



Multimodal duetting in magpie-larks: how do vocal and visual components contribute to a cooperative signal's function?



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Many animals communicate using multimodal signals, which simultaneously address different senses. Components may prompt similar or different responses when used alone, whereas the composite signal may have a similar meaning to one or both components, or a novel meaning. We used robot models to dissect the roles of visual and vocal components in the multimodal duets of Australian magpie-larks, *Grallina cyanoleuca*. Mated pairs produce antiphonal vocal duets, and coordinate them with visual duets, which usually entail alternating wing movements. Previous playback experiments show that purely vocal duets have a territorial function, but the role of visual displays is unknown. We measured territorial responses by pairs to each component independently, as well as to the multimodal signal, and analysed the choice of song and visual display used by partners during duets. Acoustic and multimodal playbacks prompted the same, strong territorial response, entailing both flight and vocal duetting by the resident pair. By contrast, purely visual playbacks did not prompt a strong territorial response. Furthermore, pairs used the same visual display within multimodal displays, independent of song type, implying that birds watch their partners when choosing the visual display, and suggesting that it could be a within-pair signal. We conclude that the vocal component of duets is a territorial signal to other pairs, whereas the visual component might either coordinate vocal duets within pairs, analogous to a conductor's baton, or have a restricted role in communication between rival pairs, perhaps especially at long range.

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Animals produce signals using single or multiple components, and perceive signals through all available sensory channels (Candolin, 2003; Hebets & Papaj, 2005; Partan & Marler, 2005; Rowe, 1999). Multimodal communication contains components that target different senses, and is widespread across taxa. Such signals can target all known senses, and include bimodal, trimodal or even more complex signals (Stevens, 2013). Signalling in multiple channels is linked with some specific benefits and costs to both the signaller and receiver (Partan & Marler, 2005), and we cannot understand multicomponent signals fully by studying their components independently (Rowe, 1999). Nevertheless, most studies on animal communication focus on one modality at a time.

The components of multimodal signals can communicate redundant or nonredundant messages (Johnstone, 1997; Møller & Pomianowski, 1993; Stevens, 2013). Multiple redundant

components can increase the efficiency of communication by providing insurance in case one component is not recognized, or by increasing the intensity of the composite signal compared with intensities of independent components (Preininger et al., 2013; Rypstra, Schlosser, Sutton, & Persons, 2009). In the fowl, *Gallus gallus*, for example, food-associated calls are typically accompanied by a distinctive visual display, with each modality acting as a backup to enhance signal efficiency. Hens need more time to begin food search when the display is silent, but the overall probability of response is similar among the multimodal, visual-only or acoustic only components (Smith & Evans, 2008). Multiple nonredundant components can convey increased information by having different roles or by targeting different recipients (Krakauer & Johnstone, 1995; Ratcliffe & Nydam, 2008). In the field cricket, *Gryllus integer*, for example, males produce long-distance calls and close-range chemical compounds. Although females demonstrate positive phono and chemotaxis, the responses to long-distance and close-range components are uncorrelated within females, suggesting that each modality has a different message (Leonard & Hedrick, 2010).

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The function of multimodal displays can be tested empirically by the analysis of responses by receivers to signal components and to full displays (Partan & Marler, 2005). Perceivers should respond with similar behaviours to signal components presented independently if components communicate redundant messages, but with different behaviours if components transmit different messages. When presented together, redundant components may lead to the same or equivalent effects, or may enhance the receiver's responses additively or even multiplicatively (Partan, 2013). Nonredundant components within complex displays may continue to elicit independent messages, produce novel responses, or modify each other (Partan & Marler, 2005).

Individuals can produce multimodal signals alone or together with others, and yet there has been no study of the role and integration of different components of multimodal signals when produced cooperatively with others. In cooperatively signalling species, communication could have two distinct types of receiver: an 'audience' addressed by the cooperative signal, and 'co-signallers' with whom an individual cooperates to form the joint signal. Additionally, if a signal is multimodal, each component could have its own target audience (Partan & Marler, 2005). Experimental study of multimodal signalling in cooperatively signalling species is therefore challenging because there could be multiple receivers and messages.

We tested whether the visual and acoustic components of Australian magpie-lark, *Grallina cyanoleuca*, duetting displays communicate equivalent or different messages, and analysed the relationship between components within the cooperative display. In many bird species, mated pairs produce acoustic duets, and some also coordinate their songs with movements to form cooperative audiovisual displays (Hall, 2009; Malacarne, Cucco, & Camanni, 1991; Todt & Fiebelkorn, 1980; Von Seibt & Wickler, 1977; Zimmer, Whittaker, & Oren, 2001). Nevertheless, such multimodal cooperative behaviours have not been broken down experimentally into their constituent parts. Magpie-lark partners produce antiphonal duets, often with a high level of coordination between partners, and these are used to defend the territory (Hall, 2000; Hall & Magrath, 2007). Birds also produce visual displays, including alternating wing movements, but their function has never been studied.

We documented how vocal and visual components are combined within magpie-lark cooperative displays, and experimentally tested their function. We used taxidermic robotic birds that produced wing movements, which we synchronized with acoustic playbacks to test the function of signal components and to analyse the integration of components from different sensory channels. The acoustic component is known to have a territorial function, so we measured behaviours used in territorial defence. In magpie-larks, playback of acoustic duets elicits a territorial defence syndrome consisting of both singing, with more duets compared to solo songs, and flying (Hall, 2000). Therefore, if the visual component transfers the same message as the acoustic one, then visual and acoustic playbacks should prompt the same territorial syndrome from focal pairs, which is likely also to be similar to the multimodal playback. Responses to multimodal signal components may differ in intensity but as long as the syndrome is maintained, the components are redundant. If, however, components prompt different responses from focal pairs, it would mean that they are nonredundant. In this case, the multimodal playback may elicit (1) a new response, a behaviour qualitatively different from either unimodal playback; (2) the same response as one of the unimodal components, meaning that one component dominates the message; (3) or a response that is a combination of behaviours given to unimodal playbacks. An additional complexity in cooperative signallers is that the partner is also a potential target, so that different components may address different receivers.

METHODS

Study Population and Species

We studied a colour-banded population of magpie-larks in and near the Australian National University in Canberra. Magpie-larks are endemic to Australia, where they commonly inhabit open woodland and suburban parks and gardens (Mulder et al., 2003; Peter, Cowling, & Higgins, 2006). Pairs defend territories throughout the year (Hall & Magrath, 2000), and the sexes are easily distinguishable by plumage differences (Disney, 1974).

Males and females each produce solo songs, and together can combine songs to form antiphonal duets. Solo songs consist of a series of short units, called motifs, which are 300–600 ms long and given at a tempo of about 1 motif/s. Individuals have a repertoire of about three to six different song types, each composed of a single, repeated motif, and an earlier study found nine motifs in the study population, but with only two used by all birds (Hall, 2006). In duets, partners alternate their motifs on average six or seven times. Each bird uses the same motif throughout a duet, but it is rare for pairs to sing a duet in which each bird uses the same motif type (Hall, 2006). Coordination is often precise, with perfect alternation of motifs and a regular tempo of about 1 motif/bird per s. Pairs that have been together longer are more likely to produce well-coordinated duets, which are a more threatening territorial signal (Hall & Magrath, 2007).

In addition to the vocal display, magpie-lark duets are typically accompanied by synchronized body movements (Hall & Magrath, 2007; Peter et al., 2006; Tingay, 1974). Most often, the movements consist of wing spreading or raising of folded wings ('shoulder' raising), but sometimes the whole body bends forward (Supplementary Videos S1–S3, respectively). Although most duets entail both a vocal and visual component, magpie-larks can give purely vocal or visual duets (P. Reş, personal observation). However, unimodal duets are relatively rare, and in our experimental sample of 188 duets only three were purely vocal and none purely visual (see Results).

Ethical Note

The use of the animals adhered to ethical guidelines for animal research in Australia (Australian Bird and Bat Banding Scheme, Environment ACT) as well as all the institutional guidelines of the Australian National University (A2014/17). Although the procedures we applied might cause temporary distress to birds, we minimized the number of recordings and playbacks consistent with experimental goals, and always kept the rate of playback below natural rates.

Robotic Models

We used a male–female pair of taxidermic robotic magpie-larks during the playback experiment (Supplementary Video S4). Each bird contained two servo motors (Power HD, Analog Micro Servo HD-1440A) that were attached to the humeri of the wings, which enabled the outstretched wings to be moved up and down. This movement corresponded to the 'wing spreading' movement, which is the most common visual display of magpie larks (76% of 370 movements observed during this study). The servo motors from one bird had a single circuit, so that the two wings moved in synchrony, while the motors of the male and female were controlled independently, so that they could be moved in alternation. Model birds were attached to a perch next to each other facing the same direction, so that they resembled a duetting pair. Movements of robotic birds were controlled together with acoustic playbacks

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