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Multimodal shifts in noise: switching channels to communicate through rapid environmental change

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A multimodal shift is the ability to switch from reliance on one sensory channel to another during communication. The shift can take place during signal production and/or perception. If environmental changes such as urbanization and climate change impair signal transmission in particular channels, it would benefit the animal to be able to switch to a relatively quieter channel. For this strategy to be successful, it requires animals to be able to send redundant information across multiple channels. I develop and explore the argument that the ability of animals to switch from a noisy channel to a relatively quiet one may be key for the animals' ability to cope with rapid anthropogenic environmental change. I review examples of multimodal shifts that occur with environmental noise as well as cases in which a predicted shift did not occur. I survey which sensory channels are used in shifts and whether the signal components are redundant or nonredundant. Most multimodal shift examples include the visual channel as one of the components. The majority of signals involved in shifts appear to be redundant, although the majority of signals involved in multimodal communication in general appear to be nonredundant, especially for chemical/visual combinations. Finally, I discuss how anthropogenic environmental changes can affect signal transmission in different channels and habitats and explain why the ability to shift channels may help animals cope with these changes. Predictions and recommendations for future work are provided.

> *Perhaps the most striking generalization that can be advanced … is the overwhelming importance of composite signals. In most situations it is not a single signal that passes from one animal to another but a whole complex of them, visual, auditory, tactile, and sometimes olfactory. There can be little doubt that the structure of individual signals is very much affected by this incorporation in a whole matrix of other signals* **(Marler, 1965, page 583)**

Animals communicate with composite signals across multiple sensory channels, as Marler (1965) eloquently described. Despite the early attention drawn to these composite, or multimodal, signals, this topic was not often studied until the 1990s and 2000s, when it experienced a surge of interest that continues to increase (Johnstone, 1996; Partan & Marler, 1999; Rowe & Guilford, 1999; see publication rates in: Leonard, Dornhaus, & Papaj, 2011; see overviews of the topic in: Higham & Hebets, 2013; Partan, 2013). Part of the reason for this interest is that multimodal signalling presents an intriguing problem. Adding signal channels potentially increases costs to both signallers and receivers in terms of energy and predation risk, so there must be adequate benefit as well. In addition, multimodal signals are complex because they can be redundant or nonredundant, for example, and components can interact in many ways (Hebets & Papaj, 2005; Partan, 2004; Partan & Marler, 2005). While this complexity invites evolutionary explanation (Johnstone, 1996), we are only beginning to understand how the ability to communicate via multiple sensory modalities affects signal structure, evolution, and ultimately the behaviour and survival of the organism.

In this essay I advance the argument that multimodality (the ability to communicate using multiple sensory channels) should benefit animals by allowing them to better cope with noise introduced by rapid environmental change (Bro-Jørgensen, 2010; Partan, 2013; van der Sluijs et al. 2011). Multimodal communication can be advantageous in noisy environments because of the opportunity to shift from a noisy to a quieter channel (Brumm & Slabbekoorn, 2005; Hebets & Papaj, 2005; Partan & Marler, 2005). Note that the terms ‘noisy’ and ‘quiet’ are used across sensory channels to describe conditions in which the channel is either impaired or clear for signal transmission. This ability to switch from

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reliance on one sensory channel to another will be referred to as a 'multimodal shift' (Partan, Fulmer, Gounard, & Redmond, 2010), and it may be particularly important in dealing with rapid anthropogenic environmental change.

Climate change, urbanization and other anthropogenic activities create acoustic, visual and chemical noise pollution that affect signal transmission in both terrestrial and aquatic habitats (Halfwerk & Slabbekoorn, 2015; Partan, 2013; Tuomainen & Candolin, 2011), discussed further below. If these rapid environmental changes can disrupt signal transmission in one or more sensory channels, and if multimodality can enable a switch to a quieter channel, then multimodal shifts should help animals better cope with change in the short term, and multimodal signalling should be favoured, evolutionarily, in the long term (see Bro-Jørgensen, 2010; Partan, 2013; Rhebergen, Taylor, Ryan, Page, & Halfwerk, 2015). Continued environmental change should favour continued multimodality, rather than sequential unimodal switches to new channels.

There is a great deal of literature on signal adjustments in response to environmental change within a *single* sensory channel. For example, birds adjust a number of acoustic parameters of their vocalizations in response to urban noise (Slabbekoorn & Peet, 2003; reviewed in: Patricelli & Blickley, 2006; Ryan & Partan, 2014), and lizards adjust visual components of their display in response to visual 'noise' such as moving vegetation or low light (e.g. Ord, Stamps, & Losos, 2010). In addition, birds may use serial redundancy in song to overcome noisy environments (Brumm & Slater, 2006). The unique advantage of multimodal signals, across sensory channels, however, is the ability to continue to transmit the message even if one channel is impaired.

Here I survey the channels, species and contexts in which multimodal shifts have been documented. I also explore examples of cases in which a multimodal shift was expected but not found. I then discuss the importance of redundancy in multimodal shifts. An assessment of the incidence of redundancy in multimodal communication allows us to make some predictions about which channels, and which taxa, are likely to be successful at multimodal shifts and therefore likely to be able to use this strategy to cope with environmental change. In the second half of this paper I review the ways in which human-induced rapid environmental change (HIREC, Sih, Ferrari, & Harris, 2011) can affect signalling channels and suggest that multimodal shifts may help animals to cope with HIREC.

EXAMPLES OF MULTIMODAL SHIFTS

> *[I]n animal communication there is extensive collaboration between the senses. The usefulness of certain modalities may be restricted by an animal's habits… When the usefulness of vision is limited by the environment or by inadequacies of the visual receptors, there tends to be more reliance on olfaction* **(Marler, 1967, page 773)**

Marler (1967) surveyed the advantages and disadvantages of each sensory channel used for communication, relating channel usage to environmental factors, and anticipated the importance of shifting between sensory channels to overcome limitations imposed by the environment. In this section I discuss two types of multimodal shifts: those related to environmental factors that occur to overcome noise in one of the channels (Brumm & Slabbekoorn, 2005; Hebets & Papaj, 2005; Partan & Marler, 2005), and those that occur for social reasons, in order to attract or avoid attention (Partan, 2013). I will discuss examples of multimodal shifts found in the literature, with cases of animals switching channels in response to abiotic environmental impediments listed in Table 1, and cases of switching due to biotic factors such as social or antipredator behaviour listed in Table 2. While most of the cases involve a shift of sensory modality during signal production (which necessitates that the receiver also change channels for perception), some of the shifts involve only perception changes, as noted in the tables and discussed below.

Figure 1 depicts the direction of the shifts between each sensory channel for the 16 studies described. The sensory channels most used in the examples are visual (13 out of 16 cases involved vision: 8 as the initial channel and 5 as the one switched to), acoustic (7 cases: 5 as the initial channel and twice switched to) and vibration (8 cases: 3 as the initial channel, and 5 times switched to). Figure 1 is not meant to be definitive but is based on the 16 examples of multimodal shifts that we found in the literature and as such is a representative reflection of what has been studied and published so far. (In addition to Web of Science citation searches, we searched with topic word strings such as 'animal communication + (multimodal or multisensory) + (shift or switch or backup)'; I encourage those publishing in this area to include these sorts of terms in their keywords.)

For immediate, individually plastic behavioural shifts (12 examples; solid arrows in Fig. 1), the most common situation observed was for an animal to shift from vision to vibration or olfaction, although other channels were possible. For population-level or evolved shifts (4 examples; dashed arrows in Fig. 1), three examples suggest that the auditory channel was ancestral, and a shift occurred to vision or vibration (over evolutionary time), and one example suggests a shift from vibration to audition. The channels used in a switch are prescribed in part by physical and environmental constraints on species' choice of modalities. In a survey of multimodal signalling examples, invertebrates tended to use vibration more than did vertebrates, while vertebrates tended to use acoustics more (Otovic & Partan, 2009). Taxonomic categories of the species involved in the 16 shifts surveyed here are indicated by colour in Fig. 1. Arachnids dominate the literature on multimodal shifts, switching between the visual and vibrational channels. All vibrational examples involved invertebrates (arachnids or insects). Amphibians and fish were found to shift primarily from the visual to olfactory channel; birds switched from acoustic to visual channels; and mammals switched among a variety of channels. Details on each study are covered below.

Multimodal Shifts Due to Abiotic Environmental Factors

Among the 10 cases in Table 1 of animals shifting channels in response to noise or environmental degradation in one of the channels, five cases involve switches from visual signalling to either vibration or olfaction when visual clarity decreases, three cases involve shifting from acoustic signalling to either vision or vibration in audio noise, and two cases involve a switch from vibration to visual. The visual-to-vibratory examples all involve courtship in spiders. Jackson (1977, 1992) observed male jumping spiders, *Phidippus johnsoni*, under natural conditions, courting outside of the nest with visual signals but using seismic signals inside the nest, where it is generally dark. This represents a shift in signal production enacted by the signaller (the male) to overcome natural environmental variability. In laboratory studies of wolf spiders, *Schizocosa ocreata*, Taylor, Roberts, and Uetz (2005) found that when males were allowed to court in dark rooms versus lighted rooms, several flexible elements of courtship changed, but those displays that occurred in both conditions were similar in structure. Stridulation, for example, was included in the displays in both the light and the dark conditions, and leg extensions, which can only be seen in the light, were also done in the dark. This is less clearly a

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