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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