Female Túngara Frogs Do Not Experience the Continuity Illusion

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In humans and some nonhuman vertebrates, a sound containing brief silent gaps can be rendered perceptually continuous by inserting noise into the gaps. This so-called "continuity illusion" arises from a phenomenon known as "auditory induction" and results in the perception of complete auditory objects despite fragmentary or incomplete acoustic information. Previous studies of auditory induction in gray treefrogs (*Hyla versicolor* and *H. chrysoscelis*) have demonstrated an absence of this phenomenon. These treefrog species produce pulsatile (noncontinuous) vocalizations, whereas studies of auditory induction in other taxa, including humans, often present continuous sounds (e.g., frequency-modulated sweeps). This study investigated the continuity illusion in a frog (*Physalaemus pustulosus*) with an advertisement vocalization that is naturally continuous and thus similar to the tonal sweeps used in human psychophysical studies of auditory induction. In a series of playback experiments, female subjects were presented with sets of stimuli that included complete calls, calls with silent gaps, and calls with silent gaps filled with noise. The results failed to provide evidence of auditory induction. Current evidence, therefore, suggests that mammals and birds experience auditory induction, but frogs may not. This emerging pattern of taxonomic differences is considered in light of potential methodological, neurophysiological, and functional explanations.

Keywords: auditory induction, continuity illusion, perceptual restoration, *Physalaemus pustulosus*, temporal induction

A common challenge faced by humans and other animals is rendering intact perceptual scenes from fragmentary sensory input. The visual system, for example, actively "fills in" missing pieces of partially occluded objects to form unified percepts of whole objects in coherent visual scenes (Kellman & Shipley, 1991;

Pessoa & De Weerd, 2003; Sekuler & Palmer, 1992). In audition, a parallel percept can occur when an ongoing sound (e.g., speech) is temporarily masked by another brief, loud sound (e.g., someone coughing). Much like the visual system, the auditory system actively fills in the masked portions to create a so-called "continuity illusion" of a complete auditory object (Bregman, 1990; Warren, 1999). Even removing a portion of a target sound and replacing it with a burst of noise can result in the illusory perception of a complete sound. This form of perceptual restoration, known as *auditory induction*, is responsible for phonemic restoration in humans (Miller & Licklider, 1950; Warren, 1970). Parallels of phonemic restoration have been demonstrated in other acoustically communicating animals, including primates (Miller, Dibble, & Hauser, 2001; Petkov, O'Connor, & Sutter, 2003) and songbirds (Braaten & Leary, 1999; Seeba & Klump, 2009). Auditory induction has also been demonstrated using much simpler stimuli, such as pure tones and frequency-modulated sweeps (Ciocca & Bregman, 1987; Kluender & Jenison, 1992; Petkov et al., 2003; Sugita, 1997). Current evidence from studies of brain imaging and event-related potentials in humans, and from single-unit recordings from primates and cats, indicates processing in the auditory cortex contributes to auditory induction (Petkov & Sutter, 2011). In the present study, we asked whether a vertebrate that lacks an auditory

cortex, but nevertheless relies heavily on hearing and sound communication, experiences auditory induction. This question is key to elucidating both the evolutionary history of auditory induction and the extent to which its underlying neural basis may be conserved among species (Petkov & Sutter, 2011).

Anuran amphibians (frogs and toads) are well known for their use of loud and conspicuous vocal signals (Gerhardt & Huber, 2002; Wells, 2007). Communication in frogs often takes place in dense choruses, where many males vocally compete to attract reproductive females, presenting females with the challenge of selecting individual calling males as mates in an environment with many sources of masking sound (Bee, 2012, 2015; Vélez, Schwartz, & Bee, 2013). No part of the amphibian brain is anatomically or functionally equivalent to an auditory cortex (Wilczynski & Endepols, 2007). Nevertheless, recent research has discovered that frogs exploit many of the same cues used by humans to perceptually organize acoustic scenes (Bee, 2012, 2015; Vélez et al., 2013). An important question is whether they also experience auditory perceptual restoration.

The hypothesis that anurans experience auditory induction has been tested previously in two studies of closely related North American treefrogs, *Hyla versicolor* and *H. chrysoscelis* (Schwartz et al., 2011; Seeba, Schwartz, & Bee, 2010). Both species produce a vocalization consisting of a train of short (10–20 ms), discrete pulses separated by short intervals of silence (50% pulse duty cycle); that is, their vocalization is a *discontinuous* sequence of sounds. Neither Seeba et al. (2010) nor Schwartz et al. (2011) found evidence supporting the hypothesis that their subjects experienced illusory pulses when small groups of consecutive pulses were removed and replaced by bursts of noise. These negative findings tentatively suggest frogs might not experience illusions of auditory continuity. However, these studies of treefrogs differ from those demonstrating auditory induction in other animals (including humans) in that the latter have typically used stimuli that are *continuous*, such as pure tones, frequency-modulated sweeps, or continuous vocalizations, including speech. Before drawing conclusions about the presence or absence of auditory induction in frogs and its significance to the phenomenon's evolutionary history, it is critical to investigate the phenomenon in frog species with naturally continuous vocalizations (Seeba et al., 2010).

Here, we tested the hypothesis that auditory induction occurs in a frog that produces a vocalization that is a natural analog of a frequency-modulated sweep. Túngara frogs, *Physalaemus pustulosus*, are small anurans distributed throughout Mesoamerica (Weigt, Crawford, Rand, & Ryan, 2005). Males attract females using a vocalization commonly referred to as a "whine" (Figure 1; Ryan, 1985). Females use the calls to localize and select a male mate by exhibiting phonotaxis to and strong preferences for certain features of male signals. Males can append suffixes ("chucks") after the whine, but often produce only whines, which are necessary and sufficient to elicit positive phonotaxis by females (Baugh, & Ryan, 2010; Ryan, 1985). Túngara frog choruses often have multiple males calling simultaneously (Ryan, 1985); hence, calls often overlap and are masked or interrupted by the calls of competing conspecific and heterospecific males and other environmental sounds.

We investigated auditory induction by measuring phonotaxis evoked by a continuous whine and discontinuous whines having
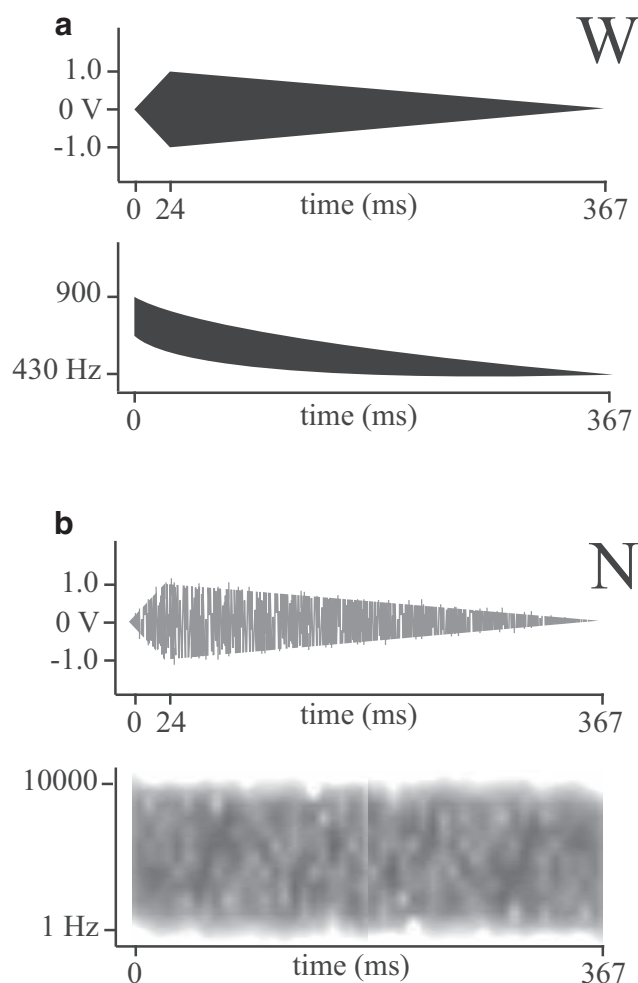

Figure 1. Stylized oscillogram (top) and spectrogram (bottom) showing the acoustic parameters for (a) the complete whine stimulus (W) and (b) noise stimulus (N).

silent gaps or gaps filled with bursts of noise. This approach permitted us to test the general hypothesis that the continuity illusion in female auditory perception can occur if gaps of silence in male calls, which render the calls unattractive, are filled with noise. Our general predictions, therefore, were that (a) continuous whines would be attractive (Baugh & Ryan, 2010; Ryan, 1985), (b) silent gaps would render whines unattractive (Wilczynski, Rand, & Ryan, 1995), (c) whines with noise-filled gaps would be more attractive than whines with silent gaps, and (d) continuous whines and whines with noise-filled gaps would be similarly attractive.

General Method

Study System

Procedures for collecting and testing frogs were approved by the Institutional Animal Care and Use Committees of the University of Texas at Austin (06041701) and the University of Minnesota–Twin Cities (0510A76966), and Autoridad Nacional del Ambiente

approved scientific permits in the Republic of Panamá. We conducted this study in the vicinity of the Smithsonian Tropical Research Institute in Gamboa, Panamá (9° 07.0′N, 79° 41.9′W) between June and August from 1998 to 2006. Protocols for collecting and testing females followed those we have described previously (Baugh & Ryan, 2009; Lea, Halliday, & Dyson, 2000; Lynch, Rand, Ryan, & Wilczynski, 2005). Subjects were returned to their site of collection within 12 hr. To prevent resampling, subjects were marked with a unique toe-clip combination following the *Guidelines for the Use of Live Amphibians and Reptiles in Field Research* (Beaupre, Jacobson, Lillywhite, & Zamudio, 2004).

Apparatus

Experiments were conducted inside a rectangular, sound-attenuating chamber (2.7 × 1.8 × 1.78 m, L × W × H; ETS-Lindgren, Cedar Park, TX) equipped with acoustic foam to reduce reverberation and located inside a temperature-controlled (~27 °C) laboratory. Acoustic stimuli were output through the soundcard of a desktop (Dell Dimension 4600) or laptop computer (Dell Latitude D610) using either SIGNAL 4.0 (Engineering Design, Berkeley, CA) or Traction® (Traction Software Inc., Providence, RI), amplified with a Crown XLS 402 amplifier (Crown Audio USA, Elkhart, IN), and broadcast through two A/D/S L210 speakers (Directed Electronics, Vista, CA) located 2.6 m apart at opposite ends of the sound chamber at equal distances from the center of the chamber. Stimulus SPLs were calibrated in dB SPL (re 20 μPa) using a GenRad, 1982 sound level meter (SLM; IET Labs Inc., Roslyn Heights, NY), with its microphone pointed toward a speaker from a central release point at the center of the chamber, equidistant from the two playback speakers. The subjects' behavioral responses were monitored using a wide-angle infrared camera (Fuhrman Diversified Inc., Seabrook, TX) mounted from the center of the sound chamber ceiling and connected to a TV monitor located outside the chamber.

Acoustic Stimuli

Our experiments shared several stimulus types in common, including a complete, uninterrupted whine (W) and a control noise (N) consisting of white noise shaped with the amplitude envelope of the whine (see Figure 1). Using the W stimulus, we also synthesized stimuli with silent gaps (WG) and silent gaps filled with noise (WGN; see Figure 2). W, WG, and WGN were synthesized based on the mean values of call parameters from the local population (Ryan & Rand, 1990). All stimuli were synthesized (20-kHz sample rate, 8- or 16-bit resolution) using either SIGNAL 4.0 or custom software (J. Schwartz, Pace University at Pleasantville, NY).

Whine stimulus (W). The W stimulus was 367 ms in duration and consisted of a continuous tone that swept downward in frequency from 900 Hz to 430 Hz (logarithmic decrease; Figure 1a). The amplitude envelope of the whine was shaped with a linear on-ramp over the first 24 ms and a linear off-ramp over the last 343 ms. This synthetic version of the whine, consisting only of the fundamental frequency, reliably elicits phonotaxis by females and evokes calling by males (Bernal, Rand, & Ryan, 2007), and differs principally from natural whines in its absence of higher harmonics.

Female túngara frogs do not discriminate, on average, between synthetic and natural whines (Ryan & Rand, 1990), and harmonics above the fundamental frequency do not influence female preferences (Rand, Ryan, & Wilczynski, 1992). Additional information on call parameters and the synthesis procedure can be found in Ryan and Rand (1990, 2003). Unless indicated otherwise, the SPL of the W stimulus was calibrated as follows: we used the SLM to adjust the SPL (fast root-mean-square [RMS], C-weighted) of a continuous, 500-Hz pure tone (the average frequency of the whine) to 82 dB. We then matched the peak-to-peak voltage of the W stimulus in software to that of the calibrated 500-Hz tone in software.

Noise stimulus (N). Following earlier work (Wilczynski et al., 1995), we used noise (N) as a stimulus in some tests, here consisting of broadband noise (1–10,000 Hz) shaped to have a duration (367 ms) and amplitude envelope (Figure 1b) equivalent to that of the W stimulus. Previous studies have shown the N stimulus to be behaviorally neutral, meaning short bursts of noise are equivalent to silence and elicit neither positive nor negative phonotaxis (Rand et al., 1992; Ryan & Rand, 1993). We calibrated the N stimulus by adjusting the peak-to-peak voltage of its envelope to match that of the W stimulus.

Whine-gap stimulus (WG). We created WG stimuli (see Figure 2) by digitally replacing portions of the W stimulus with silence. The duration of the silent gap introduced into a W stimulus to create a WG stimulus varied in different experiments, but in all cases, the overall durations of WG stimuli were equivalent to that of the W stimulus (367 ms); see subsequent sections for details. In all experiments, WG stimuli were calibrated such that the peak-to-peak voltages of the remaining portions of the whine were equal to those of the equivalent samples in the calibrated W stimulus.

Noise-filled whine-gap stimulus (WGN). To create WGN stimuli, we inserted short noise bursts into WG stimuli that filled the silent gap (see Figure 2). The WG portions of the WGN stimuli were calibrated as described above for typical WG stimuli. The spectral content of the noise, and procedures for calibrating noises, varied across experiments as described in subsequent sections.

Experimental Protocol

We conducted five separate experiments, all based on using two-alternative choice tests of phonotaxis behavior (Gerhardt, 1995). In such experiments, two alternative stimuli are broadcast antiphonally at rates that simulate two actively calling males. Experiments 1–3 were designed as *recognition tests* (Ryan & Rand, 2001; Ryan, Rand, Hurd, Phelps, & Rand, 2003), which typically pair a target signal, such as a whine (W), against an alternative consisting of a behaviorally neutral control sound, such as a burst of noise (N). The logic of a recognition test is that if the target signal is detected and recognized as the call of an appropriate mate, then it should elicit positive phonotaxis; if not, it should fail to elicit phonotaxis. In these experiments the behavioral response (phonotaxis) requires recognition of the sound as the call of a potential mate; therefore, subjects are expected to detect some sounds (e.g., noise bursts) that are not recognized as the call of an appropriate mate. Experiments 4 and 5 were designed as *discrimination tests* (Ryan & Rand, 2001), which pair two potential target signals against each other as alternatives in a choice test. If subjects do not behaviorally discriminate between the two signals,
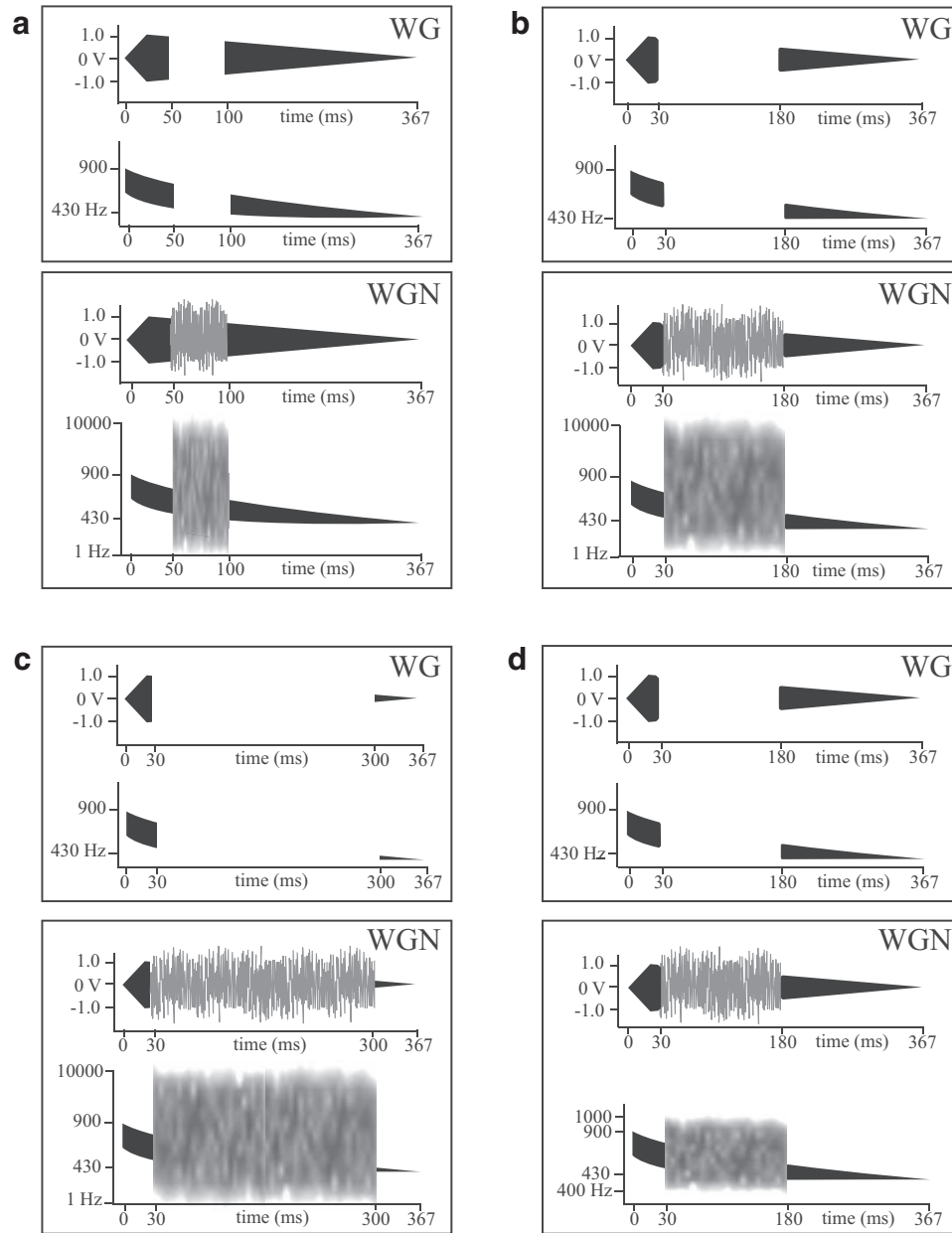
Figure 2. Stylized oscillogram (top) and spectrogram (bottom) showing the acoustic parameters for the whine stimuli with a gap of silence (WG) and with the gap of silence filled with noise (WGN). The gaps are positioned at the following locations: (a) 50–100 ms, (b) 30–180 ms, (c) 30–300 ms, and (d) 30–180 ms.

the expected outcome is that the pool of subjects that make a choice will choose each alternative in equal proportions (0.5). Behavioral discrimination between the target signals is evidenced when a proportion of subjects greater than 0.5 chooses one of the two alternatives.

An individual test began by placing a single female frog under an acoustically transparent cone at the center of the chamber (origin). We then broadcast the two alternatives antiphonally (180° out of phase) for 2 min at a rate of one stimulus per 2 s. Following this 2-min period, the cone was lifted remotely and subjects could move freely within the sound chamber. We scored a "choice" if the

subject entered within 15 min a response zone that extended 10 cm from the speaker in all directions without simply following the chamber wall. A choice of "neither" was recorded if the frog (a) remained motionless at the origin for 5 min after the cone was raised; (b) remained motionless for 2 min after exiting the origin; or (c) failed to make a choice within 15 min (Ryan & Rand, 1993). We periodically alternated the side of the chamber broadcasting each alternative stimulus to eliminate any potential side bias. Across subjects, we systematically alternated which stimulus in a pair of alternatives was broadcast first to control for a potential leading caller preference (Bosch & Márquez, 2002).

Across all experiments, 159 females were tested in a total of 379 tests, resulting in 182 phonotactic choices. Females that were tested more than once were given a minimum of 5 min between tests. In this species, there is no evidence of carry-over effects for repeated testing (Kime, Rand, Kapfer, & Ryan, 1998), and memory of stimuli decays to null expectations in less than 120 s (Akre & Ryan, 2010). Females were never tested more than once in the same experiment.

Statistical Analysis

In each experiment, we designated one of the two alternative stimuli as "Alt-1" according to the specific hypothesis being tested. We then computed one of two response variables. For recognition tests (Experiments 1–3), we computed P(Alt-1) as the proportion of all subjects in a particular test that were scored as choosing Alt-1. We used Fisher's exact tests to analyze the results in terms of their observed and expected values of P(Alt-1). For discrimination tests (Experiments 4–5), we computed P(Alt-1|choice) as the proportion of subjects choosing Alt-1 out of only those subjects meeting our choice criterion. We analyzed the results of discrimination tests using binomial tests of the null hypothesis that a proportion of subjects equal to 0.5 would choose each alternative. All statistical tests were two-tailed and we used a significance criterion of $\alpha = .05$ for each test. Additional details are provided in subsequent sections.

Experiment 1

The specific goals of Experiment 1 were to establish estimates of phonotactic responsiveness to the W stimulus and the false alarm rate when no stimulus was presented. These estimates were used subsequently as expected outcomes in Experiments 2 and 3.

Method

We performed two separate tests in this experiment. In Test 1, we muted one speaker and broadcast the N stimulus by itself from the other speaker. Thus, this test effectively paired silence from one speaker (Alt-1) against the N stimulus broadcast from the other speaker. This procedure allowed us to empirically determine the false alarm rate corresponding to the expected proportion of subjects that would be scored as making a choice when, in fact, no stimulus was present. In Test 2, we broadcast the W stimulus (Alt-1) from one speaker and the N stimulus from the other speaker. This test allowed us to determine the proportions of subjects that respond and choose the W stimulus when it was paired against the behaviorally neutral N stimulus.

Results and Discussion

In Test 1 (silence vs. N), the majority of subjects (51 of 60, 85%) failed to meet our choice criterion. Of the nine subjects (15%) scored as making a choice, four were scored as choosing silence, and five were scored as choosing the N stimulus (see Table 1). Thus, P(Alt-1) = 0.07, indicating the false alarm rate using our experimental design is about 7%. Of the nine subjects scored as meeting our choice criterion, the proportions of subjects choosing silence versus the behaviorally neutral N stimulus did not differ from 0.5 (two-tailed binomial test: $p = 1.0$).

In Test 2, 43 of 64 subjects (67%) were scored as making a choice (W vs. N; Table 1). Of these 43 subjects, 42 chose Alt-1, so that P(Alt-1) = 0.66 (see Table 1). This response rate is similar to what we found when W was paired against another putative neutral stimulus—a temporally reversed W (choices for W: 7; choices for reversed W: 0; no choices: 6; Ryan, 1993). The proportion of subjects choosing the W stimulus in Test 2 was significantly greater than the expected false alarm rate based on results of Test 1 (see Table 1).

Experiment 1 confirmed earlier work showing that bursts of broadband noise (N) are behaviorally neutral (Test 1) and that the W stimulus is recognized as an attractive call (Test 2) (Rand et al., 1992; Ryan & Rand, 1993). Together, Tests 1 and 2 allowed us to derive the following expected outcomes for Experiments 2 and 3: (a) when paired against an N stimulus, a given WG or WGN

Table 1

Summary of Outcomes From the Recognition Tests of Experiments 1–3

| Experiment | Test | Alternative 1 | | | Alternative 2 | | | Scored Choice | | | P(Alt-1) | | | |
		Stimulus	Gap (ms)	Noise level	Stimulus	Gap (ms)	Noise level	Alt-1	Alt-2	Neither	Observed	Expected	p	n
1	1	Silence	—	—	N	—	—	4	5	51	.07	—	—	60
	2	W	—	—	N	—	—	42	1	21	.66	.07[a]	<.0001	64
2	3	WG	50–100	—	N	—	—	8	0	4	.67	.07[a]	<.0001	12
												.66[b]	1.00	
	4	WG	30–180	—	N	—	—	12	0	8	.60	.07[a]	<.0001	20
												.66[b]	.79	
	5	WG	30–300	—	N	—	—	4	3	13	.20	.07[a]	.21	20
												.66[b]	<.0001	
3	6	WGN	30–300	12 dB	N	—	—	7	4	9	.35	.66[b]	.02	20
												.20[c]	.48	
												.07[a]	.0004	

Note. Shown here are the number of subjects that were scored as choosing Alternative 1 (Alt-1) and Alternative 2 (Alt-2) and as not making a choice (Neither). Also shown are the proportions of subjects that chose Alt-1 out of the total number of subjects tested (P[Alt-1]). Statistical *p* values are from two-tailed Fisher's exact tests comparing observed and expected values. W = uninterrupted whine; WG = noise stimuli with silent gaps; WGN = silent gaps filled with noise; N = control noise.
[a] From the observed value in Test 1.   [b] From the observed value in Test 2.   [c] From the observed value in Test 5.

stimulus that was behaviorally neutral should elicit a response rate equivalent to the false alarm rate of P(Alt-1) = 0.07 (from Test 1, Table 1); (b) when paired against an N stimulus, a given WG or WGN stimulus perceived as being equivalent to a W stimulus should elicit an overall response rate of P(Alt-1) = 0.66 (from Test 2, Table 1).

Experiment 2

To investigate auditory induction, it was necessary to demonstrate that introducing silent gaps into W stimuli disrupted signal recognition. Earlier work by Wilczynski et al. (1995) found that replacing a segment of the whine with a silent gap can disrupt signal recognition and reduce phonotaxis response. However, we did not simply rely on using gap durations they determined to be effective because they used a slightly shorter W stimulus (314 ms) than the one used here (367 ms). Therefore, the goal of Experiment 2 was to derive an effective WG stimulus in which the silent gap was of sufficient duration to disrupt recognition of the 367-ms W stimulus as an attractive signal when paired against a behaviorally neutral N stimulus.

Method

In three separate tests, we broadcast the WG stimulus (Alt-1) from one speaker and the N stimulus from the other speaker. Across Tests 3–5, the duration of the gap was 50 ms, 150 ms, and 270 ms, respectively (see Table 1). The temporal gaps in these three WG stimuli (and the respective frequency ranges removed) occurred between 50 ms and 100 ms (789 Hz and 706 Hz), 30 ms and 180 ms (824 Hz and 624 Hz), and 30 ms and 300 ms (824 Hz and 543 Hz) of the normal 367-ms W stimulus (Table 1; Figure 2a–c). Our decision to test this set of WG stimuli was informed by preliminary studies exploring a larger parameter space and earlier work by Wilczynski et al. (1995) that tested an extensive set of gap positions using a shorter W stimulus. To create the WG stimuli, we introduced silence at the zero crossings closest to the designated gap boundaries (± 0.43 ms).

We made two predictions for each test based on expected outcomes determined in Experiment 1. First, if the WG stimulus was behaviorally neutral, then we expected a proportion of P(Alt-1) = 0.07 of subjects (i.e., the false alarm rate) to choose the WG stimulus, based on Test 1 in Experiment 1 (silence vs. N). Second, if the WG stimulus was recognized as the call of an appropriate mate, then we expected a proportion of P(Alt-1) = 0.66 of subjects to choose the WG stimulus, based on Test 2 in Experiment 1 (W vs. N).

Results and Discussion

A silent gap of 270 ms (Test 5) was required to render a WG stimulus behaviorally neutral. Silent gaps of 50 ms (Test 3) and 150 ms (Test 4) were ineffective at doing so. In Test 3 (50-ms gap between 50 and 100 ms), eight of 12 subjects responded, and of these, all eight chose the WG stimulus over the N stimulus [P(Alt-1) = 0.67; Table 1]. This proportion was significantly higher than the false alarm rate, but not significantly different from expected for a test of W versus N (see Table 1). When a 150-ms gap was located between 30 and 180 ms (Test 4), 12 of 20 subjects responded, and

all 12 chose the WG stimulus over the *N* stimulus [P(Alt-1) = 0.60; Table 1]. As in Test 3, this proportion was not significantly different from expected for a test of W versus N, but was significantly greater than the expected false alarm rate (see Table 1). In Test 5 (270-ms gap between 30 and 300 ms), four of 20 subjects responded to the WG stimulus [P(Alt-1) = 0.20)]. This proportion was significantly lower than expected for a test of W versus N, and not different from the false alarm rate (see Table 1). Together, these results suggest WG stimuli with gap durations of 50 ms (between 50 and 100 ms) and 150 ms (between 30 and 180 ms) were still recognized as calls equivalent in attractiveness to a W stimulus in a test of W versus N. This degree of permissiveness for missing or substituted portions of the advertisement signal is congruent with other studies in this species (Rand et al., 1992; Wilczynski et al., 1995). In contrast, inserting a silent gap of 270 ms duration (between 30 and 300 ms) rendered a WG stimulus behaviorally neutral.

Experiment 3

Experiment 3 was the first of three experiments designed explicitly to test for a continuity illusion. If túngara frogs experience a continuity illusion, then filling the silent gap in a WG stimulus with noise (i.e., a WGN stimulus) should restore the perception of a complete, attractive whine continuing through the noise-filled gap. Therefore, we predicted that in a recognition test, a W stimulus and a WGN stimulus would elicit phonotaxis from similar proportions of subjects when the alternative in each case was an N stimulus. If, on the other hand, they did not experience the illusion, then a WGN stimulus should be recognized as no more or less attractive than the equivalent WG stimulus lacking the gap-filling noise when each was paired against an N stimulus.

Method

In Test 6, we broadcast a WGN stimulus (Alt-1) from one speaker and the behaviorally neutral N stimulus from the other speaker. The WGN stimulus was based on the WG stimulus from Test 5 of Experiment 2, in which the gap was 270 ms in duration and was located between 30 and 300 ms of the 367-ms whine (Figure 2c). To create the WGN stimulus, we filled the silent gap in this WG stimulus with a 270-ms burst of broadband noise (1–10,000 Hz). The voltage of the noise was adjusted in software to have a RMS amplitude that was 12 dB greater than that of the continuous W stimulus used in Test 2. The proportions [P(Alt-1)] of subjects that chose that W stimulus and the WG stimulus in Tests 2 and 5, respectively, were used as the alternative outcomes expected for our two predictions in this test of WGN versus N. We additionally compared the proportions of subjects scored choosing the WGN stimulus to those that were scored as choosing silence in Test 1 (silence vs. N) to determine whether responses to the WGN stimulus differed from the expected false alarm rate.

Results and Discussion

Eleven of 20 subjects (55%) in Test 6 were scored as making a choice. Of these 11 subjects, seven were scored as choosing the WGN stimulus [P(Alt-1) = 0.35], significantly fewer than expected based on a test of W versus N (Test 2, Table 1), but not

significantly different from those expected based on a test of WG versus N (Test 5, Table 1). The proportion of subjects scored as responding to WGN [P(Alt-1) = 0.35] was significantly higher than the expected false alarm rate [P(Alt-1) = 0.07] determined in a test of silence versus N (Test 1, Table 1). However, out of the 11 subjects scored as making a choice, the proportions choosing the WGN stimulus (0.64) over the behaviorally neutral N stimulus (0.36) did not differ from the null expectation of 0.5 (two-tailed binomial test, p = .55).

Together, results from Test 6 indicate the following. There was no evidence that the noise inserted into the WG stimulus from Test 5 to create the WGN stimulus of Test 6 restored perception of a continuous whine. Had it done so, the proportions of subjects responding and choosing W and WGN over N in Tests 2 and 6, respectively, should have been similar. They were not. Moreover, the proportion choosing WGN in a test of WGN versus N (Test 6) was not different from the proportion choosing WG in a test of WG versus N (Test 5). This result is especially noteworthy, because in the latter test (WG vs. N), the noise hypothesized to create the illusion of continuity was completely absent. That is, whether the potential illusion-inducing noise was present or absent had no bearing on differences in the proportions of subjects choosing WGN or WG when each was paired against a behaviorally neutral alternative. Although the proportion of subjects scored as responding to the WGN stimulus exceeded the expected false alarm rate, there was no indication that more subjects were scored as choosing this stimulus than were scored as choosing the behaviorally neutral N stimulus. We interpret this overall pattern of results as failing to provide support for the hypothesis that noise filling a silent gap in the whine results in the illusory perception of a continuous whine. We performed Experiment 4 to determine whether this negative result could be corroborated in an independent series of discrimination tests.

Experiment 4

To assess whether the result from Experiment 3 was an artifact of using recognition tests, we paired the same Alt-1 stimuli used in Tests 2 (W), 5 (WG), and 6 (WGN) against each other in pairwise discrimination tests. We made the following predictions according to the hypothesis that túngara frogs experience the continuity illusion. First, we predicted both the W and WGN stimuli would be chosen in proportions exceeding 0.5 when paired against the WG stimulus. Second, we predicted that the W and WGN stimuli would be chosen over the WG stimulus in equal proportions. Finally, we predicted that the W and WGN stimuli would be chosen in equal proportions (0.5) when paired against each other.

Method

In Test 7, one speaker broadcast the W stimulus (Alt-1) from Test 2 and the other broadcast the WG stimulus from Test 5. This test, therefore, directly measured behavioral discrimination between a complete, continuous whine (W) versus an equivalent stimulus having a silent gap (WG) known to disrupt signal recognition. In Test 8, one speaker broadcast the WGN stimulus (Alt-1) used in Test 6 and the other speaker broadcast the WG stimulus used in Tests 5 and 7. If subjects perceived an illusory whine continuing through the noise in the WGN stimulus, then they were expected to discriminate against the WG stimulus in favor of the WGN stimulus. In Tests 9 and 10, one speaker broadcast the W stimulus (Alt-1) and the other broadcast the WGN stimulus. In Test 9, the level of the noise burst in the WGN stimulus was 12 dB greater than that of a calibrated W stimulus (as in Test 6 from Experiment 3); in Test 10, the level of the noise was reduced to 6 dB above a calibrated W stimulus. These two tests directly measured discrimination between a complete, continuous whine and a stimulus in which subjects were hypothesized to perceive an illusory, continuous whine. We tested two noise levels relative to the signal levels (6 and 12 dB) in an attempt to identify an optimal noise level—a key parameter for inducing the continuity illusion (Riecke, van Opstal, & Formisano, 2008).

Results and Discussion

When the W and WG stimulus were paired against each other in Test 7, all subjects responded and chose the W stimulus (see Table 1). The proportion of subjects choosing the W stimulus over the WG stimulus, P(Alt-1|choice) = 1.0, was significantly greater than 0.5 (see Table 2). This result is consistent with our first prediction and established that subjects behaviorally discriminated between the W and WG stimuli in favor of the complete, continuous whine

Table 2
Summary of Outcomes From the Discrimination Tests of Experiments 4 and 5

| Experiment | Test | Alternative 1 | | | Alternative 2 | | | Scored choice | | | P(Alt-1) | | | |
		Stimulus	Gap (ms)	Noise level	Stimulus	Gap (ms)	Noise level	Alt-1	Alt-2	Neither	Observed	Expected	p	n
4	7	W	—	—	WG	30–300	—	10	0	0	1.00	.50	.001	10
	8	WGN	30–300	12 dB	WG	30–300	—	1	1	12	.50	.50	1.00	14
	9	W	—	—	WGN	30–300	12 dB	9	1	1	.90	.50	.02	11
	10	W	—	—	WGN	30–300	6 dB	9	1	1	.90	.50	.02	11
5	11	W	—	—	WG	30–180	—	20	0	15	1.00	.50	<.0001	35
	12	WGN	30–180	6 dB	WG	—	—	12	8	34	.60	.50	.50	54
	13	W	—	—	WGN	30–180	6 dB	18	2	28	.90	.50	.0004	48

Note. Shown here are the number of subjects that were scored as choosing Alternative 1 (Alt-1) and Alternative 2 (Alt-2) and as not making a choice (Neither). Also shown are the proportions of subjects that chose Alt-1 out of the number of subjects scored as making a choice (P[Alt-1|Response]). Statistical p values are from two-tailed binomial tests of the null hypothesis of an expected response proportion of .50 in a two-alternative choice test. W = uninterrupted whine; WG = noise stimuli with silent gaps; WGN = silent gaps filled with noise.

over a whine having a silent gap. The outcome was quite different when we paired the WGN stimulus against the WG stimulus in Test 8. Of the 14 subjects in this test, 12 failed to meet our response criterion, one was scored as responding to the WGN stimulus, and one was scored as responding to the WG stimulus. The proportion of responsive subjects that chose the WGN stimulus over the WG stimulus [P(Alt-1|choice) = 0.50] did not differ significantly from the expected null proportion of 0.5 (see Table 2). This result directly contradicts our first prediction, namely that both the W and WGN stimuli would be chosen in proportions exceeding 0.5 when paired against the WG stimulus.

We also predicted that the W and WGN stimuli would be chosen over the WG stimulus in equal proportions. Our data provide mixed results for this prediction. The proportion of responsive subjects that chose the WGN stimulus over the WG stimulus in Test 8 [P(Alt-1|choice) = 0.50] did not differ significantly from expectations based on a choice between W versus WG in Test 7 (P[Alt-1|choice] = 1.0; two-tailed Fisher's exact test: p = .1667). At first, this result would appear consistent with our second prediction. We note, however, that this negative result actually stems from the low number of subjects that met our choice criterion in Test 8 (N = 2 of 14). If the same proportion (P[Alt-1|choice] = 0.50) of subjects had chosen the WGN stimulus over the WG stimulus in a test with a sample size that was five times larger (i.e., n = 10 of 70), such that the total numbers of subjects scored as making a choice were equal in Tests 7 and 8 (i.e., n = 10), then the outcomes of these two tests would have been significantly different (p = .0325). Moreover, we note that the proportion of all subjects [P(Alt-1)] responding and choosing the WGN stimulus over the WG stimulus in Test 8 (n = 2 of 14) was significantly lower than expected based on the results of Test 7 (W vs. WG), in which 10 of 10 subjects responded and chose the W stimulus (two-tailed Fisher's exact test; p < .0001). Based on these additional considerations, we believe the data are largely inconsistent with our second prediction.

Our final prediction was that the W and WGN stimuli would be chosen in equal proportions (0.5) when paired against each other. The data were inconsistent with this prediction. The outcomes of Tests 9 and 10 (W vs. WGN) were the same. Of the 11 subjects in each test, 10 were scored as making a choice, and of these, nine were scored as choosing the W stimulus (P[Alt-1|choice] = 0.90) and one was scored as choosing the WGN stimulus. The proportions of subjects choosing W over WGN in Tests 9 and 10 were significantly greater than the expected null of 0.50 (see Table 1). In addition, there were no significant differences in the proportions of subjects scored as responding to the W stimulus (9 of 11) between Tests 9 or 10 (W vs. WGN) and Test 7 (W vs. WG; two-tailed Fisher's exact test: p = .4761).

Results from the discrimination tests in this experiment corroborate those from the recognition tests of Experiment 3. Subjects strongly preferred the continuous whine in the W stimulus compared to the interrupted whine in the WG stimulus. There was little evidence to suggest that subjects heard an illusory whine during the WGN stimulus. This stimulus was generally less attractive than the W stimulus and no more attractive than the WG stimulus, which subjects strongly discriminated against. Taken together, these results fail to provide support for the hypothesis that túngara frogs experience a continuity illusion.

Lastly, we note that the 270-ms gap used in Experiment 4 (ca. 74% of the total signal duration), which was sufficiently long to interfere with recognition (Test 7), might have been prohibitively long to induce the continuity illusion. Although the continuity illusion has been demonstrated in human (Kashino, 2006; Riecke, Esposito, Bonte, & Formisano, 2009; Riecke et al., 2008) and nonhuman studies (Braaten & Leary, 1999; Miller et al., 2001; Seeba & Klump, 2009) employing gaps of similar absolute duration, these gaps rarely comprise such a large proportion of the stimulus. For this reason, we used a shorter gap duration in Experiment 5.

Experiment 5

The primary purpose of this experiment was, again, to test the general hypothesis that filling a gap in a whine induces the illusory perception of a continuous whine. To this end, we performed a second, independent series of discrimination tests using W, WG, and WGN stimuli to determine the extent to which the previous negative results generalize to stimuli with other spectro-temporal features. Because the continuity illusion may depend on the duration, relative power, and notch width of the interrupting noise (Riecke et al., 2008), we investigated the possibility that the findings from our previous experiments arose due to the specific properties of the gap and noise used.

The W stimulus was the same as that used in our other tests. However, the WG and WGN stimuli had different values for the gap duration and location, and the WGN stimulus had different features for the gap-filling noise. Our predictions were the same as the three predictions outlined above for Experiment 4: (a) both the W and WGN stimuli should be chosen in proportions exceeding 0.5 when paired against the WG stimulus, (b) the W and WGN stimuli should be chosen over the WG stimulus in equal proportions, and (c) the W and WGN stimuli should be chosen in equal proportions (0.5) when paired against each other.

Method

The design and logic of the three tests of this experiment follow exactly those outlined above for Experiment 4. In Test 11, one speaker broadcast the W stimulus (Alt-1) and the other broadcast the WG stimulus. In Test 12, one speaker broadcast the WGN stimulus (Alt-1) and the other speaker broadcast the WG stimulus. In Test 13, one speaker broadcast the W stimulus (Alt-1) and the other broadcast the WGN stimulus. We conducted each test until a sample of 20 subjects had been scored as choosing one of the two alternative stimuli. This was done to eliminate the need to interpret outcomes based on what might have happened had equal numbers of subjects made choices in all tests.

The WG stimulus was based on the W stimulus and had the segment between 30 and 180 ms removed to create a silent gap (Figure 2d). This 150-ms gap was shorter than the gap used in Experiments 3 and 4 (270 ms; 30 to 300 ms), and was equivalent to the gap used in the WG stimulus of Test 4 in Experiment 2. We used linear 5-ms onset/offset ramps to shape a 160-ms noise burst so that the steady-state portion of the noise was 150 ms and was centered in the 150-ms gap. Instead of using a broadband noise burst to fill the gap in the WGN stimulus, as in Experiments 3 and 4, the WGN stimulus in this experiment included a burst of

600-Hz-wide band-limited noise (passband: 400 to 1,000 Hz; Figure 2d). We generated five unique noise bursts to fill the silent gaps, and we elicited choices from an equal number of subjects ($n = 4$) using WGN stimuli created with each noise burst to reduce the possibility of a perceptually anomalous noise stimulus.

The acoustic features of the gap-filling noise in the WGN stimuli were selected based on a consideration of stimulus processing by the anuran peripheral auditory system. Frogs have two auditory end organs that transduce airborne sound frequencies, the amphibian papilla (AP) and the basilar papilla (BP) (Frishkopf, Capranica, & Goldstein, 1968). Multiunit recordings from the inferior colliculus in túngara frogs suggest that the AP is stimulated by sound containing frequencies between 100 and 1,100 Hz while the BP has a narrower frequency band of enhanced sensitivity centered at 2,100 Hz (Ryan, Fox, Wilczynski, & Rand, 1990). Therefore, by using band-limited noise restricted to the range of the AP for the WGN stimulus, instead of broadband noise, we aimed to selectively stimulate the AP, which is the main end auditory organ that processes whines (Wilczynski et al., 1995). By omitting BP-stimulating sounds that can enhance call attractiveness we restricted our investigation to recognition of the whine. Wilczynski et al. (1995) demonstrated that merely activating a high frequency (900–560 Hz) region followed by a low frequency (640–500 Hz) region of the AP is sufficient to elicit recognition. The silent and noise-filled gaps used in the present study met this sparse stimulation requirement.

We calibrated the W stimulus to 75 dB SPL (fast RMS, C-weighted) by placing the microphone of the SLM at the origin on the floor of the sound chamber. The remaining whine portions of the WG and WGN stimuli were calibrated in software to have the same peak-to-peak voltages as the equivalent portions of the W stimulus. The level of the band-limited noise was calibrated to 81 dB SPL (slow RMS, C-weighted) at the origin by broadcasting a 10-s noise with the same bandwidth. Hence, the overall level of the noise in the WGN stimulus was 6 dB greater than that of the signal.

Results and Discussion

In Test 11 (W vs. WG), 20 of 35 subjects (57%) were scored as responding, and of these, all 20 were scored as choosing the W stimulus. The proportion of subjects choosing the W over the WG stimulus, P(Alt-1|choice) = 1.0, was significantly greater than 0.5 (see Table 2). These results demonstrated that subjects discriminate behaviorally between a complete, continuous whine and a whine having a silent gap of 150 ms located between 30 and 180 ms. In Test 12 (WGN vs. WG), 20 of 54 subjects (37%) were scored as making a choice. Of these 20 subjects, 12 chose the WGN stimulus (P[Alt-1|choice] = 0.60) and eight chose the WG stimulus. The proportion of subjects choosing the WGN stimulus in this test did not differ significantly from the null expectation of 0.5 (see Table 2). In Test 13 (W vs. WGN), 20 of 48 subjects (42%) were scored as making a choice. Eighteen of these 20 subjects chose the W stimulus (P[Alt-1|choice] = 0.90) and two chose the WGN stimulus. The proportion of subjects choosing the W stimulus over the WGN stimulus was significantly higher than the null expectation of 0.50 (see Table 2).

The overall pattern of outcomes for Tests 11–13 in this experiment was identical to that observed in Tests 7–10 in Experiment 4. Subjects discriminated in favor of a complete, continuous whine

over a whine with a gap, but inserting noise in the gap did not result in the illusory perception of a complete whine. Subjects also strongly discriminated against whines with noise-filled gaps when these were paired against complete, continuous whines. Together, these data provide little support for the hypothesis that band-limited noise is able to restore perception of a complete, continuous whine when it fills silent gaps. Thus, despite reducing the gap duration, retaining the stimulatory portions of the whine stimulus and filling the gap with band-limited noise intended to selectively stimulate critical regions of the AP, our study was unable to render WGN stimuli as attractive to females.

General Discussion

Our results are generally inconsistent with the hypothesis that túngara frogs experience the illusion of auditory continuity. Although we found that continuous whines are attractive and that silent gaps render them unattractive, corroborating previous results with this species (Ryan, 1985; Wilczynski et al., 1995), we found no indication that the perception of continuity was restored when the gap was filled with noise: whines with noise-filled gaps were no more attractive than whines with silent gaps, and both of these stimuli were less attractive than a continuous whine. This pattern of results was generalizable over different testing paradigms (recognition tests vs. discrimination tests), different gap durations, and noises with different intensities and spectral content.

Our findings are thus consistent with those from studies of auditory induction in treefrogs, which also failed to find evidence for illusory continuity (Schwartz et al., 2011; Seeba et al., 2010). Seeba et al. (2010) hypothesized that the two species of gray treefrogs did not show evidence of induction because they communicate using signals composed of discrete, temporally separated pulses. However, given that we also found no evidence of the continuity illusion in túngara frogs—which have a simple call composed of a continuous, frequency-modulated sweep, similar to those used previously to investigate induction in humans and other animals (Ciocca & Bregman, 1987; Kluender & Jenison, 1992; Sugita, 1997)—these three studies suggest that anurans may indeed lack neural mechanisms that function to restore missing or masked acoustic elements of sounds. These combined results stand in stark contrast to those from previous studies of songbirds (*Sturnus vulgaris*; Braaten & Leary, 1999; Seeba & Klump, 2009), domestic cats (Sugita, 1997), Mongolian gerbils (Kobayasi, Usami, & Riquimaroux, 2012), rhesus macaques (Petkov et al., 2003), and cotton-top tamarins (Miller et al., 2001), which confirm that birds and mammals experience auditory induction. What methodological, neurophysiological, or functional explanations might account for this emerging pattern of taxonomic differences?

At a methodological level, research on frogs has investigated auditory induction by exploiting phonotaxis in response to communication signals (this study; Seeba et al., 2010; Schwartz et al., 2011). There is no a priori reason that using communication signals as stimuli and an animal's natural behaviors as a response should make it more difficult to detect auditory induction compared to using artificial stimuli and a conditioning procedure. Studies of phonemic restoration in humans use speech to investigate auditory induction (reviewed in Warren, 1999). Braaten and Leary (1999) and Seeba and Klump (2009) found robust auditory induction in starlings using songs. While humans and songbirds

exhibit vocal learning, this mode of acquiring communication is not required for auditory induction of vocalizations, as demonstrated by research on nonhuman primates. Cotton-top tamarins (Miller et al., 2001) and rhesus macaques (Petkov et al., 2003), neither of which are vocal learners, experience auditory induction using nonlearned, species-specific vocalizations. The study by Miller et al. (2001) is also notable because it demonstrated induction using the tamarin's natural antiphonal calling behavior as an unrewarded response. The study of cats by Sugita (1997) used operant conditioning of phonotaxis to demonstrate auditory induction. While all methods for studying auditory induction in animals have limitations (Petkov & Sutter, 2011), phonotaxis toward vocal communication signals seems unlikely to impose a bias against detecting the phenomenon.

At a neurophysiological level, current evidence suggests that cortical processing contributes substantially to auditory induction. Recent EEG and fMRI studies of humans confirm a role for auditory cortex in the perceptual restoration of obscured sounds (Heinrich, Carlyon, Davis, & Johnsrude, 2008, 2011; Micheyl et al., 2003; Riecke, van Opstal, Goebel, & Formisano, 2007; Riecke et al., 2009, 2012; Vinnik, Itskov, & Balaban, 2012). Single-unit recordings from the mammalian auditory cortex in cats (Sugita, 1997; but see Micheyl et al., 2003) and rhesus macaques (Petkov, O'Connor, & Sutter, 2007) have identified neural correlates of auditory induction, consistent with the purported contribution of cortical processing (see also Kubota, Miyamoto, Hosokawa, Sugimoto, & Horikawa, 2012). Recordings from the mammalian thalamus have produced limited evidence for such correlates (Schreiner, 1980). Cortical processing is also implicated in generating a coherent perception of partially occluded visual objects (Ban et al., 2013; Hegde, Fang, Murray, & Kersten, 2008; Kosai, El-Shamayleh, Fyall, & Pasupathy, 2014; Liu, Plomp, van Leeuwen, & Ioannides, 2006; Rauschenberger, Liu, Slotnick, & Yantis, 2006; Sugita, 1999). Hence, the existing body of evidence suggests that in mammals, active cortical processing is important for perceptual restoration in multiple sensory modalities.

Evolutionary homologs of mammalian auditory cortex, including the lamination and radial columnar structure considered essential to cortical processing, are present in birds (Dugas-Ford, Rowell, & Ragsdale, 2012; Jarvis et al., 2005; Wang, Brzozowska-Prechtl, & Karten, 2010). In their study of starlings, Seeba and Klump (2009) hypothesized that neural correlates of auditory induction might be found in the avian homolog of primary auditory cortex (field L), but were more likely to be found in secondary auditory areas, such as the caudo-medial mesopallium and the caudo-medial nidopallium. This hypothesis remains to be tested. At present, therefore, it remains an intriguing possibility that evolutionarily conserved and potentially ancient cortical mechanisms underlie auditory induction in birds and mammals.

In contrast to birds and mammals, frogs lack an auditory cortex (Wilczynski & Endepols, 2007). If auditory induction requires top-down inputs originating in cortex, then it is perhaps not surprising that frogs do not experience it. However, there is little a priori reason to believe top-down processing originating in the anuran forebrain, or at "subcortical" levels of the auditory system, could not bring about perceptual restoration in frogs (e.g., Ponnath & Farris, 2014). Studies of auditory

stream segregation (Nityananda & Bee, 2011; Schwartz & Gerhardt, 1995) and auditory grouping (Farris, Rand, & Ryan, 2002, 2005; Farris & Ryan, 2011; Bee, 2010) demonstrate that frogs are capable of perceptually analyzing complex acoustic scenes (reviewed in Bee, 2012, 2015). This perceptual analysis occurs in the absence of an auditory cortex. Decades of research on auditory processing in the frog mesencephalon and diencephalon have revealed key correlates of call recognition and sound perception (Hall, 1994; Gerhardt & Huber, 2002; Narins, Feng, Fay, & Popper, 2007). For example, neurons in the inferior colliculus exhibit complex patterns of spectro-temporal tuning that function as selective feature detectors of biologically important attributes of communication signals (Hall, 1994). Lesions to this brain region impair discriminative behavioral responses by females exhibiting phonotaxis (Endepols, Feng, Gerhardt, Schul, & Walkowiak, 2003). At present, too few studies have investigated the neural underpinning of auditory scene analysis in frogs (Feng & Schul, 2007) to understand why they might be generally capable of auditory streaming and grouping, but apparently not auditory induction.

At a functional level, one hypothesis for our negative results is that auditory induction is absent in anurans because there has been no selection favoring its evolution. Two complementary features of mate choice in anurans might contribute to a general lack of selection for auditory induction. First, behavioral adaptations in male signaling behavior, in particular the redundancy provided by frequent repetitions of highly stereotyped calls (Gerhardt & Huber, 2002; Wells, 2007), might mitigate some of the need to perceptually restore obstructed signals. If a male's call were obstructed in a chorus environment, a female túngara frog might need to listen for only 2–3 more seconds until he repeated himself (Ryan, 1985). Thus female frogs have multiple opportunities to evaluate the calls of a potential mate. Second, given the consequential nature of mate choice in frogs for which errors can result in a complete loss of evolutionary fitness, selection may favor, to the extent possible, "foolproof" mechanisms of call recognition. The evolutionary costs of choosing an inappropriate or poor quality mate in error are potentially high; such errors should be especially costly in nocturnal anurans because they often mate with only one male during a reproductive cycle and base that decision almost exclusively on the acoustic features of the male call (Wells, 2007). Given these costs, there may be little evolutionary advantage to being susceptible to an auditory illusion.

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