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Synchronized Calling in a Treefrog *(Smilisca sila)*

Short Behavioral Latencies and Implications for Neural Pathways Involved in Call Perception and Production

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Abstract. A neotropical treefrog, *Smilisca sila*, exhibits an unusual ability to synchronize its calling with that of neighbors such that calls often overlap temporally. Call playback experiments measured the latency to evoked calling in response to one-note and two-note mating calls. Approximately one-half of the responses overlapped the one-note stimulus call, while 20% overlapped the two-note stimulus call. Minimum response latencies were 55 ms and 78 ms in response to the one-note and two-note calls, respectively. These data were used to evaluate the efficacy of proposed neural pathways involved in call recognition and production. Based on neural and behavioral latencies presented in those studies, it is suggested that the proposed pathways for call recognition and production might not accommodate the short behavioral latencies in *S. sila*. One possible explanation for this discrepancy is that call detection is decoupled from call recognition, the former requiring a shorter neural pathway thus permitting a shorter behavioral latency.

Introduction

Communication signals used in courtship displays function in mate attraction; to perform this function the signals must be detected and recognized by conspecifics. This function is enhanced by increasing the conspicuousness of the signal. Studies of acoustic and visual communication have postulated a number of adaptations that increase signal conspicuousness [Alexander, 1975; Green and Marler, 1980; Narins, 1982a]. For example, acoustic signals might be adapted to maximize transmission distance [Morton, 1975; Wiley and Richards, 1982; Bowman, 1983; Ryan 1985, 1986] or to stand out against background noise [Brenowitz, 1982; Ryan and Brenowitz, 1985]. Many species avoid temporal overlap with similar signals of heterospecifics and conspecifics [Cody and Brown, 1969; Littlejohn and Martin, 1969; Greenfield and Shaw, 1982; Narins, 1982b; Schwartz and Wells, 1983]. Several

authors have discussed possible neural adaptations to achieve such temporal synchrony [Narins, 1982a, 1983; Zelick, 1986].

A number of animals, however, exhibit patterns of signaling such that signals of neighbors overlap in time. This can result merely from random interactions among individuals [e.g., Walker, 1969; Greenfield and Shaw, 1982; Greenfield, 1983]. In some cases, however, signal overlap is not random but is the outcome of finely tuned behaviors. The synchronous flashing of the firefly *Pteroptyx malaccae* is perhaps the most cited example [Buck and Buck, 1968]. In this example, and in most reported cases of synchronous and overlapping signals, animals entrain to a rhythm.

Tuttle and Ryan [1982] reported a different pattern of synchronous calling in the neotropical treefrog *Smilisca sila* (Hylidae) that often results in temporal overlap among calls of neighboring males. *S. sila* produces calls that consist of a variable number of notes. Single notes are similar in possessing a complex spectral structure, and each note can vary in duration from ca. 20 to 150 ms. The call is noisy with a frequency range of ca. 1.0–3.5 kHz and a dominant frequency peak of 2.5 kHz [Tuttle and Ryan, 1982]. These frogs call relatively infrequently ($\bar{x}$ = 1.7 calls/min), and calling does not appear to follow any well-defined pattern [Tuttle and Ryan, 1982]. There is no apparent calling rhythm to which males could entrain. However, at times the calls so precisely overlap that it is difficult to discern the number of frogs that have called. Clearly, the frogs respond to the neighbor's call, and they do so rapidly. The latency from the onset of a neighbor's call to a vocal response appeared to be much shorter for *S. sila* than that reported for other anurans [e.g., Narins, 1982a]. The purpose of this study is to quantify this short behavioral latency for evoked calling and use these data to evaluate proposed neural pathways involved in call recognition and production.

Material and Methods

Study Area

Experiments were conducted in January and February, 1983, on Barro Colorado Island, Panama. Male *S. sila* call along streams, either on the ground or from bushes and trees above the stream. Males do not aggregate, and usually are spaced at intervals greater than 1 m. Most of the experiments reported here were conducted along Allee Creek. Air temperature was always 26 ± 2 °C. Tuttle and Ryan [1982] provide further information on calling behavior and calling habitat.

Playback Experiments

Conspecific calls were broadcast to evoke calling from male *S. sila*. Stimuli were natural mating calls recorded on tape loops. One stimulus was a one-note mating call with a duration of 111 ms. The other was a two-note call; the first and second notes had durations of 107 and 34 ms, respectively. The inter-note interval was 14 ms, and the total call duration was 155 ms (fig. 1).

Stimuli were broadcast from a stereo Uher tape recorder (model 4200) and a small extension speaker at an intensity of 75 dB SPL (fast setting; re: 2×10^{-5} N/m) at 0.5 m. As the stimulus was broadcast it was recorded simultaneously via a patch cord onto one channel of another stereo Uher tape recorder. The male's vocal response was recorded onto the other channel, using a Sennheiser MKH 104 microphone.

The speaker was positioned about 1 m from the calling male. The microphone was placed within several centimeters of the male; the microphone head was directed towards the calling male and away from the speaker. Although the microphone did record the stimulus as well as the male's response, the much greater amplitude of the response allowed it to be dis-

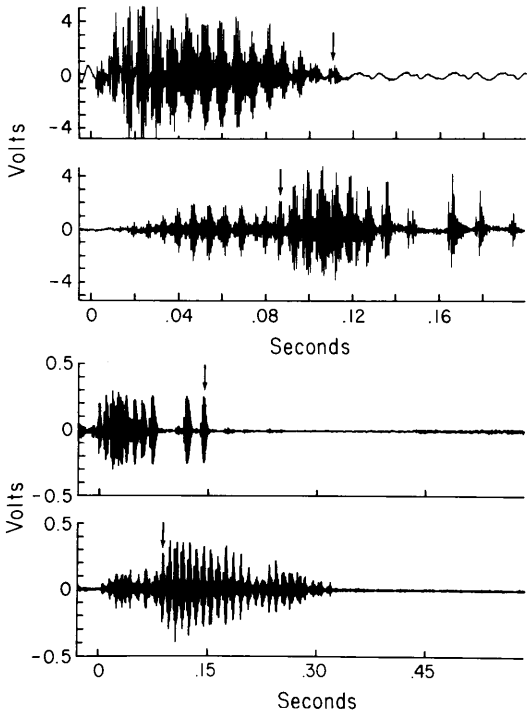

Fig. 1. Oscillograms of the stimulus and the evoked response to that stimulus. The top pair of oscillograms shows the one-note stimulus (top of that pair) and a response to that stimulus (bottom of that pair), and the bottom pair of oscillograms shows a two-note stimulus (top of that pair) and an associated response (bottom of that pair). Time scales differ between the two pairs of oscillograms in order to allow depiction of the entire response to the stimulus. The arrow in the top oscillogram of each pair, indicates offset of the stimulus, while the arrow in the bottom oscillogram of each pair indicates onset of the response.

tinguished easily from the stimulus (fig. 1). The playback experiments consisted of broadcasting a single stimulus call and recording the male's response. The rate of call presentation was always less than 1/min.

Analysis

The temporal relationship of the male's response to the stimulus call was analyzed with a DATA 6000 digital waveform analyzer. Analog signals were digitized at a rate of 10 kHz, providing a temporal resolution of 100 μs. Nyquist frequency was 5 kHz, encompassing the entire frequency range of the male's call. The onset of the male's response relative to the onset of the stimulus was determined, and poststimulus histograms were constructed.

Results

In all, 134 responses of 20 males were recorded and analyzed. There were 50 responses to the one-note stimulus and 84 responses to the two-note stimulus. A one-note response rather than a multi-note response was more likely to be evoked by either stimulus, and there tended to be an inverse correlation between the number of notes in the response and the frequency with which that response was evoked (table I). The range of notes evoked by the two-note stimulus (1–13) was greater than the range of notes evoked by the one-note stimulus (1–7), but the mean number of notes/response evoked by the one-note stimulus ($\bar{x}$ = 2.28, SD = 1.59) was greater than that evoked by the two-note stimulus ($\bar{x}$ = 2.05, SD = 2.30).

There was significant variation in both note duration and inter-note interval (table I). In response to the one-note stimulus, there were significant differences among the first 4 notes in note duration (Kruskal-Wallis test, H = 42.0, $p < 0.001$) but not in inter-note interval (H = 5.4, $p > 0.05$). Sample sizes for notes 5–7 were too small to permit statistical analysis. Among calls evoked by the two-note stimulus, there were significant differences in both note duration (H = 40.0, $p < 0.001$) and inter-note interval (H = 53.1, $p < 0.001$). Small sample sizes for notes 10–13 prohibited statistical analysis.

Table I. Mean inter-note interval and duration ± standard deviation (range) of notes in response to one-note and two-note stimuli

Note No.	Inter-note interval, ms	Duration, ms	N	Calls, n
One note stimulus				
1	114 ± 41 (58–198)	80 ± 35 (23–202)	50	23
2	110 ± 90 (11–257)	45 ± 42 (4–162)	27	9
3	58 ± 60 (19–215)	30 ± 40 (6–176)	18	8
4	56 ± 78 (28–280)	43 ± 55 (7–193)	10	6
5	97 ± 121 (33–279)	31 ± 26 (8–55)	4	1
6	26 ± 10 (18–38)	15 ± 11 (8–27)	3	1
7	29 ± 1 (28–29)	37 ± 11 (29–45)	2	2
Two-note stimulus				
1	201 ± 94 (81–813)	71 ± 62 (4–380)	84	56
2	70 ± 87 (12–281)	58 ± 74 (5–260)	28	15
3	49 ± 69 (24–280)	30 ± 46 (5–159)	13	1
4	42 ± 47 (9–171)	31 ± 30 (6–92)	12	3
5	35 ± 53 (13–175)	29 ± 28 (6–76)	9	2
6	17 ± 5 (13–26)	23 ± 30 (7–87)	7	1
7	15 ± 4 (11–23)	10 ± 5 (6–17)	6	1
8	17 ± 6 (10–26)	14 ± 11 (7–34)	5	1
9	12 ± 4 (8–16)	57 ± 64 (2–136)	4	2
10	11 ± 3 (9–13)	35 ± 36 (9–60)	2	1
13	13	37	1	1

The inter-note interval is the time from the onset of that note to the offset of the previous note, except for note No. 1, in which it is the time from the onset of stimulus to the onset of the response (note No. 1), i.e., the latency to response. N = Sample size; Calls = number of calls with each maximum number of notes.

Twenty-nine of the 50 calls evoked by the one-note stimulus temporally overlapped the stimulus call, while only 17 of the 84 calls evoked by the two-note stimulus overlapped that stimulus (fig. 2). Overlapping calls, especially, should provide insights into the minimum latency required for call recognition and production.

Overlapping calls were evoked as rapidly as 58 ms ($\bar{x}$ = 82) and 81 ms ($\bar{x}$ = 119) after onset of the one-note and two-note stimuli, respectively. The speaker broadcasting the stimulus was ca. 1 m from the male; thus the time required for the stimulus to reach the male was ca. 3 ms. Therefore, in response to the one-note stimulus the minimum latency for evoked calling was 55 ms, and the average latency of calls overlapping the stimulus was 79 ms.

Discussion

Latencies in Other Anurans

The playback experiments demonstrate clearly that *S. sila* males respond to a neighbor's call such that calls often over-

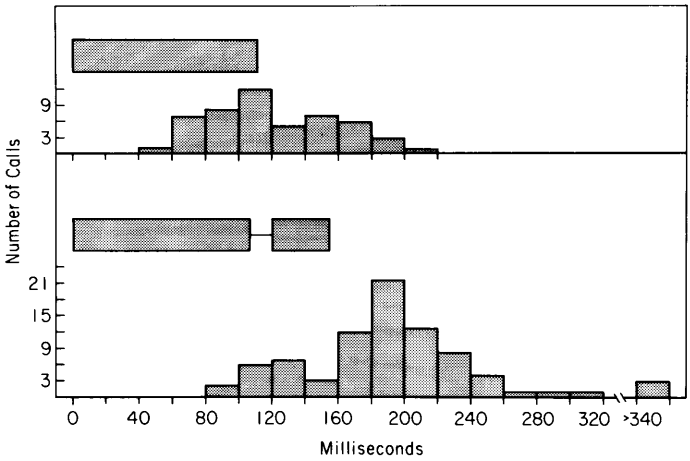

Fig. 2. Post-stimulus histogram showing the temporal relationship between the onset of the response relative to the onset of the one-note stimulus (top) and two-note (bottom) stimulus.

lap in time, and that the latency to evoked vocal response is short. Latencies were shorter in response to the one-note call than to the two-note call. This suggests that the initial notes of the calls differed in their abilities to evoke calling. The fact that intraspecific variation in the mating call might influence evoked calling is interesting and suggests further investigation but is not germane to this study. The point is that both stimuli are natural, conspecific mating calls, and both elicit evoked calling with very short latencies.

The time in which males respond to both stimulus calls is short relative to latencies reported for other vertebrates. Auditory reaction time in humans, measured in experiments similar to those presented here, were 284 ms [Broadbent and Gregory, 1962]. Auditory reaction times in duetting birds can be short, 144 ms in the the black-headed gonolek [Thorpe, 1963] and 80–90 ms in the barbary shrike [Payne, 1970]. However, it is suggested that these short latencies do not result from a stimulus-response reaction, but instead from an autochthonous calling rhythm or internal periodicity [Payne and Skinner, 1970].

The auditory latencies documented in *S. sila* are unsurpassed in other anurans that have been investigated. For example, Schmidt [1964] recorded the latency of release calling in response to various synthetic stimuli in *Pseudacris triseriata*. The stimulus that evoked responses most quickly resulted in latencies of 300–350 ms in one frog and 450–600 ms in another. Schmidt [1973] also recorded the latency of release calling in response to a touch stimulus in *Rana pipiens* – the latency was greater than 750 ms. Narins [1982a] reported minimum latencies for evoked vocal responses in two neotropical frogs, *Eleutherodactylus coqui* and *Hyla ebraccata*, of 200 and 150 ms, respectively, and characterized these responses as fast. The responses of *S. sila* can be three to four times more rapid. Wells and Schwartz [1984] reported that most responses of *H. ebraccata* were 140–200 ms after the onset of the stimulus. The average latencies of calls that overlap the one-note stimulus in

S. sila were twice as rapid. This unusual behavior in *S. sila* has implications for neural mechanisms underlying evoked calling.

Latency to Calling and Proposed Sensory-Motor Pathways

The vocal response of a male frog to the conspecific mating call involves both sensory processing of the acoustic stimulus and activation of the motor pathways that result in vocalization. The precise sensory and motor pathways involved in mating call perception and production are not derived from studies of one species. However, neurophysiological and neuroanatomical studies from a variety of species have resulted in general hypotheses of pathways involved in call perception [reviewed by Capranica and Moffat, 1983; Capranica and Rose, 1983; Wilczynski and Capranica, 1984] and call production [Schmidt, 1974; Wetzel et al., 1985]. The major centers and pathways are outlined in figure 3.

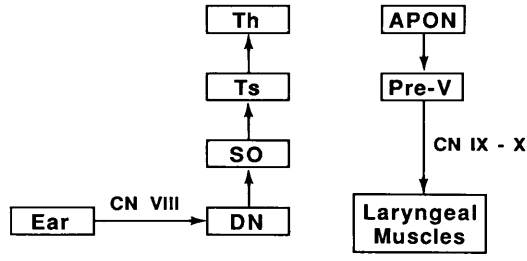

Fig. 3. A graphical representation of pathways proposed for sensory processing and production of vocalizations. Neary and Wilczynski [1986] demonstrate that the sensory and vocal systems are linked between Th and APON; Aitken and Capranica [1984] suggest linkage between SO and pre-V. DN = Dorsal medullary nucleus; SO = superior olive; Ts = torus semicircularis; Th = thalamus; APON = anterior preoptic nucleus; pre-V = pretrigeminal nucleus of the dorsal tegmental area; CN VIII-X = eighth to tenth cranial nerves.

Neural and behavioral latencies within each system allow one to consider whether latencies exhibited by *S. sila* reflect a minimum latency imposed by the response properties of the sensory and motor pathways. Furthermore, these behavioral results afford an opportunity to evaluate the efficacy of the proposed sensory and motor pathways for call recognition and production; that is, can the proposed pathways accomodate the short behavioral latencies observed in *S. sila*?

Based, in part, on the results from Capranica's [1965] study of call properties needed to elicit vocal responses from bullfrogs, Frishkopf et al. [1968] suggested that representative neural output from the amphibian and basilar papillae converge in the central auditory system for recognition of spectral properties of the mating call. They predicted the existence of a 'mating call detector' that would exhibit a synergistic response to combination tones that excited both papillae. Mudry et al. [1977] and Fuzessery and Feng [1983] have verified that areas in the thalamus do show an enhanced response to combination tones – this area of the brain appears to contain the 'AND' gates predicted by Frishkopf et al. [1968]. Complete processing of the mating call probably involves integration of temporal cues as well; Rose and Capranica [1983, 1984] showed units in the torus semicircularis tuned to rates of amplitude modulation that are characteristic of the species' mating call. The results of these studies suggest that auditory information must reach at least the level of the thala-

mus for call recognition to occur. It should be remembered, however, that some frogs might produce calls that contain energy only in those frequencies that stimulate the basilar papilla. This could include *S. sila*, which has all of its energy in the call concentrated above 1,000 Hz.

The descending motor pathway for call production has been hypothesized to start at the anterior preoptic area (APON) and pass through the hypothalamus to the pretrigeminal nucleus [pre-V; designated as the pretrigeminal nucleus of the dorsal tegmental area by Wetzel et al., 1985; see also Schmidt, 1973]. Neary and Wilczynski [1986] have recently shown the sensory and motor pathways to be linked via direct connection from the thalamus to the hypothalamus and preoptic area. A consideration of latencies to acoustic stimulation at each point in this circuit shows that evoked calling in *S. sila* probably cannot involve a passage of information completely through these neural circuits.

Latencies for calling in response to stimulation of APON are too long to reflect the true time course for motor pathway activation during calling in chorus situations in *S. sila*, and probably in other species as well. For example, Wada and Gorbman [1977] stimulated the APON in freely moving *R. pipiens* and reported the shortest latencies as 11 s. Even latencies within the proposed motor pathway can not accommodate the behavioral latencies exhibited by *S. sila*. Schmidt [1974] stimulated the posterior edge of a transection through the infundibular foramen, which receives efferents from the APON, and recorded responses in pre-V and in muscles associated with glottal opening. Latencies recorded from both pre-V and the muscles were greater than 100 ms [Schmidt, 1974, pers. commun.].

Considering the short behavioral latencies of *S. sila* relative to the longer responses within the proposed motor pathways, the results of Aitken and Capranica [1984] are of particular interest. They recorded responses from pre-V of *R. pipiens* in response to auditory stimulation and reported latencies of 10–50 ms [see also Schmidt, 1971]. These shorter neural latencies could accomodate the behavioral latencies of *S. sila*.

The pathway of the auditory stimulus that gave rise to the short latencies in pre-V reported by Aitken and Capranica [1984] was not documented. Given the latencies of pre-V after stimulation of APON in other studies, it appears that the stimulus could not have arrived via a pathway including the APON. Also, it appears that the stimulus must reach the pre-V prior to being processed by the thalamus. Fuzessery and Feng [1983] isolated single units in the thalamus of *R. pipiens* and reported latencies ranging from 26 to 75 ms, with an average neural latency of 39 ms. Thus, even without considering motor pathways, the short behavioral latencies suggest that the evolution of calling behavior in *S. sila* might be under neurophysiological constraints, and they raise suspicion as to the ability of the proposed sensory-motor pathways for call recognition and production to accommodate this behavior.

Even though it is thought that complete processing for call recognition takes place at or above the level of the thalamus, given the short behavioral latencies in *S. sila* relative to the neural latencies reported for the thalamus of *R. pipiens*, it is worth con-

sidering neural latencies at lower levels of the proposed sensory pathway. In the torus semicircularis of the Australian bullfrog *(Limnodynastes dorsalis)*, Loftus-Hills [1971] reported latencies of single units ranging from 6 to 85 ms, with most units having latencies less than 30 ms. In the torus of the fire-bellied toad *(Bombina bombina)* and the grass frog *(R. temporaria)* the shortest latencies observed were 5 and 10 ms, respectively [Walkowiak, 1980; see also Corwin et al., 1982]. If call processing in the central nervous system were restricted to the brain stem for calling male *S. sila*, these neural latencies could accommodate the behavioral latencies reported in this study. However, if sensory-motor pathways must involve higher areas of the brain – the thalamus and APON, respectively – it is difficult to reconcile these models with the behavioral latencies for evoked calling exhibited by *S. sila*. Latency in response to auditory stimulation in the thalamus is greater than 30 ms, while latencies to glottal opening even when stimulation is anterior to APON are quite long.

One resolution of this discrepancy suggests that in some situations call processing might be restricted to the brainstem and, as suggested by Aitken and Capranica [1984], auditory stimuli might reach the pre-V via a more direct route, possibly from the superior olive. This hypothetical pathway would short-circuit higher areas of the brain allegedly involved in call recognition (thalamus) and production (APON; or at least sensitization of neural circuits to acoustic triggering), and could accommodate the behavioral latencies for evoked calling reported in this study. However, Aitken and Capranica do suggest that the APON is involved in call production, and that stimulation of the pre-V via the superior olive alone probably does not result in mating call production.

There are at least three explanations for the observed disparities between behavioral and neural latencies. (1) The proposed pathways may be necessary for call recognition, but perhaps in some situations calling can be evoked merely by detection of a less specific acoustic event; thus detection and recognition are decoupled. (2) The pathways for call recognition are applicable, but the neural latencies are an experimental artifact that do not reflect the actual time course operating in free-moving, physiologically primed individuals. (3) *S. sila* is unique, at least relative to other species that have been investigated, in possessing neural adaptations allowing both call recognition and short behavioral latencies.

The first possibility, perhaps a likely one, is that complete processing of the call is not always necessary to evoke calling. It appears that in many species reproductively active males are less discriminating than females in response to conspecific calls. Loftus-Hills [1971] emphasizes this dichotomy in discussing results showing that males will respond vocally to a variety of acoustic stimuli, while the stimuli that will elicit phonotaxis from females are much more restrictive. Perhaps once a male is at the breeding site among other conspecific males, the calls are first completely processed and recognized and then the male's response to subsequent calls may be triggered without complete auditory processing. Once a male has identified the calls in a chorus as being those of conspecifics, it may be advantageous in

some situations to decouple call detection from call recognition. This could be done by short-circuiting higher levels of acoustic processing. Thus a mating call detector system may not be activated each time a male calls.

This model is consistent with the pathways proposed by Aitken and Capranica [1984]. Upon recognition of a conspecific call the APON might function in sensitizing the pre-V to acoustic inputs that might arrive via the shorter pathways. The general model of the decoupling of detection and recognition can be tested with playback experiments. This model predicts that males will be more selective in the stimuli to which they respond when they initially enter the chorus, and that subsequently less appropriate stimuli are more likely to evoke calling and do so with shorter latencies. The specific pathways involved could possibly be elucidated by attempting to elicit evoked calling from males that have been lesioned in various areas of the brain [e.g., Schmidt, 1974].

The second possibility is that the reported neural latencies are an experimental artifact. This does not seem to be true in the studies of the auditory system discussed above. Fuzessery and Feng [1983] immobilized animals with *d*-tubocurarine chloride prior to neurophysiological recordings. This procedure should not effect neural response times [Yovanof and Feng, 1983]. It is possible that physiological condition, especially hormonal state, might influence latencies. Pfaff [1980] reviews a variety of effects of estrogen on neural response properties of rats. However, although Aitken and Capranica [1984] reported an increased probability of finding auditory activity in the pre-V after hormone treatment, there were no differences in latencies in treated versus untreated frogs. Urano and Gorbman [1981] reported that injections of pituitary homogenates increased the percentage of APON neurons responsive to auditory stimulation, but they provide no evidence that latencies were affected. Yovanof and Feng [1983] showed that estradiol will influence the amplitude of evoked responses in the midbrain, but again, there is no evidence that hormonal state influences neural latencies.

Finally, this apparently unusual calling behavior in *S. sila* might reflect adaptations of the animal's neural circuitry. Although there is at least one other species that exhibits similar short behavioral latencies *(Centrolenella* sp., pers. observation), this calling behavior is certainly the exception and not the rule among anurans. If these short behavioral latencies do reflect adaptive changes in neural circuitry, *S. sila* offers interesting possibilities for comparative studies of sensory and motor pathways involved in call recognition, detection and production.

In summary, the results presented here demonstrate short behavioral latencies for evoked calling in *S. sila* and are at variance with current models of sensory-motor pathways involved in call recognition and production in anurans. One possible explanation for this disparity is that during evoked calling call detection and call recognition are decoupled, the former relying on a shorter neural pathway, perhaps restricted to the brainstem. This study presents the first evidence, to my knowledge, to suggest that complete processing of the call is not necessary to evoke calling from male anurans.

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