Lighting up sound preferences: cross-modal influences on the precedence effect in treefrogs

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Perception is frequently cross-modal, involving interactions among stimuli in multiple sensory modalities. Cross-modal integration of sensory stimuli is well established in humans and laboratory mammals, but the understanding of its mechanisms and evolution is limited by a lack of data from a broader taxonomic range in an ecological framework. Our aim in this study was to test whether the precedence effect, the bias in sound localization towards earlier arriving sounds, which is modulated by simultaneous visual stimulation in humans, is also susceptible to cross-modal effects of visual stimulation in two treefrog species, *Hyla versicolor* and *Hyla cinerea*. We used two-choice playback experiments to test whether female preferences for leading male advertisement call stimuli were enhanced or suppressed, respectively, by visual stimuli co-localized with leading or lagging call elements. In contrast to humans, strong female leader preferences were generally robust to cross-modal visual stimulation. We propose that divergence in both sensory systems and ecology has led to variation in the relative reliability of visual and acoustic cues of direction, which may explain the differences between humans and frogs. We argue that studies of cross-modal effects on sensory processing are an important tool for understanding the evolution of perceptual mechanisms.

Studying the diversity of sensory systems has significant implications for understanding biological diversity because sensory perception mediates key processes such as mate choice, habitat selection and predator—prey interactions and because the capabilities of sensory systems probably reflect the ecological and evolutionary factors that were important in diversification (Stevens, 2013). Comparative studies have provided much insight into the evolution of individual sensory systems, in particular hearing and vision (Cronin, Johnsen, Marshall, & Warrant, 2014; Dooling, Fay, & Popper, 2000; Fay & Popper, 1999; Hoy, Popper, & Fay, 1998). However, many relevant environmental stimuli have multiple properties that can be assessed by different sensory systems (Calvert, Spence, & Stein, 2004). It is increasingly clear that cross-modal interactions, the integration of stimuli from different modalities during sensory processing, have a significant role in perception (Shimojo & Shams, 2001). Cross-modal interactions are best known from psychophysical studies of humans and laboratory mammals (Calvert et al., 2004; Schroeder & Foxe, 2005) and include such phenomena as ventriloquism, an illusion in which sounds are perceived as originating from a spatially separated visual stimulus (Vroomen & Gelder, 2004), and the McGurk effect, in which the perception of spoken syllables is altered by the visual stimulus of lip movements uttering a different syllable (McGurk & Macdonald, 1976). However, knowledge of the extent and significance of cross-modal sensory integration in nonhuman animals in natural environments is limited, and there have been few attempts to identify the key ecological and evolutionary factors that determine variation in the influence of cross-modal interactions on animal sensation (Munoz & Blumstein, 2012; Partan, 2013; Ronald, Fernández-Juricic, & Lucas, 2012). Bringing the paradigms of psychophysical studies of cross-modal integration into an ecologically relevant framework is essential for generating comparative data to improve the understanding of the evolution of sensory system structure.

Studies of cross-modal integration in humans have demonstrated that the relative influence of stimuli from different modalities on the formation of a sensory percept depends on the reliability with which stimuli in each modality are perceived (Alais & Burr, 2004; Ernst & Banks, 2002). Reliability is defined as the

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variance associated with the estimate of the environmental property by the sensory system (Ernst & Banks, 2002). This finding provides a powerful framework from which predictions about the nature of cross-modal integration in animals can be made at multiple levels (Munoz & Blumstein, 2012). Within individuals, the relative reliability of information within each modality for a given sensory task may vary depending on local environmental conditions such as light or noise levels, leading to short-term adjustments to the weights given to stimuli in each modality in forming a sensory percept (e.g. Heuschele, Mannerla, Gienapp, & Candolin, 2009; Partan, Fulmer, Gounard, & Redmond, 2010). Across species, different ecological conditions and evolutionary histories lead to divergence in the capabilities of individual components of sensory systems (Endler, 1992), such that species that are highly specialized for performing a given sensory task in one modality may be less susceptible to cross-modal influences of stimuli in other, less reliably perceived modalities. Our aim in this study was to test whether the precedence effect, a cross-modal psychophysical phenomenon observed in human sound localization (Brown, Stecker, & Tollin, 2015), operates similarly in a distantly related taxon, treefrogs in the genus *Hyla*. The comparison between humans and frogs provides an excellent opportunity to test the hypothesis that variation in cross-modal integration is driven by variation in the relative reliability of stimulus perception in each sensory modality because both humans and frogs face similar challenges in localizing sounds (Bee, 2015), yet their sensory ecologies, and in particular the relative capabilities of their visual and acoustic systems, are highly divergent.

In the human precedence effect, two sounds presented in close succession from different spatial locations are perceived as originating from a single source in the direction of the first-arriving (leading) sound (Wallach, Newman, & Rosenzweig, 1949). The precedence effect facilitates sound localization in reverberant environments by reducing the influence of echoes on sound perception (Litovsky, Colburn, Yost, & Guzman, 1999). The human precedence effect is a classic example of sensory processing that was widely considered to operate exclusively in a single sensory modality, audition, but that has been recently demonstrated to be fundamentally cross-modal (Brown et al., 2015). Specifically, the precedence effect is enhanced when a visual stimulus (a flashing light-emitting diode; LED) is associated with leading sound sources, and weakened when a visual stimulus is associated with lagging sound sources, suggesting that information on the spatial location of visual cues is incorporated into the perception of sound location in humans (Bishop, London, & Miller, 2011). Sound localization in challenging acoustic environments is also important for animals to select mates, avoid predators and search for prey (Bee & Micheyl, 2008; Bradbury & Vehrencamp, 2011; Gerhardt & Huber, 2002). Across animal taxa, sound localization is commonly biased towards the direction of the leading of two temporally overlapping sounds, and in many cases this can be attributed to the precedence effect (Dent & Dooling, 2004; Greenfield, Tourtellot, & Snedden, 1997; Marshall & Gerhardt, 2010; Wyttenbach & Hoy, 1993). To our knowledge, no study has examined whether precedence effects in nonhuman animals are influenced by visual stimulation, and are therefore cross-modal, as they are in humans. On the one hand, the prevalence of multimodal signalling provides the appropriate sensory context for cross-modal localization (Hebets & Papaj, 2005; Higham & Hebets, 2013). On the other hand, the susceptibility of the precedence effect to cross-modal influences may depend on the environmental conditions in which signalling takes place and the architecture and capabilities of the sensory system.

We studied cross-modal influences on the precedence effect in two treefrog species, grey treefrogs, *Hyla versicolor*, and green treefrogs, *Hyla cinerea*. As in humans, sound localization is important for social behaviours in anuran amphibians; in particular, females both evaluate and localize mates largely on the basis of acoustic characteristics of male advertisement calls (Gerhardt & Bee, 2007; Gerhardt & Huber, 2002). Mate selection in many frog species takes place in choruses, large, dense aggregations of signalling males, in which the inevitable environmental degradation of sounds, combined with the potential for overlap and interference from the calls of multiple males signalling in close proximity, creates severe challenges for the localization of individual signallers (Schwartz & Bee, 2013). When two males' calls overlap in time, the precedence effect would provide a simple mechanism for females to focus on and localize one of the two males, and indeed females usually prefer leading (first-arriving) calls (Höbel & Gerhardt, 2007; Klump & Gerhardt, 1992). For instance, in *H. versicolor*, female phonotaxis was strongly biased towards a loudspeaker that broadcast synthetic advertisement call pulses that led those of a second loudspeaker by 2–18 ms (Marshall & Gerhardt, 2010). These results suggested that precedence effects are important in sound localization in *H. versicolor*. In *H. cinerea*, females prefer leading calls over a wide range of overlap levels (Höbel & Gerhardt, 2007; Klump & Gerhardt, 1992), which is also consistent with the operation of the precedence effect.

We studied cross-modal influences of visual stimuli on acoustic precedence effects in frogs in the context of the general hypothesis that the potential for cross-modal integration depends on the relative reliability of acoustic and visual cues for localization of mates. At first glance, there seems to be little scope for visual stimuli to influence the precedence effect because acoustic communication is the predominant signalling modality in most frog species, and most important social behaviours are performed at night, under poor visual conditions (Gerhardt & Huber, 2002). Furthermore, the precedence effect is a particularly robust phenomenon in frogs, overriding preferences for not only other acoustic signal characteristics used to discriminate between conspecific males (Höbel, 2010), but also signal characteristics that allow for discrimination between males of different species (Marshall, Schwartz, & Gerhardt, 2006). However, it is increasingly apparent that vision has important effects on mating behaviour in nocturnal anurans (Gomez et al., 2009; Hödl & Amézquita, 2001; Reichert, 2013; Sztatecsny, Strondl, Baierl, Ries, & Hödl, 2010), and in some cases visual cues can alter the expression of female preferences for male acoustic signal characteristics (Reichert & Höbel, 2015). Some frogs produce specific visual signals that complement, or even replace, acoustic advertisement calling (Grafe & Wanger, 2007; Preininger, Boeckle, Sztatecsny, & Hödl, 2013). In many other species, the inflation of the vocal sac is a conspicuous visual cue that coincides with sound production (Rosenthal, Rand, & Ryan, 2004; Starnberger, Preininger, & Hödl, 2014; Taylor, Klein, Stein, & Ryan, 2011); this visual information could be integrated with acoustic signal leadership preferences to form a cross-modal percept of the location of a calling male. These studies of multimodal signalling are important in demonstrating that suitable ecological conditions exist for the evolution of cross-modal integration. However, frogs are also responsive to a broader range of visual stimuli than those associated with calling males, including showing robust phototaxis to simple light stimuli under a variety of conditions (Jaeger & Hailman, 1973; Reichert, Galante, & Höbel, 2014). This is significant because it allows for experiments to replicate the psychophysical paradigms used in humans. Furthermore, the use of a visual stimulus such as light that is not actually used by the focal species as a mating signal reduces the likelihood of interpreting results as indicating cross-modal integration when in fact they were actually caused by enhancement effects in multimodal mate choice, in which case it is unknown whether an animal's altered

response to stimuli in multiple modalities is driven by either separate unimodal perceptions or a combined cross-modal perception (Partan & Marler, 1999). Thus, we tested for cross-modal influences on the anuran precedence effect by using a flashing LED as a visual stimulus (Bishop et al., 2011).

We tested the hypothesis that precedence effects on the localization of advertisement calls in two treefrog species, *H. versicolor* and *H. cinerea*, are influenced by cross-modal visual stimulation. Specifically, we used two-choice playback tests to determine whether female leader preferences were strengthened when a visual stimulus (flashing LED) was associated with the leading acoustic stimulus and weakened when a visual stimulus was associated with the lagging acoustic stimulus. We conducted two series of control trials to rule out alternative phenomena that could have produced these results. First, we investigated whether females were more likely to orient towards calls associated with a visual stimulus because the LED is inherently attractive. Previous studies demonstrated robust phototaxis in these species, and thus it was important for us to assess the effects of the visual stimulus in isolation (Jaeger & Hailman, 1973; Reichert et al., 2014). We used single-speaker playbacks to compare the relative attractiveness of unimodal acoustic and visual stimuli, and used two-choice playbacks to test whether the addition of an LED to one of the two playback speakers would induce a preference when no preference is expressed in acoustic-only trials. If the LED is an especially attractive stimulus, then any effects of visual stimuli on female leader preferences would probably be caused by a unimodal attraction to light rather than a cross-modal influence on the precedence effect. Importantly, if visual stimuli are highly attractive but do not actually alter female leader preferences, this would indicate that the precedence effect in frogs is highly robust to cross-modal influences. Second, we investigated whether females oriented to sounds associated with visual stimuli to test whether the LED captured the perception of the auditory event, as in the ventriloquist illusion (Vroomen & Gelder, 2004). If this were the case, any cross-modal effects on female leader preferences would be unrelated to the perception of signal timing and instead explained by the predominance of vision over sound in localization. We interpret our findings in the context of the potential ecological and evolutionary factors that generate diversity in sensory processing mechanisms.

METHODS

We performed tests with both species in May 2015, during the natural breeding season in the sampled populations. Female *H. versicolor* were collected from two ponds in Ozaukee County, Wisconsin, U.S.A. Females were captured in amplexus and then brought to our laboratory on the night of capture, where they were placed in melting ice to prevent oviposition. Prior to testing, females were acclimated by placing them in a darkened box until they reached the test temperature of 20 °C. Female *H. cinerea* were collected from ponds at the East Texas Conservation Center in Jasper County, Texas, U.S.A. Females were captured in amplexus, tested the same evening, and then released at the capture pond. Female *H. versicolor* were marked with a subcutaneous fluorescent tag to ensure individual identification and preventing multiple testing of the same individuals. Female *H. cinerea* were not marked, but the short duration of the study relative to the refractory period for female oviposition (G. Höbel, personal observation) and the large number of frogs at the study site made it highly unlikely that the same female was tested twice. This research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research and the current laws for animal care in the United States. Experimental procedures were approved by the University of Wisconsin-

Milwaukee Animal Care and Use Committee (ACUC protocol 13-14 #38).

Stimulus Generation

The acoustic stimuli were synthesized in R (Version 3.1.0) software (R Development Core Team., 2015), using the seewave package (Sueur, Aubin, & Simonis, 2008). Stimulus characteristics were chosen to replicate the average advertisement call of males in the study populations; the use of artificial call stimuli reduces the problems of pseudoreplication associated with the use of natural advertisement call recordings (McGregor et al., 1992). The synthetic call for *H. versicolor* (Fig. 1b, c) had the following characteristics: total duration = 900 ms, fundamental frequency = 1071 Hz with an amplitude of −10 dB relative to a second (dominant) frequency harmonic = 2142 Hz, number of pulses = 18, pulse duration = 25 ms (80% linear rise and 20% linear fall time), interpulse interval = 25 ms. The call was followed by 2.1 s of silence for a total call period of 3 s. The synthetic call for *H. cinerea* (Fig. 1a) had a duration of 150 ms, a rise time of 25 ms and a fall time of 50 ms. Each call was a continuous tone with three frequency bands of equal energy (900, 2700 and 3000 Hz). The call was followed by 650 ms of silence for a total
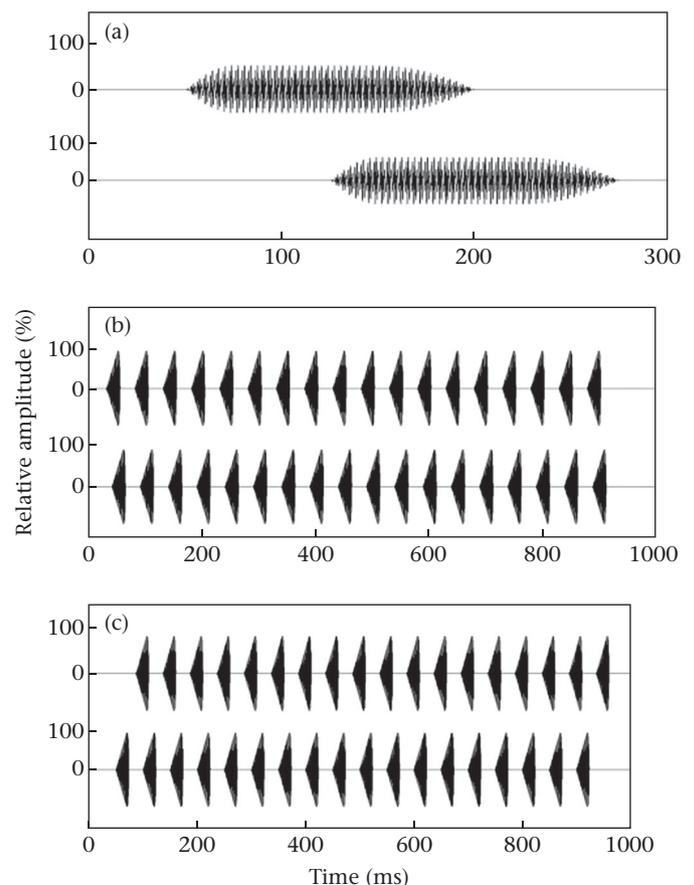
Figure 1. Waveform displays of advertisement call stimuli depicting call- and, for *H. versicolor*, pulse-timing relationships. Stimuli were generated as stereo files such that the call depicted on the upper channel was played from one speaker and the call depicted on the lower channel was played from the other speaker. (a) Overlapping *H. cinerea* advertisement calls. The leading call is depicted on the upper channel. (b) Overlapping *H. versicolor* advertisement calls in which the leading call (upper channel) also has leading pulses. (c) Overlapping *H. versicolor* advertisement calls in which the lagging call (upper channel) has leading pulses. Note that to illustrate the fine structure of the advertisement calls, we do not depict the entire duration of the silent interval (i.e. the total call period).

call period of 800 ms. For two-speaker choice tests, we used Audacity software (version 2.02, http://audacity.sourceforge.net/) to adjust the relative timing of the calls on each audio channel to generate the final stimulus files.

For both species, the visual stimulus was an LED with a wavelength of 470 nm. LEDs were used for consistency with human studies (Bishop et al., 2011), and the treefrog visual system is highly sensitive to 470 nm light (King, Douglass, Phillips, & Baube, 1993). The onset and offset of the LED was synchronized with that of one of the two acoustic stimuli. The LED was placed atop the speaker so that it was approximately co-localized with the source of sound. The speakers were hidden behind the screen of the test arena (see below), but the LED was inserted into a hole cut in the screen so that it was visible in the arena. The brightness of the LED was measured as 0.04 lx at the female's release point with an Extech EA31 light meter (Extech, Waltham, MA, U.S.A.).

Test Procedure

Females were placed in an acoustically transparent release cage in a circular arena at a distance of 1 m from each of the two playback speakers. We broadcast the test stimuli to females through two speakers (RadioShack Optimus XTS-40; RadioShack Corporation, Fort Worth, TX, U.S.A.) placed 90 degrees apart along the arena's edge, facing its centre. The speakers had a flat frequency response over the range of the playback stimuli. The female was held in the release cage for the first cycle of the selected test stimulus (i.e. for the duration of one call period); the release cage was then lifted and the female was allowed to move freely about the arena. A choice was defined as an approach to within 10 cm of one of the speakers; this area was designated the 'choice zone' and was demarcated by black tape placed on the floor of the arena. Trials in which females failed to make a choice within 5 min or crossed the choice zone incidentally while wandering along the arena's walls were considered as nonresponses. The amplitude of the acoustic playbacks was set to 85 dB SPL at the female's release point using a sound pressure level meter (Extech 407764; fast RMS, 'C' weighting). In *H. versicolor*, trials took place within a semi-anechoic chamber in the laboratory. Female movements were observed and recorded remotely using an infrared video camera (EQ150, EverFocus USA, Duarte, CA, U.S.A.) mounted above the arena. In *H. cinerea*, trials were conducted in an enclosed shed near the collection site and female movements were monitored visually with illumination provided by a dim red light mounted above the arena's centre. Background noise levels were not measured for the trials with *H. cinerea*, but we consider it unlikely that noise influenced our results because the test arena was in a shed that was distant from ponds with active choruses, and because trials were conducted after males stopped calling for the evening. Individual females' responses were measured to multiple stimuli, presented in random order, within the same test session (see below).

The primary measure of a female's response was whether or not she approached a given speaker. In *H. versicolor*, we also quantified the directedness of response towards the chosen speaker by measuring the female's approach angle from the video recordings. We defined the approach angle as the angle formed by the straight line between the chosen speaker and the female's release cage and the line between that speaker and the position of the female after her first movement to exit the release cage. We chose this position to measure angular orientation in order to estimate the female's perception of sound location under controlled signal timing conditions; in these closed-loop tests of sound localization (Klump, 1995), as females moved towards one speaker the sound from that speaker would arrive at the female sooner. Approach angles were measured from still images of video files using ImageJ

software (version 1.46K; National Institutes of Health, Bethesda, MD, U.S.A.). No video recordings were available for the measurement of approach angles in *H. cinerea*.

Test of Cross-modal Influences on the Precedence Effect

To test for cross-modal influences on the precedence effect we compared females' responses to leading advertisement call stimuli in unimodal (acoustic-only) trials, and in multimodal trials with an LED broadcast along with each repetition of either the leading or lagging stimulus. In *H. cinerea*, we used an overlapping call stimulus in which the leading call began 75 ms before the lagging call (Fig. 1a). In *H. versicolor*, we tested two different stimuli because call leadership is confounded with pulse leadership. Although a previous study showed no evidence for female preferences for call leadership in *H. versicolor* (Klump & Gerhardt, 1992), leading-call preferences are common in other anuran species (Höbel & Gerhardt, 2007), and we therefore controlled for call leadership to better isolate the effects of leading-pulse preferences. For the first stimulus, the call with leading pulses was also the leading call: the onset of the lagging call was delayed by 12.5 ms (i.e. 50% of pulse duration) relative to the leading call (Fig. 1b). For the second stimulus, the call with leading pulses was the lagging call: the onset of the call with leading pulses was delayed by 37.5 ms relative to the call with lagging pulses (Fig. 1c).

Control Experiment 1: Attractiveness of Visual Stimulus

We tested the inherent attractiveness of the LED by presenting females with the following one-choice tests: (1) the LED alone, (2) the advertisement call alone and (3) the advertisement call combined with the LED. We also performed a series of two-choice trials to test the hypothesis that if the LED is inherently attractive, then adding the LED to one of the two playback speakers would induce a preference when no preference had been expressed in acoustic-only trials. We compared females' responses to unimodal and multimodal variants of these stimuli: (1) perfectly synchronous calls from both speakers and (2) perfectly alternating calls (i.e. the call on speaker 1 was broadcast 180° out of phase with respect to the call on speaker 2; call period = 5 s for *H. versicolor* and 400 ms for *H. cinerea*).

Control Experiment 2: The Ventriloquist Effect

We tested for the ventriloquist effect by presenting females of both species with an advertisement call broadcast from one speaker and an LED broadcast simultaneously from the other speaker. The ventriloquist effect hypothesis predicts that females would approach the LED rather than the advertisement call in this test.

Statistical Analyses

In *H. cinerea*, 20 females were each tested with all of the stimuli, presented in random order. In *H. versicolor*, 20 females were tested with the precedence effect stimuli as well as the single-speaker stimuli of Control Experiment 1 and the stimulus in Control Experiment 2, presented in random order. Because a greater number of stimuli were required in *H. versicolor*, a separate sample of 53 females was used to test the two-speaker stimuli of Control Experiment 1. Each of these females was tested with both the unimodal and multimodal versions of the synchronous and alternating stimuli.

For all two-speaker stimuli, we used two-tailed binomial tests to determine whether females chose one of the alternatives more

often than the null expectation of equal stimulus attractiveness. To test the hypothesis that cross-modal stimulation altered female leadership preferences, we compared the proportion of females responding to the leading stimulus in the unimodal and corresponding multimodal conditions with generalized linear mixed models using JMP version 12 software (SAS Institute Inc., Cary, NC, U.S.A.) with the presence/absence of the LED as a factor and female identity as a random effect to control for multiple testing of individual females. For single-speaker tests, we present the proportion of females that responded to the stimulus along with females' response latencies, a measure of female motivation to approach the stimulus that is known to differ for responses to unimodal acoustic and visual stimuli (Bush, Gerhardt, & Schul, 2002; Reichert & Höbel, 2015). We compared approach angles between responses to unimodal and multimodal stimuli using Moore's test, a paired circular statistical test of equality of mean angles (Pewsey, Neuhäuser, & Ruxton, 2013). For comparisons of angles involving independent groups of females, we used the Watson–Wheeler test, a nonparametric test of angular homogeneity. Circular statistics were implemented in the package circular (Agostinelli & Lund, 2013) in R version 3.2.1 software. All statistical tests were two-tailed and performed at $\alpha = 0.05$.

RESULTS

Visual Influences on the Precedence Effect

Female *H. cinerea* had strong and statistically significant preferences for leading advertisement calls in the unimodal trial (Fig. 2). Adding an LED to the leading call had no effect on leader
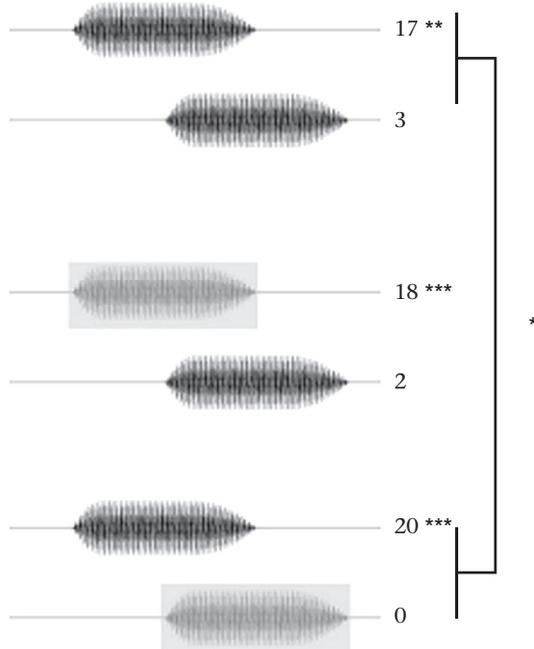
Figure 2. Results of unimodal and multimodal tests for leading call preferences in *H. cinerea*. Female leader preferences were tested for unimodal stimuli (no accompanying visual stimulus; top row), and multimodal stimuli with an LED appended to either the leading (middle row) or lagging (bottom row) call. The timing relationship between the stimuli is illustrated by the waveform displays. The grey shading indicates that the LED was associated with that call. Next to each pair of stimuli are the numbers of females that chose each stimulus; asterisks denote the statistical significance of binomial tests of the null hypothesis of randomly allocated responses. Bars connecting pairs of stimuli and associated asterisks denote the statistical significance of generalized linear mixed models comparing responses to the two stimuli. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

preferences (generalized linear mixed model: $\chi^2_1 = 0.23$, $P = 0.63$; Fig. 2). There was, however, a significant effect of adding the LED to the lagging call, with all 20 females responding to the leading call ($\chi^2_1 = 4.40$, $P = 0.04$; Fig. 2). This outcome does not support the hypothesis that LEDs suppressed the precedence effect because female leader preferences were even stronger in the multimodal than in the unimodal condition.

In *H. versicolor*, females had strong preferences for calls with leading pulses in unimodal trials (Fig. 3a, c). There was no effect of call leadership on preferences for pulse leadership ($\chi^2_1 = 1.41$, $P = 0.23$; Fig. 3a, c). When the LED was paired with the leading-pulse call, females selected this call unanimously, both when the leading-pulse call was also the leading call (Fig. 3a) and when the leading-pulse call was the lagging call ($\chi^2_1 = 1.41$, $P = 0.23$; Fig. 3c). The approach angles for multimodal stimuli with the LED on the leading-pulse call did not differ from the angles for the acoustic-only stimuli (Moore's test: leading call, leading pulse: $R = 0.76$, $P = 0.20$; lagging call, leading pulse: $R = 0.43$, $P = 0.61$; Fig. 3b, d). When the LED was paired with the lagging-pulse call, females had a nearly unanimous preference for the leading-pulse call when it was also the leading call ($\chi^2_1 = 1.41$, $P = 0.23$; Fig. 3a), and there was no difference between approach angles to the multimodal and unimodal stimuli ($R = 0.85$, $P = 0.14$; Fig. 3b). However, when the LED was paired with a lagging-pulse call that was also the leading call, females still responded more often to the leading-pulse call, but their preference for this call in multimodal trials was significantly reduced compared to the unimodal trials ($\chi^2_1 = 4.72$, $P = 0.03$; Fig. 3c). Furthermore, for this stimulus approach angles were oriented more accurately towards the leading-pulse speaker in the acoustic-only trial than in the multimodal trial, although this difference was not statistically significant ($R = 1.0$, $P = 0.06$; Fig. 3d).

Attractiveness of Visual Stimuli

Females of both *H. versicolor* and *H. cinerea* always responded to single-speaker presentations of both conspecific advertisement calls and the conspecific advertisement call with a concurrent LED flash. Female *H. versicolor* also usually responded to the presentation of the LED without an accompanying acoustic stimulus ($N = 16/20$ females), although they approached this more slowly than they did advertisement calls (mean $\pm$ SE latency; call alone: 39.5 ± 5.7 s; LED alone: 138.3 ± 18.3 s; call plus LED: 34.6 ± 3.5 s; $\chi^2_2 = 44.1$, $P < 0.001$). Mean approach angles did not differ for responses to the LED alone compared to the advertisement call alone ($R = 1.03$, $P = 0.06$; Fig. 4a), or for the LED alone compared to the advertisement call plus LED ($R = 0.75$, $P = 0.22$; Fig. 4a). However, there was a significant difference in approach angles between responses to the call alone and to the call plus LED, with females moving more directly towards the speaker in response to the latter stimulus ($R = 1.61$, $P < 0.001$; Fig. 4a). Only three of 20 female *H. cinerea* approached the LED without an accompanying acoustic stimulus. Those females that responded to the LED approached this stimulus more slowly than they approached stimuli including an advertisement call (mean $\pm$ SE latency; call alone: 53.45 ± 8.0 s; LED alone: 165.0 ± 30.0 s; call plus LED: 52.7 ± 7.7 s; $\chi^2_2 = 33.1$, $P < 0.001$).

Females of neither species had a speaker bias in two-choice audio playbacks of synchronous or alternating advertisement calls (binomial tests: all $P > 0.2$). In *H. cinerea*, adding an LED did not induce a preference for one of the synchronous or alternating calls: females chose equally the call with and without the LED (Fig. 5a). In *H. versicolor*, however, females significantly preferred the call with the LED for both synchronous and alternating stimuli (Fig. 5b). For both control stimuli in *H. versicolor*, approach angles were not
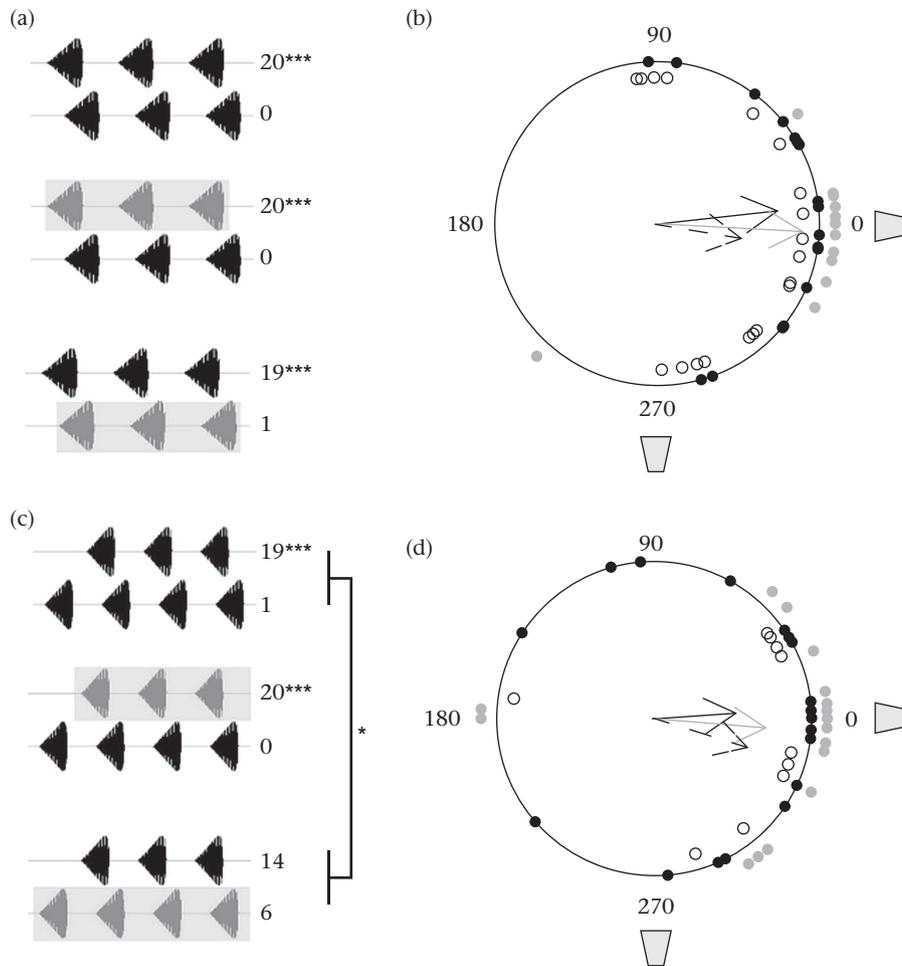
Figure 3. Results of unimodal and multimodal tests for leading pulse preferences in *H. versicolor*. (a) Female preferences for stimuli in which the call with leading pulses was also the leading call. Numbers, asterisks and shading as in Fig. 2. (b) Approach angles for choices made for the stimuli depicted in (a): unimodal trials (black arrow, solid black points), and multimodal trials in which the LED was on the leading-pulse call (grey arrow, solid grey points) or on the lagging-pulse call (dotted arrow, open points). Orientation of arrow represents direction of the mean vector; length of the arrow is rho, a measure of dispersion. Longer arrows indicate more concentrated data points. The point at which the arrows originate is the female release point in the arena. Only choices to the leading-pulse stimulus, located at 0°, are depicted. The location of the lagging-pulse stimulus is depicted at 270°. Note that in practice we alternated the speaker positions; this does not affect angle measurements, which were calculated relative to the two speaker positions. (c) Female preferences for stimuli in which the call with leading pulses was the lagging call. Only the beginning of each call is depicted in (a) and (c). (d) Approach angles for choices made to the leading-pulse stimulus for the stimuli depicted in (c): unimodal trials (black arrow, solid black points), and multimodal trials in which the LED was on the leading-pulse call (grey arrow, solid grey points) or on the lagging-pulse call (dotted arrow, open points).

significantly different for approaches to the speaker in the unimodal trial compared to approaches to either the speaker with or without the LED in the multimodal trial (synchronous, chose LED: $R = 0.04$, $P = 1.0$; synchronous, did not choose LED: $R = 0.68$, $P = 0.28$; Fig. 5c; alternating, chose LED: $R = 0.85$, $P = 0.13$; alternating, did not choose LED: $R = 0.88$, $P = 0.14$; Fig. 5d). However, females that chose the speaker with the LED had a more directed response to the chosen speaker than did females that chose the speaker without the LED (Watson–Wheeler tests, synchronous: $W = 12.1$, $P = 0.002$; Fig. 5c; alternating: $W = 8.3$, $P = 0.015$; Fig. 5d).

The Ventriloquist Effect

In both species, 19 of 20 females chose the speaker broadcasting a male advertisement call over a spatially separated LED (binomial test: $P < 0.001$). An examination of approach angles showed that female orientation in *H. versicolor* was actually directed away from the LED on average (Fig. 4b). Thus we found no evidence for visual capture of audition under our experimental set-up.

DISCUSSION

In both *H. versicolor* and *H. cinerea*, strong leader preferences that are probably attributable to the precedence effect were largely robust to cross-modal influences of visual stimuli. In *H. cinerea*, the LED was generally unattractive and simply may not have been salient for female sound localization. In *H. versicolor*, however, given our finding that the LED was highly attractive when presented without an acoustic stimulus and that visual stimuli have strong effects on the attractiveness of other acoustic signal characteristics (Reichert & Höbel, 2015), the robustness of the precedence effect to the influence of visual stimulation was surprising. Nearly all of our tests, including analyses of both individual choices and approach angles, showed no cross-modal influences on the precedence effect in *H. versicolor*. There was an effect of adding an LED to a leading call with lagging pulses on *H. versicolor* pulse leadership preferences, but even here the preference was only weakened, not reversed. This species thus presents a clear contrast with humans, in which there were strong cross-modal influences on the precedence effect in a similar task (Bishop et al., 2011). In
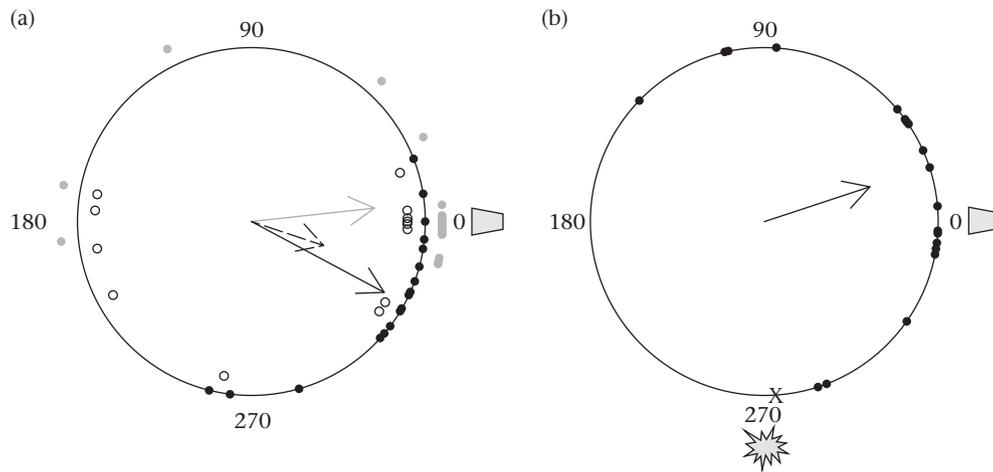
Figure 4. Approach angles of female *H. versicolor* to (a) the single-speaker stimuli of Control Experiment 1 and (b) the call versus LED stimulus of Control Experiment 2. Arrow orientation and length as in Fig. 3. In (a) approach angles are shown to the unimodal advertisement call (black arrow, solid black points), the unimodal LED (dotted arrow, open points) and the multimodal call plus LED stimulus (grey arrow, solid grey points). The stimuli were located at 0°. In (b), the advertisement call was broadcast from a speaker located at 0°. The location of the LED is depicted at 270°. The arrow corresponds to females that chose the advertisement call stimulus; the single instance of a female choosing the LED is depicted with an X.
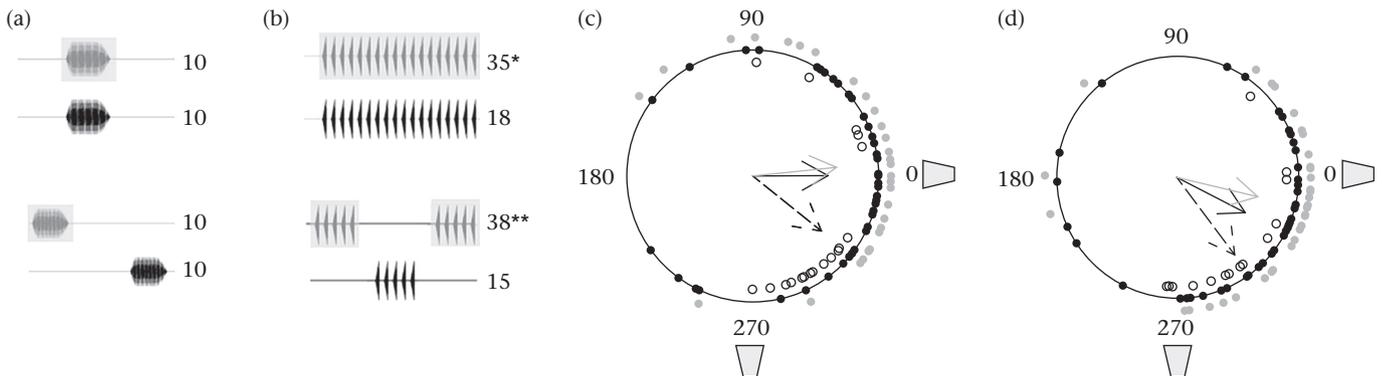
Figure 5. Results of tests for female preferences for synchronous (top row) and alternating (bottom row) advertisement calls in (a) *H. cinerea* and (b) *H. versicolor*. The alternating calls in (b) are truncated for illustration purposes. Numbers, asterisks and shading as in Fig. 2. In (c) and (d), approach angles are shown for responses of female *H. versicolor* to synchronous and alternating advertisement calls, respectively. Angles measured with respect to the chosen speaker, located at 0° (alternative speaker located at 270°) for unimodal (black arrow, solid black points), and multimodal trials in which the female chose the speaker with the LED (grey arrow, solid grey points) or the speaker without the LED (dotted arrow, open points). Arrow orientation and length as in Fig. 3.

treefrogs, the processing of directional cues for sound source localization is apparently at most only weakly cross-modal and instead takes place largely in isolation in the acoustic modality. This implies that the sensory processing architecture responsible for the precedence effect might be divergent in humans and frogs.

Cross-modal integration may be weaker in frogs than humans because of frogs' sensory ecology. In humans, the reliability of cues in each modality often determines their relative influence on the perception of a multimodal stimulus (Alais & Burr, 2004; Ernst & Banks, 2002). Therefore, one explanation for our finding that acoustic stimuli dominated the localization process in frogs is that visual stimuli do not provide reliable directional cues. Indeed, nocturnal anurans localize mates under dim light conditions, which impose a trade-off between visual sensitivity and spatial resolution (Warrant, 2004). Anurans are highly sensitive to small quantities of light (Jaeger & Hailman, 1973), which suggests that they have balanced this trade-off in favour of visual sensitivity, although to our knowledge the visual spatial resolution abilities of nocturnal anurans have not been measured. Anurans with better visual spatial resolution capabilities, such as is likely to be the case in diurnal species, may be more likely than nocturnal anurans to show cross-modal integration of acoustic and visual cues. To our knowledge, this has only been studied in one species, the diurnal dart-poison frog, *Epipedobates femoralis*, in which localization of spatially separated visual and acoustic cues was dominated by a visual stimulus when stimuli were separated by 12 cm or less and by an acoustic stimulus when stimuli were separated by 25 cm or more (Narins, Grabul, Soma, Gaucher, & Hödl, 2005). We encourage further study of the hypothesis that the reliability of perception in a given modality and the dominance of that modality in a sensory task are linked because it may be a powerful general explanation of variation in cross-modal integration between species.

Two additional results from our study are also consistent with the hypothesis that the influence of visual stimuli is related to the relative reliability of sound and vision as location cues, but in this case the effect operates within species in response to changes in the context of the sensory task. First, the localization of a single advertisement call, as in our control trials, is a very simple task that the acoustic system would be expected to handle reliably, and there was no effect of the addition of a co-localized visual stimulus in this case. Our test for the ventriloquist effect also involved the

broadcast of a single acoustic stimulus, this time with a spatially separated visual stimulus. Once again, in this test we found no evidence for an effect of the visual stimulus. Female túngara frogs, *Engystomops pustulosus*, also preferentially localized acoustic stimuli over the spatially separated visual stimulus of a robotic frog with an inflatable vocal sac (Taylor et al., 2011). Second, and in contrast, in the control trials with synchronous or alternating advertisement calls, sound localization may have been difficult because there were no differential timing cues. Visual cues influenced female approach angles to these stimuli in *H. versicolor*. Females oriented more accurately when approaching the LED speaker than when approaching the speaker without an LED, suggesting that either the LED improved localization in the former case or impaired localization in the latter case. If the LED indeed had improved localization, this suggests that when the acoustic stimuli for localization are less reliable, visual stimuli are weighted more heavily in the localization process.

Hyla cinerea females were not attracted to LEDs in isolation and LEDs did not induce a female preference for otherwise neutral synchronous or alternating calls. This finding was surprising given previous demonstrations of robust phototaxis in *H. cinerea* (Jaeger & Hailman, 1973). In contrast, the LED was clearly an attractive stimulus for *H. versicolor*. Females responded readily to LEDs when these were presented with no accompanying acoustic stimuli, and LEDs biased female responses to synchronous or alternating calls. It is not clear why the two species differed in their response to LEDs. Neither species showed evidence of cross-modal modulation of the precedence effect, and our findings from *H. versicolor* are particularly compelling because strong leader preferences were maintained despite the attractiveness of the visual stimulus. One important consideration is that we used an LED, rather than a naturally occurring visual stimulus, in order to use a comparable design to psychophysical studies in humans (Bishop et al., 2011). It is possible that different results may have been obtained if we had used other types of visual stimuli that incorporate different types of visual stimulation (e.g. movement) or that simulate natural environmental stimuli such as the vocal sac of a calling male (e.g. Rosenthal et al., 2004; Taylor et al., 2011), and this should be investigated in future studies.

Comparing the effects of visual stimuli on the acoustic precedence effect in frogs and humans also gives some insights into divergence in the neural architecture of sensory systems in these distantly related taxa. Tympanal hearing evolved independently in anurans and mammals, although some form of sensitivity to airborne sounds may have a common evolutionary origin in tetrapods (Christensen-Dalsgaard & Carr, 2008). Anuran tympana are internally coupled and act as pressure difference receivers with an inherent directionality, while mammalian tympana are uncoupled and most processing of binaural directional cues takes place in the central nervous system (Christensen-Dalsgaard, 2005). Although much remains to be understood about the processing of directional cues in both taxa, the increased displacement of directional processing towards the central nervous system in mammals may result in increased interaction between acoustic and visual stimulus processing centres, and thus the cross-modal influences on the precedence effect observed in humans (Bishop, London, & Miller, 2012; Rohe & Noppeney, 2016).

Conclusions

Preferences for acoustic signals associated with the precedence effect were generally not modified by visual stimuli in two treefrog species. This is one of the first investigations of cross-modal influences on the precedence effect in nonhuman animals. The comparative study of both precedence effects and cross-modal

integration remains in its infancy, in part because many of the experimental paradigms for human studies require reporting of perceptual phenomena by observers, and obtaining similar data from animals is difficult without extensive conditioning (Brown et al., 2015; Gerhardt, 1995). We argue that tests of cross-modal integration are an important alternative approach because they rely on simple stimulus manipulations that can be readily applied across taxa, and that may drastically alter the expression of response behaviours. We have proposed hypotheses to explain the differences between frogs and humans based on both the functional significance of visual stimuli in the environment and the structure of the auditory system. We encourage researchers to apply this experimental paradigm to other taxa, which will enhance our knowledge of not only the evolutionary factors that have led to diversity in sensory processing mechanisms, but also the comparative understanding of human and animal hearing.

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