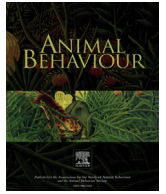




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Interactions between complex multisensory signal components result in unexpected mate choice responses

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Multimodal (multisensory) signalling is common in many species and often facilitates communication. How receivers integrate individual signal components of multisensory displays, especially with regard to variance in signal complexity, has received relatively little attention. In nature, male túngara frogs, *Physalaemus pustulosus*, produce multisensory courtship signals by vocalizing and presenting their inflating and deflating vocal sac as a visual cue. Males can produce a simple call (whine only) or a complex call (whine + one or more chucks). In a series of two-choice experiments, we tested female preferences for variation in acoustic call complexity and amplitude (unimodal signals). We then tested preferences for the same calls when a dynamic robotic frog was added to one call, generating a multimodal stimulus. Females preferred a complex call to a simple call; when both calls contained at least one chuck, additional numbers of chucks did not further increase attractiveness. When calls contained zero or one chuck, the visual stimulus of the robofrog increased call attractiveness. When calls contained multiple chucks, however, the visual component failed to enhance call attractiveness. Females also preferred higher amplitude calls and the addition of the visual component to a lower amplitude call did not alter this preference. At relatively small amplitude differences, however, the visual signal increased overall discrimination between the calls. These results indicate that the visual signal component does not provide simple enhancement of call attractiveness. Instead, females integrate multisensory components in a nonlinear fashion. The resulting perception and behavioural response to complex signals probably evolved in response to animals that communicate in noisy environments.

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Communication in both human and nonhuman animals typically incorporates multiple sensory systems (e.g. visual plus acoustic) that may facilitate signal transmission and reception (Hebets & Papaj, 2005; McGurk & MacDonald, 1976; Narins, Hödl, & Grabul, 2003; Partan & Marler, 1999; Uetz, Roberts, Clark, Gibson, & Gordon, 2013). These multisensory (multimodal) signals are thought to improve detection, discrimination or memorability of the signals by receivers and are widespread in diverse taxa (for review see Hebets & Papaj, 2005; Partan & Marler, 2005; Rowe, 1999). For example, bird signals may consist of conspicuous plumage plus vocalizations (Patricelli & Krakauer, 2010), frogs produce acoustic and visual displays (Preininger, Boeckle, Freudmann, et al., 2013), spiders produce both visual and seismic

displays (Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013), and some fish combine conspicuous visual courtship displays with acoustic signals (Maruska, Ung, & Fernald, 2012).

How signals are detected and perceived by receivers (typically females) is important because this influences mate choice and dictates which males in a population gain matings. Recent studies have demonstrated substantial variation in how females evaluate individual signal components within complex courtship displays. For example, females may evaluate individual components of complex courtship signals in different contexts, at different temporal or spatial scales (Uy & Safra, 2013), and may vary their attention towards different signal components (Hebets et al., 2013); furthermore, interaction among signal components may generate unexpected patterns of mate preference (Hebets & Papaj, 2005; Taylor & Ryan, 2013).

Frogs are an excellent model system to investigate multimodal communication. They use acoustic signals during reproduction to

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convey information about reproductive state and territorial boundaries. Their stereotyped acoustic advertisements are easily synthesized, females respond readily to synthetic signals (Gerhardt & Huber, 2002; Ryan, 2001), and there is considerable information about the mechanisms that underlie signal production (Ryan & Guerra, 2014; Zornik & Kelley, 2011) and perception (Bee, 2015; Wilczynski & Ryan, 2010). In addition, a variety of species incorporate visual cues into their reproductive displays and these visual cues can be reproduced in playback experiments (Starnberger, Preininger, & Hödl, 2014; Taylor, Klein, Stein, & Ryan, 2008).

The túngara frog, *Physalaemus pustulosus*, has been extensively studied in the context of sexual selection and communication (Ryan, 1985; 2011). It is a small (ca. 30 mm), brown frog, common in Panama and throughout much of Middle America. The animals reproduce at night during the wet season from May to November. Males congregate in small ponds or puddles and vocalize. The male's vocalizations can be a simple call consisting of a whine (W) only, or they can include up to seven additional notes called chucks (C), to the whine, creating a complex call (see Fig. 1). Complex calls are five times more attractive than simple calls (Gridi-Papp, Rand, & Ryan, 2006). The vocalizations are accompanied by a conspicuous and synchronous inflation of an elastic vocal sac, and females are known to assess both the vocalization and movement of the vocal sac (Taylor, Klein, & Ryan, 2011; Taylor et al., 2008; Fig. 1). The vocal sac typically reaches close to its maximum volume approximately 250 ms after the onset of the whine (typical call is 350 ms). The vocal sac volume increases a small additional amount when chucks are produced. After assessing potential mates, females will approach a male; he then clasps her in amplexus. When the female begins to oviposit her eggs, the pair builds a foam nest and deposits the eggs in the nest (Ryan, 1985).

The call (acoustic modality) is the dominant feature of this signalling system, as it is for most frog species (Gerhardt & Huber, 2002; Kelley, 2004; Ryan, 2001). In several species the visual stimulus of the vocal sac inflation–deflation also serves as a cue or a signal component (Narins et al., 2003; Starnberger et al., 2014; Taylor, Buchanan, & Doherty, 2007). Female túngara frogs prefer a call that is accompanied by a vocal sac inflating synchronously with the call, but strongly reject a call that is accompanied by an asynchronously inflating vocal sac (Taylor et al., 2008; Taylor, Klein, Stein, et al., 2011). In dense choruses, significant call overlap occurs among male calls and generates discrimination challenges for female receivers (Bee & Micheyl, 2008; Gerhardt & Huber, 2002; Ryan, 2001; Schwartz, Buchanan, & Gerhardt, 2001; Vélez, Schwartz, & Bee, 2013). Frogs have evolved auditory mechanisms to improve discrimination in these noisy conditions. For example,

directional hearing allows females to identify callers when they are spatially separated and some species appear to rely on 'dip listening,' that is, identifying callers during periodic, brief windows when the background chorus noise subsides (Nityananda & Bee, 2012; Vélez & Bee, 2011). The addition of a visual component probably further improves detection and discrimination (Preininger, Boeckle, Freudmann, et al., 2013; Preininger, Boeckle, Sztatecsny, & Hödl, 2013; Starnberger et al., 2014; Taylor, Klein, Stein, et al., 2011).

Although studies of multimodal signalling are common, very little is still known about how signal components interact to influence receiver responses (Higham & Hebets, 2013; Partan, 2013). In this study, we were interested in better understanding audio-visual integration. Although superficially it appears to be simple, assigning sounds to their sources is not always an easy task, especially for animals such as frogs that communicate vocally in noisy environments. One mechanism for assigning sounds to their source is to integrate the timing of the sound with an associated visual cue. This audiovisual integration has been well studied in humans, cats, macaques and barn owls (Knudsen & Knudsen, 1989; Stein, 2012; Stein & Meredith, 1993), but very little is known about audiovisual integration outside of relatively large-brained vertebrates. In túngara frogs, preference for call variation is distance, and thus amplitude, dependent (Akre & Ryan, 2010). At farther assessment distances (e.g. >50 cm) the addition of more chucks to a whine does not make the call more attractive; that is, two chucks or three chucks are no more attractive than one. At higher amplitudes, such as those that females experience at close listening distances, more chucks do increase call attractiveness (Akre & Ryan, 2010). All else being equal, higher amplitude calls are also more attractive (Ryan & Keddy-Hector, 1992), but it is unknown how variance in amplitude or chuck number influences female choice in a multimodal context. Although it is often not explicitly stated, studies of multimodal signalling often treat each signal modality as if they are cognitively independent. For example, researchers often study signal components as independent entities that influence behaviour (sensu Partan & Marler, 1999). We should note, however, that Partan and Marler (1999) did not assume that signals are always cognitively independent. Regardless, behavioural and/or neuroanatomical data in humans (Gerdes, Wieser, & Alpers, 2014; Ghazanfar & Schroeder, 2006; McGurk & MacDonald, 1976; Shore & Dehmel, 2012), birds (Patricelli, Uy, Walsh, & Borgia, 2002) and cats (Stein & Meredith, 1993) provide strong evidence that the senses are truly integrated, such that the perception of one component influences perception of another (Stein, 2012). In light of this, we examined how different levels of audio signal complexity interact with a visual component to influence female choice. Specifically, we asked: (1) how do different numbers of chucks (call complexity) influence female mate choice decisions at relatively low playback amplitudes? (2) how do different amplitudes of the same call influence female choice? and (3) how does the addition of a visual component alter the relative value of these same acoustic signals?

METHODS

Test Arena

We performed all experiments at the Smithsonian Tropical Research Institute (STRI) in Gamboa, Republic of Panama. We collected mated pairs of túngara frogs at choruses between 1930 and 2100 hours. After collection, we placed pairs in a light-safe cooler in the laboratory in total darkness for a minimum of 1 h prior to testing to ensure that the female's eyes were dark-adapted.



Figure 1. Calling male túngara frog in a pond. The conspicuous inflated vocal sac is clearly visible below the male's mouth.

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