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TESTS FOR CALL RESTORATION IN THE GRAY TREEFROG *HYLA VERSICOLOR*

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ABSTRACT

Phonemic restoration, a form of temporal induction, occurs when the human brain compensates for masked or missing portions of speech by filling in obscured or non-existent sounds. We tested for temporal induction and related abilities in females of the Gray Treefrog *Hyla versicolor*. The number of pulses in calls is used by females for assessment of males. Accordingly, an ability to "restore" or interpolate between masked or otherwise sonically degraded portions of calls could help females during mate choice in noisy choruses. In phonotaxis experiments, we employed unmodified calls and those that had a centrally placed gap, a region overlapped by a portion of another call or filtered noise, or replaced with filtered noise. When offered call alternatives with equivalent numbers of clear pulses, we found that females discriminated against calls with gaps two or more times greater than the natural 25 ms interpulse interval. When a gap was replaced with a zone of call overlap or noise (so, again the call durations of the alternatives were unequal), females discriminated either in favour (overlap) of the modified stimuli or failed to discriminate (noise). However, when the unmodified and modified stimuli were the same duration, females discriminated against the latter. Normal calls were also chosen when paired against calls with multiple noise sections. Pulses formed from noise bursts were attractive, but less so than normal pulses. In single speaker tests, standardized rates of movement did not differ between calls containing noise segments of different duration. Our results therefore do not indicate that females of the Gray Treefrog employ a form of temporal induction that is fully restorative. However, the data indicate that acoustically anomalous sections of calls can retain attractive potential provided acoustic energy and pulses are present.

Keywords: gray treefrog, communication, temporal induction, phonemic restoration, acoustic interference

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INTRODUCTION

The natural environment impacts the process of communication between animals in a wide range of ways (Bradbury & Vehrencamp 1998; Endler 2000; Ryan & Kime 2003). For example, sound signals may be attenuated and degraded as they are transmitted through the atmosphere and vegetation (Ryan & Sullivan 1989; Lang 2000) while the sounds of animals themselves may render signal detection, discrimination and interpretation a challenge for those individuals attempting to communicate (Wollerman & Wiley 2002; Langemann & Klump 2005). In choruses of anuran amphibians, in which many individuals often call within a shared active space, these problems may seem insurmountable. Nevertheless, males successfully advertise a variety of information (e.g. their location, species identity, individual identity, condition, etc) to both other males and females that are searching for a mate (Zelick *et al.* 1999; Gerhardt & Huber 2002; Wells & Schwartz 2006). It seems certain, therefore, that the consequences of calling in aggregations has had a substantial effect on the evolution of behavioural and physiological attributes of males and females that relate to communication and acquiring mates within choruses (Feng & Ratnam 2000; Feng & Schul 2006). Particular adaptations may facilitate mating during particularly noisy periods and can be reflected in responsiveness to the spatial and temporal heterogeneity that characterizes the sound environment of anuran breeding assemblages – although the *precise* ways putative adaptations function may be unknown, unclear or ambiguous. For example, the timing of calls or their components can be changed, perhaps to reduce the likelihood of acoustic interference with other callers (Klump & Gerhardt 1992; Narins 1992; Schwartz, 1993) or to occupy a leading position in a calling/singing sequence of a group of males and so favour certain males by taking specific advantage of innate features of the auditory system of potential mates (see Greenfield 2005 for a discussion of signal timing and the precedence effect). Males may elevate their call rate, duration or complexity (Wells 1988; Schwartz 2001) to increase their relative attractiveness to females *or*, under some circumstances, to increase the chances that their signals can be detected in the background din of a chorus (Schwartz *et al.* 2001). Multiple explanations may, of course, be valid.

For some time, it has been known that auditory mechanisms exist in humans that alter our perceptions of sounds such that portions that have been obscured through masking, and so should be perceived as missing are, in fact, perceived as present (for review see chapter 6 in Warren 1999). The general process responsible for this illusion of continuity is temporal (or auditory) induction of which "phonemic restoration" is a particular manifestation. Phonemic restoration occurs when the substitution of a sound such as white noise for a phoneme restores the missing phoneme to a human listener. The efficacy of this kind of perceptual illusion, which is not limited to speech components, depends not only on the information present in the sound before and after the missing segment but also on the characteristics of its substitute. Forms of temporal induction in humans have been a subject of considerable research for over fifty years (Samuel 1996; Warren 1999), while only limited recent work has focused on other taxa. Evidence for temporal induction as reflected in reduced discrimination by cats between tonal glides with internal gaps + noise inserts and tonal glides without gaps was reported by Sugita (1997). Sugita also identified cells in the cat auditory cortex that responded in a fashion consistent with the behaviour. Braaten & Leary (1999) found that trained European starlings responded in a manner concordant with temporal induction when 300 ms internal sections of conspecific song were replaced with white noise (for a more recent study of European starlings see Seeba and Klump 2009). When white noise was inserted in the middle of the whistle syllable from the combination long call of cotton-top tamarins, animals responded no differently than they did to a normal whistle. This was not the case when the whistle contained a central gap (Miller *et al.* 2001). Macaques exhibited induction when noise bursts were positioned within gaps in tones, frequency-modulated sweeps and a natural "coo" vocalization (Petkov *et al.* 2003). To date, however, there have been no published studies designed to test the possibility that anuran amphibians engage in an analogous process. Given the potential for signal disruption and masking of calls within anuran choruses (Langemann & Klump 2005; Feng & Schul 2006), frogs seem ideal candidates for such research. Background noise levels can be extremely high and fluctuate in a way that can partially obscure portions of advertisement calls from receivers (e.g. Schwartz & Wells 1983). In dense assemblages of conspecifics, the masking potential of the background din is greatest and the chance that call overlap among neighbouring males will degrade important temporal information is a potent threat (Schwartz 1987; Schwartz *et al.* 2001). For female frogs an ability to perceptually or cognitively reconstruct parts of calls that have been subjected to masking or otherwise sonically degraded could have profound fitness benefits, especially if call attributes are utilized in mate assessment.

In this study, we used phonotaxis experiments using a variety of anomalous synthetic calls to test whether females of the Gray Treefrog *Hyla versicolor* have an ability to restore segments of calls that were obscured acoustically or replaced by filtered noise, other calls or silent gaps. *Hyla versicolor* is an excellent species with which to explore this issue. Acoustic interference in choruses can pose problems for effective communication during the breeding season (e.g. Schwartz 1987; Schwartz *et al.* 2001). Moreover, the influence of call features on female selectivity has been extensively studied (Gerhardt and Huber 2002), facilitating the design of biologically relevant tests and interpretation of results. Males give entirely pulsed advertisement calls that vary in pulse number (i.e. call duration) both within and among individuals. Pulse shape, pulse duration and interpulse interval are utilized by females for call recognition (Gerhardt 2001), and females discriminate against calls if these features are obscured during, for example, call overlap among males (for a recent treatment see Schwartz & Marshall 2006). Call rate and call pulse number facilitate assessment of potential mates (Gerhardt 2001). In particular, in two-choice phonotaxis tests, females have displayed robust discrimination in favour of longer relative to shorter duration advertisement calls. Under some circumstances, this preference is maintained even if the call rate of longer calls is reduced by a factor equivalent (or nearly so) to the factor differential in duration between longer and shorter calls (Klump & Gerhardt 1987; Gerhardt *et al.* 1996; Schwartz *et al.* 2001). Males of the Gray Treefrog are extremely sensitive to their acoustic milieu and rapidly and robustly append pulses to their calls in response to the calls of other males while simultaneously reducing call rate (Wells & Taigen 1986; Schwartz *et al.* 2002). Among-male differences in call duration can translate into fitness payoffs to females who select males with longer calls (Welch *et al* 1998; Welch 2003).

Although the pulses within the advertisement calls of *H. versicolor* may not be strictly analogous to the phonemes of human speech, they and their accompanying intervals are critical structural elements of calls. In noisy choruses, restoration of these elements could aid females in both call recognition and assessment of neighbouring males based on call duration. In addition to addressing the possibility of such a form of temporal induction in Gray Treefrogs, our experiments also bear on the question of whether females can assemble segments of disrupted calls. This ability would not afford the equivalent advantage for accurate male-male assessment as call element restoration, given the extremely strong discrimination against very brief calls (Gerhardt *et al.* 2000; Schwartz *et al.* 2001); however, assembly could still reduce assessment inaccuracy. Although restoration would not be expected for calls incorporating anomalous sections lacking sound energy (Warren 1999), we undertook some tests using calls with silent gaps for a number of reasons: (1) to help assess, in a relative sense, the negative impact of partial call interference because gaps lack any fine temporal information and acoustic energy, (2) to help define the acoustic constraints on call segment assembly (i.e. some quiet gaps may be treated as an inter-call interval rather than a segment within a single call and this may preclude assembly), (3) to help delineate the temporal constraints on call segment assembly or any interpolative process. Some of these issues will be more thoroughly addressed in another paper (Schwartz *et al.* in prep.).

METHODS

General procedures

We captured gravid females of *Hyla versicolor* in amplexus at a pond in the Blue Mountain Reservation in Peekskill, NY, USA during evenings in May and June of 2004–2009. The frogs were separated from their mates and maintained until testing (typically the following day) in plastic containers either in an ice-filled cooler or refrigerator in order to delay oviposition. Following testing, we released our subjects at their site of capture. The handling and use of study animals was approved by the Pace University IACUC (Protocol No. 8). We performed phonotaxis experiments inside a temperature-controlled (~20ºC) chamber floored with waterproof low-pile carpet and walled with echo-attenuating acoustic foam at Pace University (Pleasantville, NY; chamber inner dimensions –255 cm long × 225 cm wide × 195 cm high, Ultimate Walk-Ins, Inc., foam – Silent Source HFX-4). Infrared illumination (Marlin P. Jones & Assoc. Inc. part # 11665OP) of the "choice arena" and a closed circuit video security system enabled us to observe female phonotaxis from outside the chamber. During each test, individual females were confined briefly in and then released (via an externally-controlled pulley) from an acoustically-transparent screen cage on the floor of the arena.

We used a Commodore Amiga 600 computer, a Realistic SA-10 amplifier and Realistic Minimus 0.3 speakers to broadcast synthetic stimulus calls (8-bits per sample; 20 KHz) that were modelled after the natural calls of *H. versicolor* (Schwartz unpublished software). We adjusted sound amplitudes with a calibrated (Gen Rad 1562 A) Gen Rad 1982 Precision Sound Level meter (flat weighting, fast RMS response). These adjustments were made using broadcasts of identical "normal" calls (i.e. lacking gaps, overlapped sections, noise) from both speakers so that we could be confident that the amplitude of the pulsed sections of alternative stimuli would have equivalent sound pressure levels. In most tests, except as noted below, we set sound playback levels of call alternatives at the central female release point at 85 dB SPL (dB re 20 µPa). In all tests, stimulus rates were 15/min per speaker.

Unless otherwise noted, stimulus calls were broadcast in alternating fashion from speakers at opposite sides of the arena (1 m from the central release point) and each subject was exposed to the call stimuli for 30 seconds prior to lifting of the release cage. Females displayed discrimination by moving to within 10 cm of one of the speakers within the maximum allotted time of 10 minutes or less.

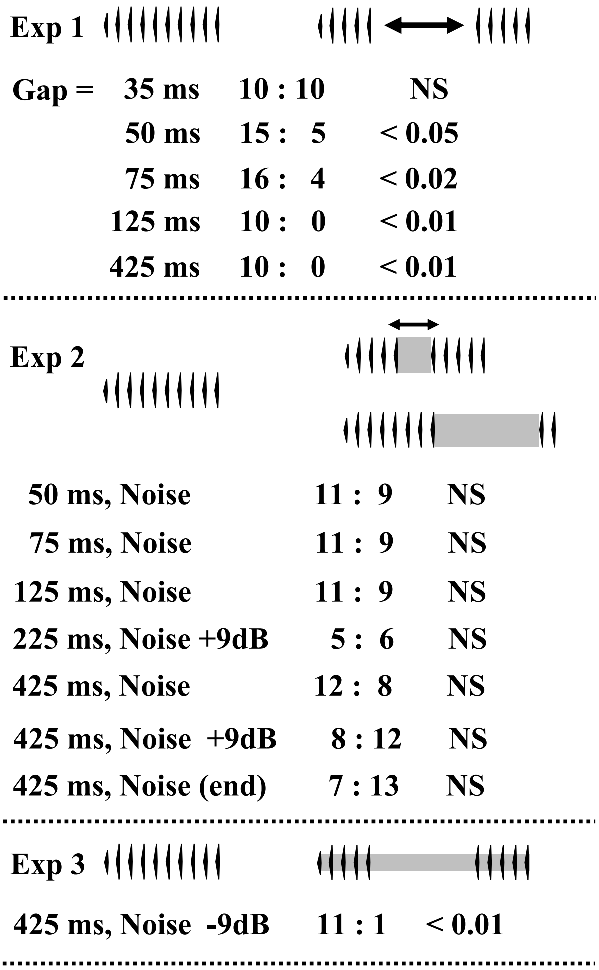
Because we ran a large number of tests, to aid the reader, in the next section we present specific experimental details, our rationale and predicted results followed by the outcome of our experiments.

METHODOLOGICAL SPECIFICS AND RESULTS

Experiment 1

Our principal goal in Experiment 1 was to examine the sensitivity of females to the presence of silent gaps within advertisement calls and check for the possibility of restoration of missing call pulses. Restoration was considered unlikely based on previous data from humans (e.g. Warren 1999) and other taxa (e.g. Braaten & Leary 1999; Miller *et al.* 2001). Moreover, sensitivity to and discrimination against calls with gaps was considered likely given the response behaviour of neurons that 'count' interpulse intervals in the anuran midbrain. These cells can be reset to a count of zero following abnormally long gaps between call pulses (Edwards *et al.* 2002). In one set of tests we offered females a choice between 10-pulse calls with the normal timing of pulses and 10-pulse calls in which we had inserted a centrally placed gap (gap durations = 35, 50, 75, 125 ms; Figure 1, top). Thus the only difference between call alternatives was one anomalous interpulse interval in the gap stimulus. In subsequent tests using calls with the 125 ms gap, we selectively attenuated the normal call stimulus (by 3 and 6 dB SPL) in order to gauge the strength of the observed female preference for the normal call. We also gave females a choice between a normal 9-pulse call and a 10-pulse call with a central 425 ms gap. Thus in this test, the call alternatives had the same number of normal interpulse intervals. Fifty ms is the mean pulse period (pulse start to pulse start; pulse duration = 25 ms, quiet interval = 25 ms) of males at the experimental temperature. Therefore the 75, 125 and 425 ms gaps represent the intervals (pulse end to pulse start) resulting from removal of 1, 2, or 8 pulses from within a call. We predicted that if females ignored the increased interpulse interval of the gap stimuli or assembled the separated pulse strings, they would fail to discriminate in tests with call alternatives with equal numbers of pulses. If females perceptually restored missing pulses (unlikely given the lack of acoustic energy in the gap), we predicted that they would discriminate in favour of some gap stimuli (125 ms gap, 425 ms gap and perhaps the 75 ms gap) because of the preference of females for longer calls with more pulses (Gerhardt 2001).

Females discriminated against all calls containing gaps that were greater than 35 ms (Figure 1, top). This was true even when the



Gap =	35 ms	10 : 10	NS
	50 ms	15 : 5	< 0.05
	75 ms	16 : 4	< 0.02
	125 ms	10 : 0	< 0.01
	425 ms	10 : 0	< 0.01

50 ms, Noise	11 : 9	NS
75 ms, Noise	11 : 9	NS
125 ms, Noise	11 : 9	NS
225 ms, Noise +9dB	5 : 6	NS
425 ms, Noise	12 : 8	NS
425 ms, Noise +9dB	8 : 12	NS
425 ms, Noise (end)	7 : 13	NS

425 ms, Noise -9dB	11 : 1	< 0.01

Figure 1. Representation of call alternatives (10 pulses long in all cases but one) offered to females in Experiments 1-3. The number of females that chose each call is indicated below each pair of calls along with a P-level for a two-tailed binomial test. For Experiment 1 (call with normal interpulse intervals versus call with a central gap), the double arrow indicates that a range of gap durations (35-425 ms) were used. In the last test of this experiment, the normal alternative to the call with the 425 ms gap contained only nine pulses (see text). For Experiment 2 (call with normal interpulse intervals versus a call with a noise insert), the anomalous call alternative with the 125 ms noise insert is illustrated on the top right (calls with central 50, 75, 225 and 425 ms noise inserts not shown). The call with the non-centrally placed (end) 425 ms noise insert is shown below. In Exp. 3, the noise was superimposed over the entire call alternative which had a gap of 425 ms. Noise +9dB or Noise -9dB indicates greater or lower relative amplitude of the noise segment. Anomalous sections of calls with noise are shown in grey.

normal call had fewer pulses than the call with the gap (425 ms 10-pulse gap call versus 9-pulse normal call). Additionally, attenuation of the normal call by 6 dB failed to reverse discrimination against the call with the 125 ms gap (15:5, $P < 0.05$). Our results therefore demonstrate a profound sensitivity to silent gaps within calls and, as expected, data are inconsistent with restoration of missing call pulses by females.

Experiment 2

In Experiment 2, we offered females a choice between a 10-pulse normal call and a 10-pulse call in which a section of filtered noise had been inserted (50, 75, 125, 225 ms or 425 ms) to replace, respectively, either 1 pulse and 1 interpulse interval, 1 pulse and 2 interpulse intervals, 2 pulses and 3 interpulse intervals, 4 pulses and 5 interpulse intervals or 8 pulses and 9 interpulse intervals. For all but one of the tests (using a non-centrally located 425 ms noise insert following the eighth call pulse), this noise entirely occupied the central portion of the call that unnatural silent gaps occupied in gap stimuli used in Experiment 1 (Figure 1, middle). Thus all the calls with noise were longer than the normal call alternative, and for all stimuli the noise abutted the preceding and following neighbouring pulses. The noise was computer generated white noise that had been digitally filtered to resemble the spectrum of the calls of *H. versicolor* and thus was similar in frequency profile to that of a natural chorus (Fig 7). In single speaker tests, this noise (85 dB SPL, Fast RMS) alone elicited phonotaxis (within 5 min) in approximately one third of females when offered in bursts of duration (866 ms) equivalent to that of an 18-pulse call (8 responded : 15 did not respond) or 425 ms (6 responded : 14 did not respond). For the tests with the 50 and 125 ms inserts, we created 5 different versions of each call type containing a noise insert and sequentially presented these to successive females as we ran our choice tests to ensure that responses would not be due to some idiosyncratic aspect of a particular noise segment. For most tests, the noise level was adjusted digitally so as to match the sound level (Fast RMS) of the associated call portions. Calls were presented at 85 dB SPL. However, for the test using a call with a 225 ms insert and one of the two tests using a call with a central 425 ms noise insert, the insert was presented at an SPL 9 dB greater (85 dB SPL, Fast RMS) than the surrounding portions of the call (76 dB SPL) and the normal call alternative (76 dB SPL). Tests of phonemic restoration have demonstrated that restoration is achieved when masking noise rather than a gap is inserted in a signal (Warren 1999). Therefore the results of this experiment and those of Experiment 1, allowed us to test for this possibility. Based on previous preference tests

(Gerhardt *et al.* 2000), we predicted that females should discriminate in favour of the longer anomalous calls (e.g. those with 125, 225, and 425 ms inserts) if missing pulse structure was restored. We increased the likelihood of detecting restoration (especially if restoration was partial) with the longer inserts. Use of a range of insert durations might also allow us to detect some upper limit to restoration, should it occur. We inserted noise into call gaps rather than attempting to simply mask part of the call to be certain that no pulses within the anomalous section of calls would be audible to any of our subjects. We elevated the noise SPL (by 9 dB relative to the pulsatile portions of the anomalous call and the normal call alternative) in two tests to evaluate whether possible failure to restore missing call elements could be due to insufficient energy of the noise insert relative to the intact pulsed portions of the call. We maintained the noise amplitude at 85 dB SPL to prevent signal clipping by our speakers.

In Experiment 2, females failed to discriminate when the central portion of a call was replaced by a block of noise lasting 50, 75 or 125 ms (Figure 1, middle). Similarly, females failed to discriminate between normal 10 pulse calls and those with noise inserts when we subsequently tested females using calls with longer, relatively louder or asymmetrically positioned noise inserts. Tests of independence also failed to reveal a significant impact of these manipulations on the female choice results (noise duration: 225 ms (noise +9 dB) and 425 ms (noise +9 dB), Fisher's exact test, $P = 1.0$; noise amplitude: 425 ms inserts, $P = 0.343$; noise position: 425 ms inserts: $P = 0.205$). However, our results clearly demonstrate that the presence of a noise segment increased call attractiveness relative to a call with a gap of equivalent duration (e.g. compare results with central 425 ms gap in Experiment 1 to those with central 425 ms insert in Experiment 2; $P = 0.029$; also see Experiment 7).

Experiment 3

Experiment 3 also offered females calls with 10 pulses. In this case, however, the abnormal call had a central gap of 425 ms and was overlapped by an 866 ms segment of filtered noise. The amplitude of this noise segment was set at 9 dB SPL below that of the overlapped call and the normal call alternative. Our rationale was to more closely simulate the natural situation in which the din of the background is superimposed over the entire call rather than just a section of the call. The much lower amplitude of the noise relative to the call ensured that the internal temporal structure of the call was not masked and so acoustically resembled a situation in which a female was within a couple of metres of a vocalizing male. We predicted that without restoration of the central portion of the abnormal call, females would discriminate against it. With restoration, we predicted either discrimination for the abnormal call or no preference (because the pulsatile portions of the abnormal call were partially obscured by the noise).

There was significant discrimination in favour of the normal 10-pulse call when a noise burst of lower amplitude was superimposed over the alternative call incorporating a central 425 ms gap (Figure 1, bottom). Thus we found no evidence of restoration in the stimulus overlapped by noise.

Experiment 4

In Experiment 4, call alternatives were normal 10-pulse calls and calls in which the 125 ms or 225 gap of stimuli used in Experiment 1 had been replaced by either 4 or 8 call pulses. These pulse groups had double the pulse rate of a normal call and so these two stimuli simulated a situation in which a mid section of a normal call (lacking a gap) was overlapped (in pulse alternation) by either a string of two or four pulses (Figure 2, top).

Previous experiments have demonstrated that this form of pulse timing (180 degree phase shift) during call overlap is more detrimental than when pulses partially (Schwartz & Marshall 2006) or fully (Schwartz 1987) overlap. Each partially overlapped call had a leading and trailing non-overlapped section consisting of five and six pulses, respectively, separated by an overlapped section. The call with the 125 ms anomalous section had a total of 14 pulses (2 extra pulses interleaved within a 12-pulse call) and the call with the 225 ms anomalous section had a total of 18 pulses (4 extra pulses interleaved within a 14-pulse call). Although pulse structure was not missing (and thus not in need of restoration) in the anomalous calls, using calls with overlapped sections allowed us to test responses to stimuli that exhibited a form of disruption frequently encountered in nature and also facilitated comparison with results using calls lacking some internal pulse structure (some stimuli from Experiment 1 and 2).

We found that when the central portion of a call consisted of an overlapped section, females, in contrast to results of the previous experiments, discriminated against the normal 10-pulse call (Fig 2, top).

Experiment 5

In Experiment 5, an 18-pulse call was paired with six alternatives (Figure 2, bottom). Each of the alternatives was identical in total (beginning–to–end) duration to the normal call. In one test (Test

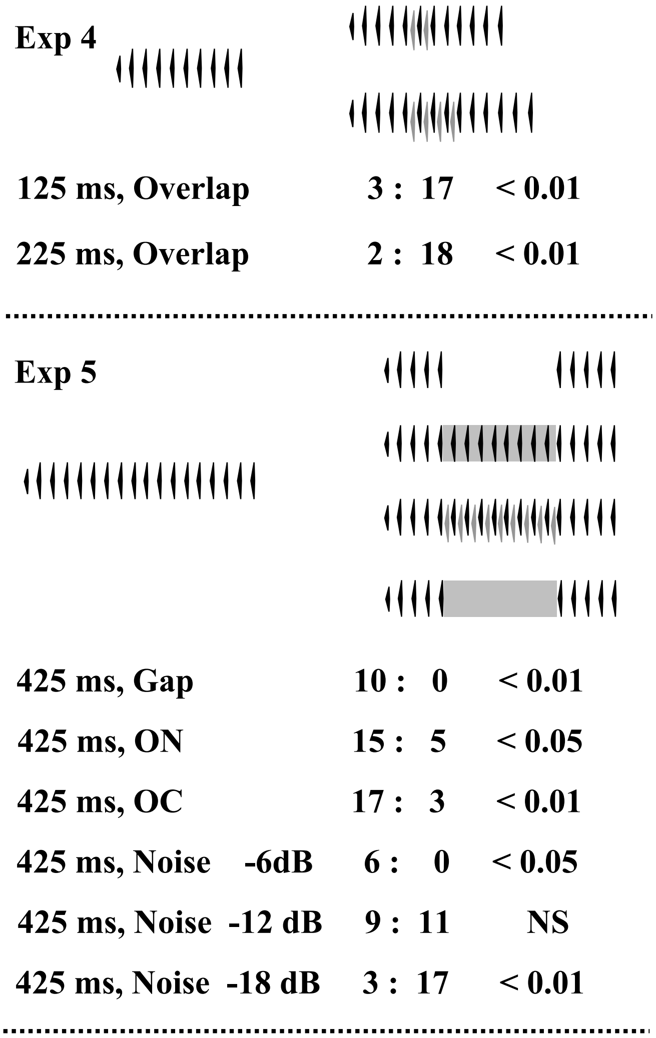


Figure 2. Representation of call alternatives offered to females in Experiments 4-5. The number of females that chose each call is indicated below each pair of calls along with a P-level for a two-tailed binomial test. In Experiment 4, the alternative to the 10 pulse normal call was either a 12 or 14-pulse call (see Methods) with its central portion (either 125 or 225 ms) overlapped by pulses of another call. For Experiment 5 (18 pulse normal call), equal duration anomalous call alternatives with either the central section missing (Test 5a; 425 ms gap = missing 8 pulses), overlapped by filtered noise (Test 5b; ON), overlapped by a 9-pulse call (Test 5c; OC), or replaced by filtered noise (Tests 5d-5f; Noise). In Tests 5d-5f, the normal call alternative was attenuated by 6, 12 or 18 dB SPL relative to the call with noise. Anomalous sections of calls with noise and pulse strings are shown in grey with extra pulses slightly offset vertically so that they may be easily recognized.

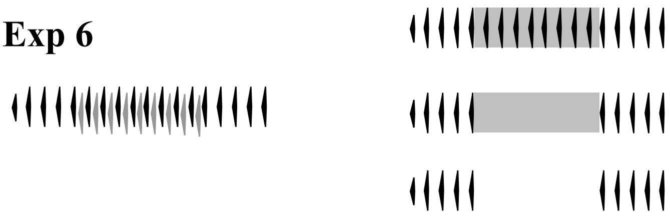
5a), the alternative call was a call in which the middle 8 pulses had been removed leaving a gap of 425 ms. In a second test (Test 5b) the alternative was a call in which this middle section was overlapped by filtered noise. The noise and this call were output using the same channel of the Amiga computer with the noise level adjusted so that it would match the level (fast RMS) of the non-overlapped pulsed portion of the call. This level relative to the call was comparable to that which a female could encounter during an approach to a male advertising within the chorus din. In a third test (5c), the middle section of the alternative call was overlapped by a 9-pulse call. As in experiment 3, the pulses in the overlapped section interleaved. In a final series of tests (5d, 5e, 5f), the alternative call contained the 425 ms noise insert used in Test 5b. However, in the series the relative amplitude of the normal 18-pulse call was lowered in 6 dB steps (from -6 dB to -18 dB). In Test 5a, and 5c call stimuli were presented at 85 dB SPL. In Test 5b, call alternatives were presented at 82 dB SPL rather than 85 dB SPL to prevent clipping of the speakers when the noise and call pulses overlapped. In Test 5d-5f, the alternative to the normal call was presented at 85 dB SPL. We ran these tests for the following reasons. The tests made use of calls close to the average duration of those used by males (18 pulses) in the field, facilitated assessment of possible differences in the impact of forms of call disruption, and also tested for signal restoration in calls in which pulse structure was obscured by noise or missing. Given the results of Experiment 2, which failed to demonstrate induction, Tests 5d-5f allowed us to estimate the strength of the preference for a normal call relative to one containing a noise insert.

In Tests 5a-5c of Experiment 5, females discriminated in favour of the normal call, independent of the form of the anomalous section of the call alternative (Figure 2, bottom). Thus when calls were identical in duration, call overlap, filtered noise and missing pulses reduced their attractiveness. The final three tests (5d-5f) indicate that discrimination for a normal call can be eliminated with a 12 dB reduction in amplitude. An 18 dB amplitude reduction reversed the preference.

Experiment 6

In Experiment 6, we paired an 18-pulse call in which the middle section had been overlapped by a 9-pulse call (as in test 5c) with three alternatives (Figure 3, top). In test 6a, the alternative had its middle section overlapped by filtered noise. In Test 6b the acoustic elements were identical to those of Test 6a except that the central pulses of the call overlapped by the noise segment had been removed. We did this because we could not be certain that the overlapped section of

Exp 6



425 ms, ON	**15 : 10**	**NS**
425 ms, RN	**19 : 1**	**< 0.01**
425 ms, Gap	**10 : 0**	**< 0.01**

Exp 7

0 dB	**15 : 2**	**< 0.01**
- 6 dB	**17 : 3**	**< 0.01**
- 9 dB	**16 : 4**	**< 0.05**
- 12 dB	**16 : 6**	**NS**
- 15 dB	**15 : 6**	**NS**
- 18 dB	**13 : 7**	**NS**

Figure 3. Representation of call alternatives offered to females in experiments 6-7. The number of females that chose each call is indicated below each pair of calls along with a P-level for a two-tailed binomial test. For Experiment 6, an 18-pulse call with its middle section overlapped by a pulse string was the alternative to a call of equal duration with either the central section overlapped by filtered noise (Test 6a; ON), replaced by filtered noise (Test 6b; RN), or missing (Test 6c; Gap). In Experiment 7, call alternatives were a 10-pulse call with a centrally-placed 425 ms noise insert (noise relative amplitude indicated) versus a 10-pulse call with centrally-placed 425 ms gap. Anomalous sections of calls with noise and pulse strings are shown in grey with extra pulses slightly offset vertically so that they may be easily recognized.

the pulsed call was effectively masked from all subjects in Test 6a (although this was also the case for Test 5b, results of that test were such that [see below] a test comparable to test 6b was unnecessary). In Test 6c, the alternative had its middle section replaced by a gap. As in Experiment 5, all stimuli were presented at 85 dB SPL except when call pulses were overlapped by noise (stimuli of Test 6b = 82 dB SPL). Experiment 6 allowed us to test the relative attractiveness of calls suffering from different forms of signal disruption in a more direct fashion than Experiment 5.

When paired with a call with the middle section overlapped, females discriminated against an identical duration call with a gap (Test 6c) and a call in which the central portion had been replaced by noise (Test 6b). However, in Test 6a in which the noise was mixed with the central pulses, females failed to discriminate (Fig, 3, top).

Experiment 7

Previous tests had demonstrated that noise inserts or noise overlap did not enhance call attractiveness relative to a normal call, and thus results were certainly inconsistent with full restoration of missing or obscured pulse structure. In Experiment 7, we offered the stimulus with the noise insert of Test 6b (5 pulses + 425 ms noise insert + 5 pulses) against the same call but with a gap lacking the noise. Because the alternative (gap) stimulus lacked acoustic energy within its mid-section, this experiment allowed us to directly test for even a small contribution of the unstructured noise insert to call attractiveness. Recall that the results of Experiment 2 when compared with those of Experiment 1 were consistent with such a contribution. In a series of tests, we lowered the relative amplitude of the noise insert in a 6 dB and then 3 dB increments (0 dB-18 dB SPL) to estimate the amplitude at which any discrimination in favour of the noise containing stimulus would disappear and possibly be reversed.

Females showed strong discrimination against a call with missing pulses relative to a call of identical pulse number in which a central gap was replaced by noise (Figure 3, bottom). Significant discrimination was eliminated when the amplitude of the noise insert was reduced by 12 dB SPL, although a non significant asymmetry in choices remained when the relative amplitude was further lowered.

Experiment 8

Noise in our previous tests was presented in calls as a single segment. However, in a natural chorus with fluctuating levels of background noise it is possible that multiple sections of an individual call,

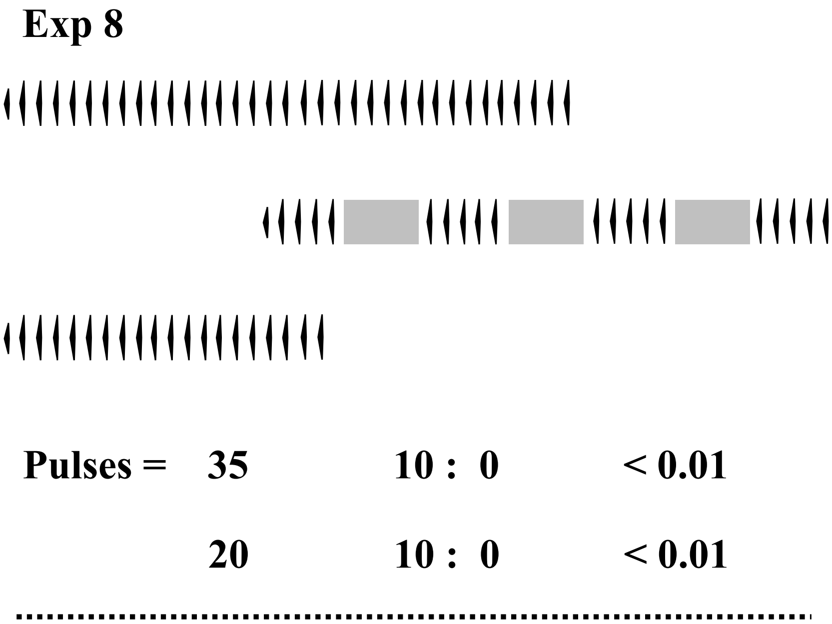


Figure 4. Representation of call alternatives offered to females in Experiment 8. The number of females that chose each call is indicated below each pair of calls along with a P-level for a two-tailed binomial test. In both tests, the anomalous call alternative (right) contained 20-pulses and three noise segments, each replacing five pulses and their intervening interpulse intervals. The normal call alternative contained either 35 pulses (and thus was the same duration as the anomalous call; Test 8a) or contained 20 pulses (Test 8b).

especially if it is long, could be masked in some portions while not masked in others. It might also be that restoration of masked portions is facilitated by multiple repetitions of audible pulse sequences interspersed with masked sections. Accordingly, in Experiment 8 we conducted two tests in which a normal call was offered against a call containing three noise segments that replaced a series of five-pulse strings interspersed evenly among five-pulse strings (Figure 4). In Test 8a, the normal call alternative contained 35 pulses and thus was equivalent in duration to the abnormal alternative. In Test 8b, the normal call alternative contained 20 pulses and thus the same number of pulses as the abnormal call. In these tests, the noise bursts were bordered by 25 ms silent intervals and so just five pulses and four interpulse intervals were replaced by noise. Because interpulse intervals of appropriate duration facilitate firing of neurons in the auditory midbrain of anurans (Edwards *et al.* 2002), we reasoned this might improve the chance of signal restoration. If full restoration occurred, we predicted that females would not discriminate in Test 8a but would prefer the abnormal alternative in Test 8b. If there was partial restoration, we predicted discrimination against the abnormal alternative in Test 8a but discrimination in its favour in Test 8b.

In both tests, females showed a unanimous preference for the normal stimulus. Accordingly there was no evidence of even partial signal restoration of the noise-containing segments of the abnormal alternative call.

Experiment 9

The aforementioned experiments employed temporally unstructured noise inserts. Full restoration would have required females to restore both interpulse intervals as well as pulse shape. In Experiment 9 we attempted to make the task easier by incorporating some of this fine temporal structure within noise-incorporating stimuli. The anomalous call alternatives of Experiment 9a had normal pulses replaced by pulses formed by rectangular shaped (25 ms) noise inserts. The noise pulses were created by zeroing out sections of the noise insert employed in the initial 425 noise insert test and thus the amplitude of resulting noise pulses was not altered. However, the pulse shape was abnormal. We conducted one test using a string of 4 noise pulses (occupying a gap of 225 ms) and two tests using a string of 8 noise pulses (occupying a gap of 425 ms). In all tests but one of those using 8 noise pulses, the anomalous section was centrally located (Figure 5). The third test of Experiment 9a, using asymmetrically positioned noise pulses, allowed us to test for an effect of position. In Experiment 9b, the normal alternative to a call with 8 centrally-placed noise pulses was an 18-pulse call rather than the 10-pulse call alternative used in Experiment 9a. Thus the normal and anomalous call had the same number of pulses, and so Experiment 9b evaluated whether the noise pulses were as attractive as normal pulses as opposed to attractive *per se* (Experiment 9a).

In all tests of Experiment 9a, females discriminated in favour of the calls with pulses formed by noise (Figure 5). However, when the normal call alternative contained the same number of pulses as the anomalous call (Experiment 9b), females discriminated in favour of the former stimulus.

Experiment 10

In Experiment 10a, we employed a single-speaker design to assess the attractive potential of two 10-pulse stimuli containing an individual noise insert of either 125 ms or 425 ms (Figure 6, top). Our previous

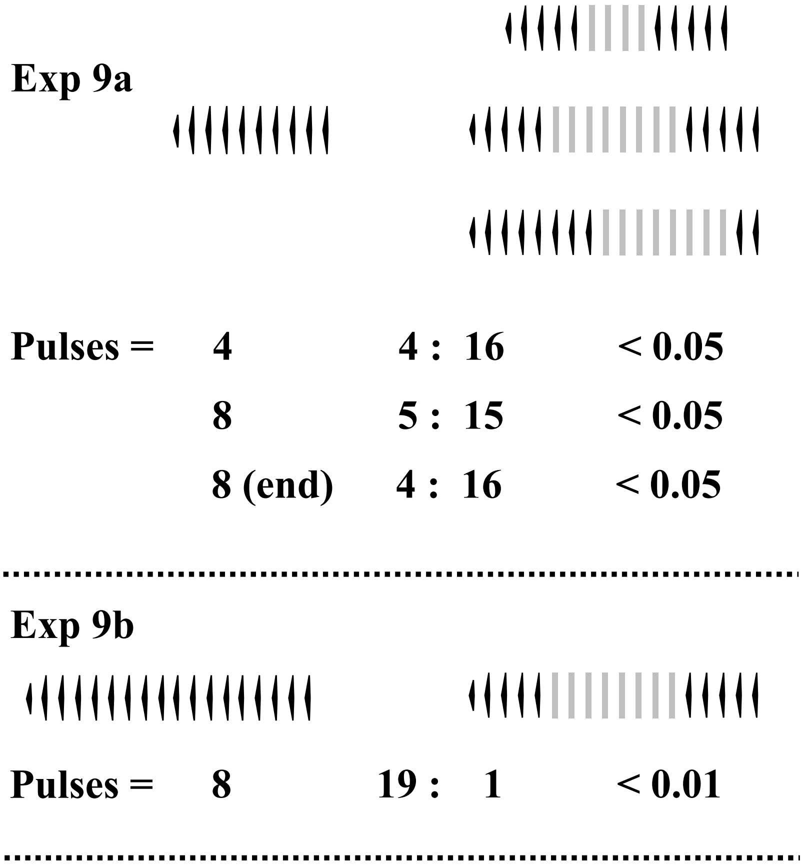


Figure 5. Representation of call alternatives offered to females in Experiment 9. The number of females that chose each call is indicated below each pair of calls along with a P-level for a two-tailed binomial test. Call alternatives were a normal 10-pulse call versus an 18-pulses calls with some pulses (grey, number indicated) formed from noise (Experiment 9a). In Experiment 9b alternatives were a normal 18-pulse call versus an 18-pulse call with 8 central pulses formed from noise. In the final test of Experiment 9a, the noise pulses were placed near the end of the call.

two-stimulus choice tests had garnered no support for temporal induction. However, discrimination tests can be very sensitive to differences in attractiveness among the alternatives. Thus induction that yielded weak restoration might have been missed in some of our tests pairing call alternatives (i.e. some restoration of call sections occurred but females nevertheless discriminated against the less than perfectly restored anomalous calls). To evaluate this possibility, we employed a single-speaker design and two 10-pulse stimuli containing an individual noise insert of either 125 ms or 425 ms. We assessed call attractiveness by determining ‘phonotaxis scores’ using methods similar to those of Schul and Bush (2002). This metric is calculated by forming the ratio of the average approach time to a standard stimulus and the approach time to the experimental stimulus (T_{av}stand / Texp) for each female. Thus a phonotaxis score of one indicates an equivalent response to the experimental stimulus and the standard call, a score greater than one indicates that the experimental stimulus elicited a more expeditious approach than the standard, and a score of less than one indicates that the experimental stimulus elicited a less speedy approach than the standard.

Each female was first tested twice with a standard call of 18 pulses. Data (approach time) from the first test was not used as this test served only to accustom the female to the test chamber and check the approximate stability of her response time to the standard call. Subsequently each female was tested with one of the experimental stimuli (chosen randomly for each subject). This was followed by another test with the standard, a test with the remaining experimental stimulus and a final test with the standard. Thus exposure to each of the test stimuli was bracketed in time by a test with the standard call stimulus. For calculation of phonotaxis score, we used the mean approach time of each female to the standard stimulus presented immediately before and after exposure to the experimental stimulus. We waited a minimum of 5 minutes between successive tests of the same female, and females were exposed to three repetitions of the stimulus call before the top of the release cage was removed. The subjects that did not reach the broadcast speaker within 10 min were to receive a score of “0”. However, all females responded within the allotted time.

If temporal induction occurred in our tests, we reasoned (see Bush *et al.* 2002) that females should have higher phonotaxis scores to the longer stimulus (containing the 425 ms noise insert) than to the shorter stimulus (containing the 125 ms noise insert). Additionally, the response times to the longer stimulus could be similar to those during the temporally proximate broadcasts of the standard stimulus (because, if “restored”, this experimental call would be perceived as having the same number of pulses as the 18-pulse standard call).

We found that the phonotaxis scores and thus standardized female approach times to the two experimental stimuli did not differ significantly (Phonotaxis Scores: with 125 ms insert = 0.845 [SE = 0.069], with 425 ms insert = 0.985 [SE = 0.068]; Paired t-test, $t = -1.53$, $P = 0.1447$, $n = 17$ females). However, the phonotaxis scores to the longer anomalous stimulus were not significantly different from 1.0 ($t = 0.22$, $P = 0.8276$) indicating a similar rate of movement to this stimulus and the temporally proximate standard calls.

Given the non-significant difference in phonotaxis scores obtained in the single speaker presentations, we conducted a discrimination

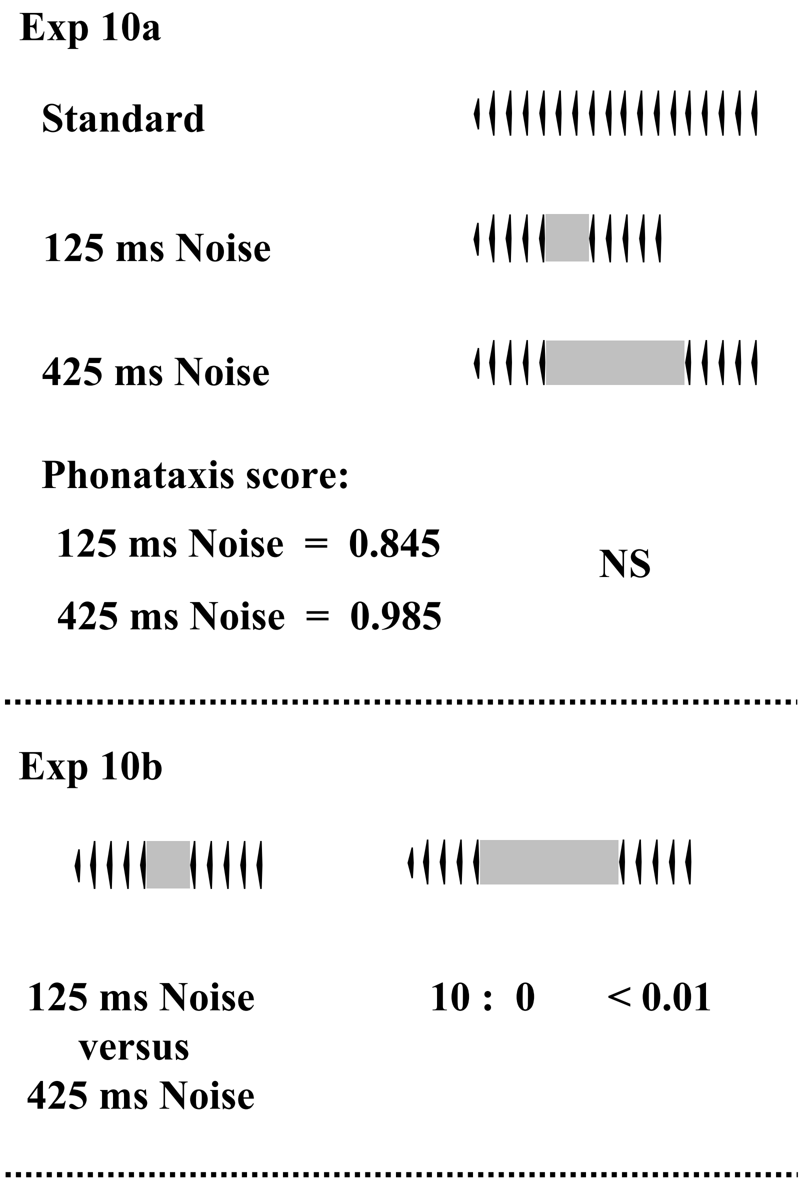


Figure 6. Representation of calls offered to females in Experiment 10. In Experiment 10a, females were presented with calls from a single speaker that were either normal in structure (18-pulse Standard) or contained 10 pulses and a central noise insert (125 ms Noise, 425 ms Noise). Phonotaxis scores for these anomalous calls, which did not differ significantly (Paired t-test), are provided. In Experiment 10b, the anomalous calls were offered as alternatives. The number of females that chose each call is indicated below each pair of calls along with a P-level for a two-tailed binomial test.

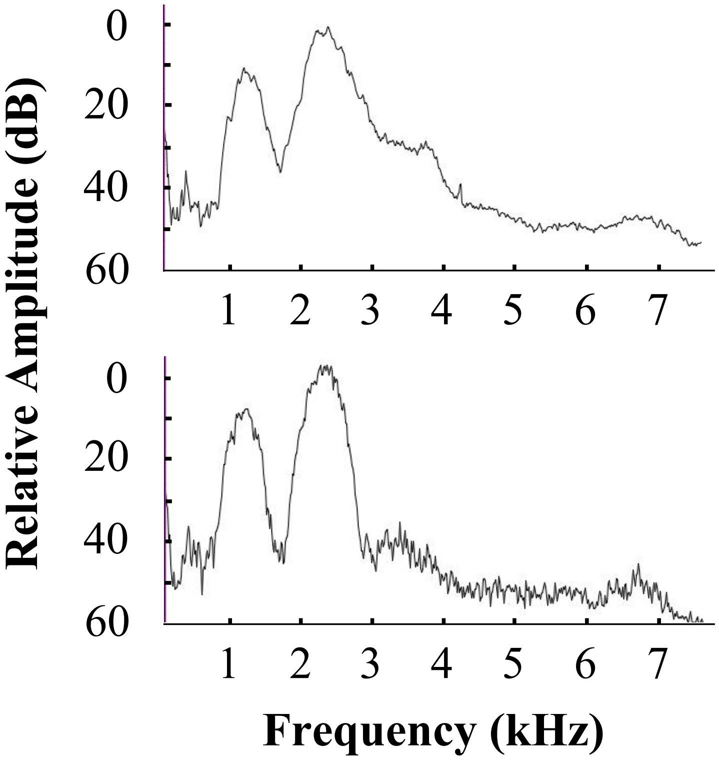


Figure 7. Top. Spectrum (Hanning window, 2048 point FFT) of a natural chorus of Gray Treefrogs (recorded in the field using an Azden ECZ-360, and Marantz PMD 360 tape recorder). Bottom. Spectrum of synthetic chorus noise that was used for noise inserts in some experiments. Both sounds were digitized from the output of a Gen Rad Precision Sound Level meter with its microphone located at the female release point within the choice arena.

test (Exp. 10b) with the two calls used as experimental stimuli in Exp 10a. Females exhibited a unanimous (10: 0) preference for the call alternative with the 125 ms noise insert (Figure 6, bottom), a result inconsistent with restoration of the entire noise insert in the anomalous calls.

DISCUSSION

We believe our results, when considered in their entirety, are inconsistent with the hypothesis that temporal induction is utilized by females of the Gray Treefrog *H. versicolor* during mate assessment in noisy choruses. Our data also provide information on the relative importance of different forms of acoustic disruption to advertisement calls. In particular, they indicate that females are very sensitive to the absence of acoustic energy within calls producing silent gaps.

In Experiment 1, females ignored calls in which a normal interpulse interval had been increased in duration by 10 ms (from 25 to 35 ms). However, we found that placement of a central gap as brief as 50 ms elicited significant discrimination against the anomalous call. This interpulse interval is shorter than that produced by removing just 1 pulse (75 ms). All call alternatives used in this first experiment had equal numbers of pulses (10) and so all gap stimuli had longer total call durations than stimuli lacking gaps. Restoration of missing acoustic content should have elicited discrimination in favour of the call with the 425 ms gap, the 125 ms gap and perhaps a non-significant preference for the call with the 75 ms gap because the alternatives to the normal 10-pulse call would have been perceived as an 18, a 12 and an 11-pulse call, respectively. The discrimination against calls with missing pulses can be quite strong. A reduction in the sound pressure level of the normal alternative by 6 dB was insufficient to eliminate the significant preference in its favour when it was paired against a call missing 2 pulses (125 ms gap). This result also argues against the hypothesis that discrimination against the gap stimuli was due to their lower total energy content relative to normal 18, 12 and 11-pulse calls. Schul and Bush (2002) have demonstrated that *H. versicolor* females are sensitive to increases in interpulse intervals of greater than about 20 ms when these occur throughout the call, and Edwards *et al.* (2002) have found that neurons in the auditory midbrain of two other species of anurans “count” interpulse intervals and respond after test subjects have been exposed to a threshold number. Anomalous intervals (i.e. gaps between pulses that are too short or too long) can reset this integration process. If such neurons exist in *H. versicolor* and play a role in shaping preferences for longer calls, our results using gap stimuli may, in part, be a consequence of neural resetting. The results of additional choice experiments (Schwartz *et al.* in prep.) designed to more rigorously test this hypothesis are consistent with this interpretation.

Research on human subjects has shown that phonemic restoration occurs when noise masks or substitutes for portions of speech (Warren 1999). Therefore, we also ran tests in which noise or call segments obscured or replaced pulse elements. In Experiment 2, when offered 10-pulse calls with filtered noise inserts of 50, 75 or 125 ms, females failed to discriminate. When we lengthened the duration of the noise insert (to 225 ms or 425 ms), which should have rendered discrimination easier if restoration occurred, or increased noise amplitude (by 9 dB) relative to the pulsed portion of the call, which could have facilitated restoration, females again failed to discriminate. Allowing females to hear more normal pulses before the noise section did not qualitatively change our results (Exp. 2: 425 ms insert with noise near the call end). Induction was also not evident when multiple noise bursts were interspersed throughout a call (Exp. 8). In fact, in spite of three opportunities for restoration of missing call structure, all females discriminated against the longer anomalous call even when it was paired against a normal call containing the same number (20) of pulses. If noise overlapped an entire call with a large gap (425 ms, Exp. 3), females discriminated in favour of the normal call, in part, presumably because the pulse structure of the overlapped call was partially obscured by the noise of lower amplitude. In humans and other taxa similar acoustic arrangements are not conducive to induction (e.g. Petkov *et al.* 2003). Our results using pulse strings simulating overlapped sections of stimulus calls were different (Experiment 4). In these situations, females discriminated in favour of the longer anomalous calls, even though the overlapped sections had a pulse repetition rate that was double the normal rate at the test temperature. Thus, although results are inconsistent with temporal induction, they may further demonstrate that all forms of call disruption are not equivalent and that when calls are partially overlapped by signals with a normal pulse structure, the resulting call segment contributes (albeit in a weakened fashion) to the attractive potential of the entire call. Our findings are in agreement with previous research that has shown that although they are typically less attractive than calls of equal duration that are not overlapped, overlapped calls (or those suffering partial overlap) will elicit female phonotaxis (Schwartz & Marshall 2006).

In Experiments 1-4, our normal call alternatives were only 10 pulses long and thus, while within the normal range of variation, were shorter than the average advertisement call duration. Because female preferences for longer calls (i.e. those with more pulses) are accentuated when call alternatives are shorter rather than longer (Gerhardt *et al* 2000), any restoration of pulses would have been more easily detected in our experiments than if we had used longer call alternatives. In part to test behaviour using calls of average duration, we employed call alternatives equivalent in duration to an 18-pulse call in Experiments 5-6. Thus these experiments also differed from the previous tests because call alternatives were identical in duration. In Experiment 5, an indication of pulse restoration was absent when the anomalous call was interrupted by a gap (425 ms). Overlap of the same portion of the call by filtered noise or a pulse string significantly reduced call attractiveness relative to a normal call. The data from Tests 5d-5f, in which the relative amplitude of the normal call was lowered relative to the call containing a 425 ms noise insert, are consistent with expectations based on results of Experiment 2. They indicate that a call with pulses replaced by noise suffers a major reduction in relative attractiveness. Additional experiments directly tested and again demonstrated that an absence of pulses is more detrimental than overlap by pulses from another call (Exp. 6) or replacement by an equivalent segment of noise (Exp. 7). However, call overlap by pulses is roughly equivalent to overlap by filtered noise (Exp. 6, ON), provided the pulses are incompletely masked – as was the case here (Schwartz *et al.* unpublished data). In natural choruses, the potential of the natural din of the chorus to mask a male's calls depends, in part, on the distance from the male of a listening female (Gerhardt & Klump 1988). Therefore, as a female approaches a small group of males in close proximity, the negative impact on mate assessment of acoustic overlap among neighbours should become progressively more important than that of the background din. Clearly, the consequences of both forms of interference depend on the precise form, intensity and timing of the interfering sounds (Schwartz & Marshall 2006).

It would seem unlikely that our failure to detect temporal induction in females of *H. versicolor* is due to an increased degree of difficulty relative to tests performed with humans or other species. In humans, for example, phonemic restoration requires that missing phonemes be replaced with a signal containing appropriate spectral energy, namely at frequencies present in the deleted or masked phoneme (Warren *et al.* 1972). Moreover, the context of a sentence in which a phoneme is expunged can affect how a listener hears the missing phoneme. Clearly, in our study, complications associated with "context" were not present and the spectral composition of our noise segments was well matched to that of our synthetic advertisement calls. In humans, phonemic restoration has been reported using noise segments of over 300 ms (Bashford *et al.* 1988). In the studies of other taxa, positive results were obtained with noise inserts of 300 ms (starlings – Braaten & Leary 1999), 110 ms (cats – Sugita 1997), ~280 ms (tamarins – Miller *et al.* 2001) and 56 ms (macaques – Petkov *et al.* 2003). Thus we feel that our noise inserts were of reasonable durations to test for comparable abilities in treefrogs. Moreover, we failed to observe restoration over a range of noise intensity levels including those above and below that of our stimulus calls. There is, however, an important aspect of the structure of the treefrog calls that may have increased the complexity of the task of restoration in most of our experiments. The advertisement calls consist of both pulses and intervening interpulse intervals. Our use of continuous segments of noise would require that females not only "restore" absent pulses using acoustic energy in the noise but also the intervals that normally lack acoustic energy. In fact, when we employed pulses constructed from noise (Exp. 9a), females discriminated in favour of the longer anomalous calls. However, the preference reversed in Experiment 9b which offered females a normal call alternative with an identical number of pulses (18 rather than 10). Therefore, Gray Treefrog females failed to exhibit even a rather limited form of signal restoration

(restoration of pulse shape). Although the rectangular noise pulses were somewhat attractive, in a natural chorus, background noise would not be packaged in discrete bursts timed to precisely coincide with the pulses of a male's call. It seems likely that the anomalous pulse shape (with an abrupt as opposed to a normal envelope rise) contributed to the reduced attractive potential of the noise pulses relative to normal pulses. This idea remains to be tested. It would also be useful to test for induction in anuran species for which the call is a continuous sound rather than one composed of a series of brief subunits. In other studies of temporal induction in animals, noise was inserted into acoustic units considerably longer than the 25 ms pulses of *H. versicolor*. The pulses of Gray Treefrogs are too short to make placement of noise within these segments practical or naturally relevant. Nevertheless, induction might be possible in female Gray Treefrogs over such brief time scales.

In many of our tests (e.g. those using relatively short or low amplitude normal call alternatives), we carefully chose our call alternatives to reveal even a small contribution of induction. Nevertheless, a potential criticism of the experiments discussed thus far is that we employed tests of discrimination that would be less likely to detect (because responses can be more sensitive to stimulus differences; Bush *et al.* 2002; Phelps *et al.* 2006) weak or partial induction than a single speaker (no-choice) design. In our final experiment (10), we did, however, estimate call attractiveness by timing female approaches to a single speaker. We found that phonotaxis scores did not differ significantly for 10-pulse calls containing either a 125 ms or a 425 ms noise insert. With full restoration, the former stimulus would have been perceived as a 12-pulse call and the latter as an 18-pulse call and elicited a significantly lower phonotaxis score than the latter call (Bush *et al.* 2002; Schwartz *et al.* in prep.). The fact that rates of approach to the standard (normal) 18-pulse call were similar to that of the longer anomalous call is, however, consistent with temporal induction. We suggest that this explanation is unlikely given the aforementioned results from other experiments (considered in their entirety) and the outcome of Exp. 10b. Recall that in Exp. 10b, we paired the two anomalous calls used in Exp. 10a against one another, and unanimous discrimination occurred against the longer call! Because both alternatives contained the same number of pulses and a noise insert, even partial restoration of pulse structure should have resulted at worst in a lack of discrimination and at best discrimination in favour of the longer call. We suspect that responses to noise or noise-containing stimuli are idiosyncratic. Thus, although noise with an appropriate spectral profile can under some circumstances add to the relative attractiveness of a call or elicit vigorous phonotaxis, the percept experienced by the female to the noise is not similar to a pulse train. In fact, we think the discrimination paradigm was better able to test for such a percept in our subjects than a single speaker test.

A satisfactory explanation for why our tests with Gray Treefrogs failed to show evidence for temporal induction may relate to differences in and the availability of higher-levels of sound processing in the central nervous system among anurans as compared to some other vertebrates (Seeba *et al.* 2010). Whatever the reason(s), we believe our results eliminate one possible mechanism by which receivers in *H. versicolor* might improve call-based assessment under the extremely noisy conditions often present in chorusing aggregations. They are also in agreement with recent data of Seeba *et al.* (2010) on the closely related treefrog *H. chrysoscelis*. Previous work has demonstrated that directional cues provided by the auditory system can improve extraction of fine-temporal information (pulse structure) during call overlap (Schwartz & Gerhardt 1995). It is likely that such cues can improve call and call element detection when, for example, a female is oriented so that a calling male is spatially separated from the chorus noise (Schwartz & Gerhardt 1989; Bee 2007). This situation is increasingly more probable as a female approaches a male. The more pronounced increase in amplitude of a male, as compared to that of the background chorus, accompanying approach will also increase the signal to noise ratio. Therefore, it may be that accurate assessment is only possible once a female is relatively close to a group of callers (Klump & Gerhardt 1988). At this time increases in the call duration and pulse effort by males that detect the female may also contribute to improved call detection. For example, in the grasshopper *Chorthippus biguttulus*, noise tolerance, assayed using a turning response, improves, within a certain duration range, with increasing stridulation signal duration (Ronacher *et al.* 2000). Whether similar duration-linked improvements in call detection in background noise occur in *H. versicolor* is currently under investigation.

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