RESEARCH HIGHLIGHTS

How signals interact in multimodal displays: Insights from a robotic frog

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Abstract

In Focus: Caldart, M. V., M. B. dos Santos & G. Machado (2021). Function of a multimodal signal: a multiple hypothesis test using a robot frog *Journal of Animal Ecology*, https://doi.org/10.1111/1365-2656.13620. Animals can communicate using signals perceived by different sensory systems, and many combine multiple sensory modalities in their display repertoires. Why these multimodal displays evolve and how they function to transmit information between individuals are crucial questions in behavioural and evolutionary research. Most empirical studies addressing these questions assume, even if implicitly, that signals of different modalities have independent effects on receiver responses. Nonetheless, the potential for interactions between signals as an explanation for the function of multimodal displays has been recognized for over two decades. Caldart et al. (2021) use a robotic frog and a receiver-based approach to test four alternative hypotheses for the function of multimodal (acoustic + visual) displays in the stream-dwelling frog *Crossodactylus schmidti*. Their results lend support to an inter-signal interaction mechanism, whereby inclusion of visual signals modifies the context in which an acoustic display is interpreted. In contrast, the results in Caldart et al. (2021) are less consistent with the hypotheses that emphasize the quality-related information encoded in different signal modalities and a hypothesis that focuses on signal transmission across heterogeneous environments. These results showcase how experimental manipulation of different signal modalities and tests of multiple alternative hypotheses are key to clarifying the function of multimodal displays.

KEYWORDS
acoustic, agonistic, communication, inter–signal interaction, visual

Many animals communicate using composite signals that can be perceived by more than one sensory modality in their intended receivers (Candolin, 2003; Mitoyen et al., 2019; Rowe & Halpin, 2013). While the ultimate causes for the evolution of such multimodal communication have been a focus of behavioural ecology research for more than two decades (Bro-Jørgensen, 2010; Rowe, 1999), a majority of empirical studies assume that the alternative modalities have independent effects in shaping receiver responses (but see Hughes, 1996; Taylor, Klein, & Ryan, 2011; Vicente & Halloy, 2017). In the absence of inter-signal interaction,

two general types of selection account for the evolution of multimodal signals. Selection may act on the information content of signals of different modalities (content-based selection) or on the degree to which these signals are effectively transmitted, perceived and processed by receivers (efficacy-based selection; Hebets & Papaj, 2005). Nonetheless, an alternative form of selection may arise when the behavioural response elicited by a signal modality depends on the presence of another signal, which stimulates a different sensory system (Hebets & Papaj, 2005). In this case, responses to multimodal displays are shaped by the

interaction between the two signals and may differ qualitatively from responses to unimodal signals (Partan & Marler, 1999).

An interesting form of inter-signal interaction occurs when a novel signal modality modifies the context in which a primary signal is interpreted (Hebets & Papaj, 2005; Hughes, 1996). It is widely acknowledged that signals of different modalities may have non-additive effects when displayed simultaneously or sequentially (Candolin, 2003; Narins et al., 2003; Partan & Marler, 1999). Yet, few studies have considered alternative signal modalities in an explicit contextual relationship (Hughes, 1996; Taylor, Klein, & Ryan, 2011; Vicente & Halloy, 2017). Such a consideration can allow researchers to assess the relative importance of inter-signal interactions vs. content-based and efficacy-based functions. Caldart et al. (2021) used a simple experiment and carefully drawn predictions to undertake this task in the stream-dwelling frog *Crossodactylus schmidti*, and found that visual signals (toe flags) that are emitted with aggressive calls escalate agonistic interactions between males. Importantly, visual displays are not correlated with common proxies of male quality, and on their own, elicit very limited responses from territorial males across signalling environments. These results suggest that toe flagging displays in *C. schmidti* may signal greater aggressive motivation in males that are already engaged in an acoustic contest.

Acoustic displays are the main form of communication in courtship and agonistic interactions in anurans (frogs and toads) (Wells, 2010). Nevertheless, visual displays have evolved multiple times in distinct lineages (Starnberger et al., 2014). Because anurans must inflate their vocal sacs to produce calls, multimodal displays often involve the colour or movement of this structure (Starnberger et al., 2014). However, limb movements, such as waving hands and flagging feet are also used as visual displays in a diverse array of taxa (Grafe & Wanger, 2007; Hartmann et al., 2005; Krishna & Krishna, 2006; Lindquist & Hetherington, 1996). Most of these behaviours have been described in species that inhabit fast-flowing streams and cascades in tropical rainforests, including *C. schmidti* (Caldart et al., 2014). In these environments, rushing water may often dampen acoustic signals, suggesting a role for visual displays in improving transmission efficacy against high background noise (Grafe et al., 2012). However, even if efficacy-based selection may account for the evolutionary origin of visual displays, it does not preclude the subsequent co-option of such signals for other functions.

To understand the current function of multimodal agonistic displays in *C. schmidti*, Caldart et al. (2021) built on a detailed understanding of the natural history of this species (Caldart et al., 2011; Caldart et al., 2014). Males of *C. schmidti* are diurnal and territorial. When an intruder approaches a defending male, their interaction typically starts with an exchange of aggressive calls, which may turn into multimodal displays by the inclusion of visual signals, such as toe flagging, limb lifting, running-jumping and body jerking (Caldart et al., 2014, 2021). In addition to efficacy-based selection via message transmission in a high-noise backdrop (Figure 1b), Caldart et al. (2021) hypothesized that multimodal displays may be under content-based selection, if the inclusion of visual signals reveals useful information for males assessing the quality of a rival (Figure 1a).

This information may for example relate to an additional quality trait, or provide a more accurate assessment of the same quality trait signalled by the acoustic display.

Male conflicts in *C. schmidti* may be resolved by the exchange of visual and acoustic displays, with one male eventually retreating, but multimodal displays may even escalate to physical combat (Caldart et al., 2014). This previous observation suggested to Caldart et al. (2021) that visual signals may also modify the context in which acoustic displays are interpreted. Specifically, visual cues may signal aggressive motivation and the probability of further escalation, but without providing additional information on male quality (Figure 1c). This latter alternative would imply a current role of inter-signal interaction in determining the function of multimodal displays in *C. schmidti*.

Caldart et al. (2021) used an electromagnetic robot, programmed to emit acoustic and visual signals identical to those produced by living males, and focused on the responses of receivers, their quality proxies and local environmental settings to evaluate the support for content-based selection, efficacy-based selection and inter-signal interaction (Figure 1). Robotic models have been successfully employed in studies of animal communication and multimodal signalling over the last two decades (Narins et al., 2003; Taylor et al., 2008, 2011). Such robots allow researchers to manipulate individual components of complex signals and investigate how the presence, timing and order of these components influence receiver responses. Caldart et al. (2021) capitalize on these previous developments and exposed resident males of *C. schmidti* to a conspecific robot that displayed acoustic, visual or multimodal signals.

The responses to multimodal displays in *C. schmidti* are shaped by the interaction between acoustic and visual components. First, Caldart et al. (2021) showed that the probability and latency of response is similar whether resident males are exposed to acoustic or multimodal signals, suggesting that visual signals in a multimodal display do not act as a backup for signal transmission. Moreover, using two quality traits in anurans, body size and body condition, Caldart et al. (2021) found no correlation between the quality trait and the rate of emission of signals of either modality in resident males. The dominant frequency of aggressive calls is however correlated with body size, as is often the case in anurans (Gingras et al., 2013). Taken together, these results indicate that while acoustic displays may provide quality-related information, additional visual signals do not, at least for the quality traits so far examined. Finally, the inclusion of toe flags in an otherwise acoustic display qualitatively modifies receiver responses. Resident males that responded to multimodal displays included more visual signals, and both their acoustic and visual responses persisted for a longer period after the end of the robotic frog stimulus.

There are many possible explanations for the function of multimodal displays (Hebets & Papaj, 2005). Thus, while challenging, studies that address multiple alternative hypotheses on the same system are crucial to determine the relative importance of these diverse mechanisms. Even though multiple forms of selection likely act on any given signal, Caldart et al. (2021) found most support for inter-signal interaction determining the function of multimodal agonistic displays

	Signal function		Response examples		Key predictions
(a) Content-based selection	'quality'		receiver 1	receiver 2	Responses of differente signal modalities are correlated to **different** quality traits across receivers
	U1	quality trait 1 →			
	U2	quality trait 2 →			
	M	quality trait 1 → / quality trait 2 →			
	'redundant'		receiver 1	receiver 2	Responses of different signal modalities are correlated to **the same** quality trait and to each other across receivers
	U1	quality proxy 1 →			
	U2	quality proxy 2 →			
	M	quality proxy 1 → / quality proxy 2 →			
(b) Efficacy-based selection	'efficacy backup'		environment 1	environment 2	Multimodal signals have a higher probability of eliciting a response across environmental gradients, when signals of different modalites have reduced **transmission** in differnt environments
	U1	channel 1 →			
	U2	channel 2 →			
	M	channel 1 → / channel 2 →			
(c) Inter-signal interaction	'context'		unimodal	multimodal	Inclusion of a contextual signals **alters the response** to a primary signal. Only the primary signal elicits a response on its own.
	U1	primary signal →			
	U2	contextual signal →			
	M	primary signal → / contextual signal →			

FIGURE 1 Alternative hypotheses and key predictions for the function of multimodal (acoustic + visual) agonistic displays in *C. schmidti*, tested in Caldart et al. (2021). Terminology follows Hebets and Papaj (2005). Yellow and blue arrows represent signals of two different modalities. Examples of possible responses under each hypothesis are drawn for each unimodal display (U1 and U2) and for the multimodal display (M). (a) Under content-based selection, different modalities provide additive information about male quality. Such information may relate to different quality traits ('quality' hypothesis), such as body size and body condition. In this scenario, both types of unimodal signals should elicit a receiver response, and responses in the two signal modalities should correlate with different quality traits. Receiver 1 in this example has a higher value for quality trait 1 and receiver 2 has a higher value for quality trait 2. Alternatively, the two signal modalities may provide information on the same quality trait ('redundant' hypothesis) which is expected to result in a more accurate message. Here, a positive correlation between the two modalities in receiver responses is expected. (b) Under efficacy-based selection, different signal modalities improve signal transmission, perception or processing under different circumstances. Caldart et al. (2021) focused on the 'efficacy backup' hypothesis, whereby each signal modality acts as a backup in environments where the other signal is transmitted less effectively, for example visual signals can be a backup for acoustic signals in noisy environments, and acoustic signals may function as a backup for visual signals in darker conditions. Here, we expect that the probability and latency of receiver responses vary along environmental gradients only when exposed to unimodal displays. If the stimulus is multimodal, these response metrics should be consistently highly across environments. (c) Inter-signal interaction implies that responses to multimodal signals are qualitatively different from responses to unimodal signals. Caldart et al. (2021) explored the 'context' hypothesis, according to which a signal modality acts to modify the context in which a primary signal is interpreted. Here, the contextual signal alone should not elicit a response and should not be correlated with male quality

in *C. schmidti*. This interaction is mediated by a contextual relationship between visual and acoustic signals. Such relationships between alternative signal modalities may be commonplace. Caldart et al. (2021) suggested that contextual relationships between signals may be particularly important when the message coded in a signal is expected to change as interactions progress, for example if motivation increases in an escalating agonistic interaction or as a female approaches a courting male. Finally, an important step beyond assessing the current function of a multimodal display is to understand the sources of between- and within-individual variation in the use of alternative signal components. The results of Caldart et al. (2021) suggest that integrating context dependence hypotheses in studies of multimodal displays is a promising research avenue towards this goal.

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