaene 1994), is it possible that some arbitrary selection rule is used? For example, when two or more call sources are equivalent in SPL, a male might simply respond to the left (or right) one and ignore the others, implying the existence of a form of 'handedness' among individuals. Or, subtle anomalies in spectral and envelope features of the various sources may influence certain males more than others. This level of discrimination is conceivable given findings on the ability of ranid frogs to differentiate among familiar and unfamiliar neighbours (Davis 1987; Owen & Perrill 1998). Alternatively, the specific orientation of a male with respect to the surrounding call sources may cause some sources from an equivalent set to be perceived as louder than others from that set (see Jorgensen & Gerhardt 1991 on directional hearing in hyliid frogs; see Wang & Narins 1996 and Wang et al. 1996 on ranid frogs). Because we could not monitor the orientations of the males within the translucent polyethylene bags, this possibility cannot be discarded. But, even this last rule would be an arbitrary one from the perspective of potential receivers: While one neighbour would be perceived by the focal male as louder than another, local females would, on average, perceive both neighbours as equally loud and render them equivalent competitors for the focal male.

Why would *P. pustulosus* select particular neighbours and respond to them exclusively rather than distributing their responses randomly among those neighbours calling at equivalent SPL? Perhaps the fundamental neural mechanisms underlying attention operate by consistently 'locking on' to the same subset of present stimuli rather than by switching among subsets. From an adaptationist perspective, it is also possible that a male would more effectively compete with neighbours for local females by responding fully to some neighbours and ignoring others completely. This question may be resolved via modelling, and a Monte Carlo simulation developed to examine the evolutionary stability of inhibitory-resetting mechanisms (Greenfield et al. 1997) is being adapted for this purpose.

Because *P. pustulosus* direct attention toward particular call sources and ignore others with very similar features, it is possible that the frogs associate direction with call characteristics. Thus, their general ability to redirect attention almost immediately in response to simulated chorus dynamics was initially surprising. But, males may encounter frequent changes in the positions and calling of neighbours in natural choruses, and such redirection may be essential for responding to those neighbours who are the strongest competitors at a given time. Possibly, males evaluate their neighbours' calls constantly and update the application of the selectivity algorithm every few seconds.

These possibilities suggest that anuran chorusing can represent a complex social feature involving various rules modifiable by substantial plasticity. In some cases, the finely tuned rules that generate the collective phenomenon of chorusing may have evolved under intense sexual selection pressures originating in psychoacoustic precedence effects.

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