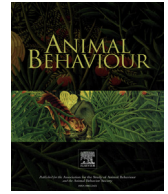




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Multimodal shifts in noise: switching channels to communicate through rapid environmental change



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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.

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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 Brø-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.




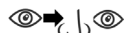


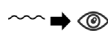



Figure 1 depicts the direction of the shifts between each sensory channel for the 16 studies described. The sensory channels most used in the examples are visual (13 out of 16 cases involved vision: 8 as the initial channel and 5 as the one switched to), acoustic (7 cases: 5 as the initial channel and 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 (Otvic & 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

Table 1
Multimodal shifts associated with abiotic environmental factors

Species	Reason for shift	Initial channel	Channel shifted to	Context/function of signal	Components are redundant or nonredundant	Components are obligate or flexible partners	Shift in signal production or just perception	Individual facultative shift, or population level shift	Method of study	Source	
Jumping spider (<i>Phidippus johnsoni</i>)	Dark nest	Visual (courtship display)		Vibration (tugging and jerking silk of nest)	Courtship	Presumably redundant	Flexible	Production	Individual	Field observations	Jackson (1977, 1992)
Wolf spider (<i>Schizocosa ocreata</i>)	Darkness	Visual (leg extension, wave, tap, arch)		Vibration (stridulation)	Courtship	Redundant	Some of each	Presumably perception	Individual	Lab; observed courtship in light vs dark	Taylor et al. (2005)
Wolf spider (<i>Rabidosa rabida</i>)	Darkness	Visual (leg wave)		Presumed vibration (stridulation)	Courtship	Redundant	Flexible	Production	Individual	Lab; observed courtship in light vs dark and in varying vibratory transmission conditions	Wilgers and Hebets (2011)
Alpine newt, <i>Mesotriton alpestris</i>	Darkness	Visual (tail and body postures and displays)		Olfactory/visual (fanning tail, which conducts pheromones to female)	Courtship	Presumably redundant	Flexible	Production	Individual	Lab; observed courtship in light vs dark	Denoël and Doellen (2010)
Stickleback fish (<i>Gasterosteus aculeatus</i>)	Turbid water	Visual (colour & size)		Olfactory (unspecified)	Mate choice	Nonredundant	Obligate	Perception (by experimental design)	Individual	Lab; tested mate preference in visual, olfactory, or both channels	Heuschele et al. (2009)
Wolf spider (<i>S. ocreata</i>)	Substrate not conducive to vibration	Vibration (stridulation)		Visual (leg wave, tap, arch, leg tufts)	Courtship	Presumably redundant	Some of each	Perception (by experimental design)	Individual	Lab; observed response to courtship in varying visual and vibratory transmission conditions	Scheffer et al. (1996)
Wolf spider (<i>S. ocreata</i>)	Substrate not conducive to vibration	Vibration (stridulation)		Visual (leg wave, arch)	Courtship	Presumably redundant	Flexible	Production	Individual	Lab; observed signals on substrates varying in vibratory transmission	Gordon and Uetz (2011)
Humpback whale, <i>Megaptera novaeangliae</i>	Wind noise	Acoustic (vocalizations)		Acoustic/visual (surface generated signals e.g. tail slaps)	Social behaviour	Unspecified	Flexible	Production	Individual	Field observations and audio recordings	Dunlop et al. (2010)
Eastern grey squirrel, <i>Sciurus carolinensis</i>	Urban environment	Acoustic (response to alarm bark)		Acoustic/visual (response to tail flag as well as alarm bark)	Response to simulated alarm signals	Redundant	Flexible	Perception (by experimental design)	Population (urban vs rural squirrels)	Field playback of a/v robotic stimulus	Partan et al. (2010)
Frogs: Hylodinae (<i>Hylodes</i>), Myobatrachidae (<i>Taudactylus</i>), Hylidae (<i>Litoria</i>), Ranidae (<i>Staurois</i>)	Noisy stream or waterfall	Presumed acoustic, based on comparative phylogenetic evidence		Visual (foot flagging and other visual signals)	Intraspecific communication including both courtship and agonism	Unspecified	Flexible	Production	Population (evolved reliance on visual)	Comparative meta-analysis of visual signal repertoires and habitat proximity to fast-flowing streams	Hödl and Amézquita (2001)

Note that in many cases the signal in the initial channel continues to be produced along with the signal in the new channel; see text for details.

Table 2
Multimodal shifts associated with biotic factors (social or antipredator)

Species	Reason for shift	Initial channel	Channel shifted to	Context/function of signal	Components are redundant or nonredundant	Components are obligate or flexible partners	Shift in signal production or just perception	Individual facultative shift, or population level shift	Method of study	Source	
Chimpanzee, <i>Pan troglodytes</i>	Attract attention when conspecific not looking	Visual (e.g. arm raise, or facial expression)	 → 	Tactile (e.g. poking, throwing object at)	Attention-getting signal given to conspecific to initiate interaction	Unspecified	Flexible	Production	Individual	Outdoor enclosures; behavioural observations	Tomasello et al. (1994)
Chimpanzee, <i>P. troglodytes</i>	Attract attention when caretaker not looking	Visual (gestures, pouts, presentations, etc.)	 → 	Acoustic (calls and attention-getting sounds)	Attention-getting signal given to caretaker	Presumably redundant	Flexible	Production	Individual	Lab; observed responses to caretaker facing towards or away	Leavens et al. (2010)
California ground squirrel, <i>Spermophilus beecheyi</i>	Confront IR-sensitive snake predators	Visual (tail flag)	 →  → 	Visual/heat (tail flag with IR heat)	Antipredator	Unspecified	Flexible	Production	Individual	Lab: IR-video of squirrels interacting with IR-sensitive and IR-insensitive snakes	Rundus et al. (2007)
Chickens, <i>Gallus gallus</i>	Avoid attention of dominant conspecific	Acoustic/visual (food calls and tidbitting display)	 → 	Visual (tidbitting display alone)	Mate attraction by subordinate males	Redundant	Flexible	Production	Individual	Naturalistic enclosures; behavioural observations	Smith et al. (2011)
Katydids (Tettigoniidae)	Avoid acoustic bat predators	Presumed acoustic	 →  → 	Vibration (tremulations) with shorter songs	Mate attraction	Presumably redundant	Unspecified	Production	Population (evolved reliance on vibration)	Field recordings	Belwood and Morris (1987)
Cicada (Cicadidae)	Unspecified, but presumably larger body size enabled acoustic production	Presumed vibration (tymbals utilized to vibrate substrate, based on comparative phylogenetic evidence)	 → 	Acoustic (tymbals now utilized to make airborne sound)	Intraspecific signalling	Unspecified	Unspecified	Production	Population (evolved ability to produce airborne sound)	Comparative review	Strauß and Lakes-Harlan (2014)

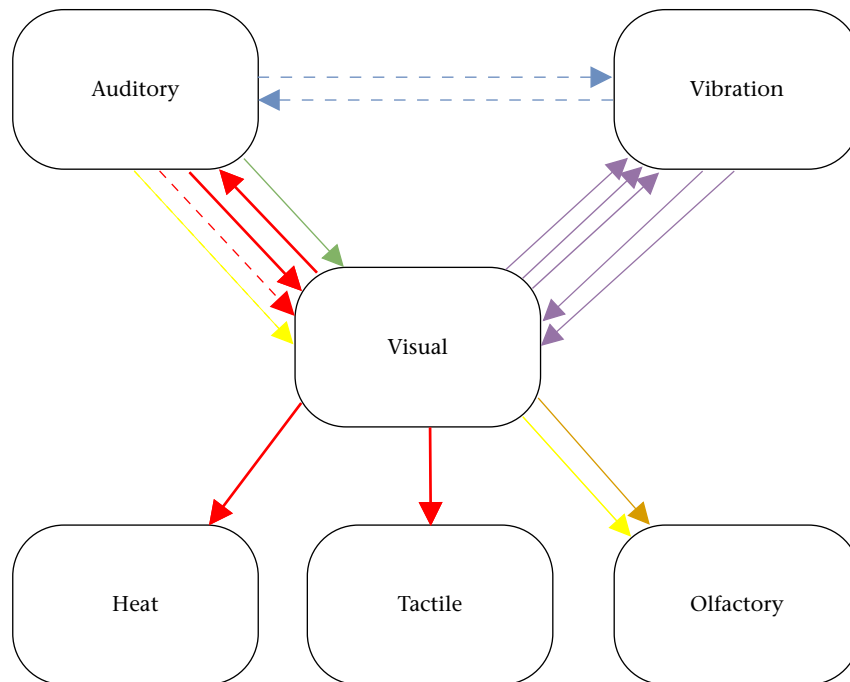


Figure 1. Sensory channels and direction of shift for the 16 multimodal shifts found in the literature (details in Tables 1, 2). Each arrow represents one study (most of the studies were of a single species, but some included multiple species). Solid arrows: immediate, context-dependent individual facultative shifts; dotted arrows: population-level shifts. Colour represents taxa: red = mammals; green = birds; yellow = amphibians; orange = fish; blue = insects; purple = arachnids.

shift in production but it suggests that having redundant visual and seismic components allows females to shift their perception of the signal under different light conditions (Taylor et al. 2005).

Similarly, Wilgers and Hebets (2011) set up laboratory trials in which male wolf spiders, *Rabidosa rabida*, were allowed to court females either in the light or in the dark, and on substrates that either did or did not transmit seismic signals. They found that males adjusted their signalling behaviour in the dark, when they tended not to give a visual leg-wave display. Although the occurrence of this leg-wave display was not dependent on the seismic transmission condition, it is reasonable to infer that in the dark, males are using other cues (presumably seismic) to court. This example involves a production shift in emphasis from more to less visual signalling behaviour. Since seismic signals themselves were not documented, it is unclear whether the shift also involves an increase in production of the seismic signal, or whether it is mainly a shift in female perception from the visual to the seismic modality, without a change in seismic production.

There are also examples in spiders of reverse shifts from the vibratory to the visual channel (Table 1). Scheffer, Uetz, and Stratton (1996) found that although wolf spiders (*S. ocreata*) rely primarily on stridulation for courtship, they can use their conspicuous visual leg tufts to court successfully using vision alone, in habitats where vibration transmission is curtailed. They conducted a laboratory study in which they allowed males to court females with both visual and vibratory transmission available, visual transmission only, or vibration transmission only. Females responded with receptivity displays in all conditions as long as the male leg tufts were intact, but when males had leg tufts temporarily removed, the female response dropped (Scheffer et al. 1996). This study did not document signal structure from the males, but rather found that females could shift in terms of perception. Later, Gordon and Uetz (2011) studied the male signals of the same species on a variety of substrates differing in seismic vibration transmission. They documented flexibility in male signal production. When males were on

substrates not conducive to vibration transmission such as soil and rocks, the spiders performed more visual leg waves and arches than they did on leaf litter, which transmits vibration. This example represents a shift in production.

Another modality that serves as a backup to the visual channel is olfaction. Denoël and Doellen (2010) found that male alpine newts, *Mesotriton alpestris*, produce relatively more visual components of courtship displays in the light, but relatively more of the fanning display, which includes the olfactory channel, in the dark. Heuschele, Mannerla, Gienapp, and Candolin (2009) found that threespine stickleback fish, *Gasterosteus aculeatus*, rely more on visual than olfactory signals for mate choice in clear water, but in turbid water their reliance on olfaction increases. They allowed females to choose to spend time near one of two males, with access to the olfactory channel alone, visual channel alone, or both together. Since male communication behaviour was not coded, it is not known whether there was flexibility in signal production by the males; this shift is in the behaviour of the female receivers. Importantly, Heuschele et al. (2009) found that the females actually changed mate preference in turbid water, indicating that there may be long-term consequences in terms of population traits as water becomes more polluted.

The other three examples in Table 1 of animals shifting channels in response to environmental noise all start with auditory signalling and then, presumably because of acoustic noise, shift to include the visual channel. Partan et al. (2010) conducted field playback experiments with eastern grey squirrels, *Sciurus carolinensis*, in both rural and urban areas, to determine whether the squirrels rely on one channel more than another in the different habitats. Squirrels were presented with a mechanical model of a conspecific that flicked its tail, produced alarm barks, or did both. Squirrels in urban areas responded more to the visual signals of alarm (tail movements) than rural squirrels did, although both populations responded equally to audio signals of alarm. Since squirrels in both areas produced both barks and tail flicks, this shift in emphasis

from responding primarily to audio in rural areas, but to visual as well as audio in urban areas, represents a shift in terms of perception, not production. In this study noise levels were not measured, so there may be other explanations for the results, but the finding is consistent with the prediction that urban audio noise would lead to increased reliance on visual signalling.

Acoustic signal transmission can be impaired by natural sources of noise, such as wind, as well as by anthropogenic sources. Wind can impair acoustic transmission in both airborne and underwater habitats. Dunlop and colleagues (Dunlop, 2016; Dunlop, Cato, & Noad, 2010) documented migrating humpback whales, *Megaptera novaeangliae*, communicating vocally under less windy conditions and shifting to communicating nonvocally under more windy conditions. The nonvocal behaviours included breaching and slapping the tail or pectoral fins on the surface of the water, all of which produced louder sounds than the vocalizations, which the authors suggest helps to overcome wind noise. Dunlop et al. (2010) mention that the surface-generated behaviours also have a visual component, so I include this as an example of a potential multimodal shift in production, from reliance on audio to reliance on visual in combination with audio, in the presence of acoustic environmental noise. In addition, I suspect that a perceptual shift may occur in terms of sensing the surface impacts as low-frequency vibrations perceived via changes in skin pressure, if recipients are close enough, as well as through hearing.

The final example of a multimodal shift due to environmental noise is a bit different in its time scope. Hödl and Amézquita (2001) suggested that frog species living by noisy streams have evolved a reliance on visual communication because the auditory channel is impaired. They conducted a comparative study of frog signalling behaviour and habitats and found that foot-flagging behaviour (a visual signal) was associated with species living in fast-flowing stream habitats. Since most other members of clades with foot-flagging frogs communicate vocally, we have good evidence that foot flagging is derived (Mangiamele et al. 2016; Pyron & Wiens, 2011), and this example represents a shift in signal production from audio to visual channels over evolutionary time.

Multimodal Shifts Due to Biotic Factors

In addition to shifting channels in response to abiotic factors, animals have also been documented to shift channels in response to biotic factors involving social or antipredator behaviour (Table 2). The first three examples of social shifts in Table 2 all involve facultative signal adjustments in mammals from visual to other modalities (acoustic, tactile, or heat), primarily to draw attention to the signaller. Tomasello, Call, Nagell, Olguin, and Carpenter (1994) observed gestural behaviour among captive chimpanzees, *Pan troglodytes*, in an outdoor field station to discover whether signallers adjust the modality of their behaviour based on the attentional state of the recipient. They found that the chimpanzees used silent visual gestures only when the recipient was looking, and used tactile signals (poking) more often when the recipient was not looking. The chimpanzees also gave multimodal audio/visual signals and audio/visual/tactile signals that occurred in both contexts. Similarly, Leavens, Russell, and Hopkins (2010) found captive chimpanzees to be sensitive to gaze direction and attention of caretakers. When caretakers holding desired food items were facing them, the chimpanzees solicited them with a wide variety of visual gestures and displays, but when caretakers turned away, the proportion of vocalizations and other nonvisual attention-getting behaviours (such as clapping and banging the cage) increased. Both of these examples show flexibility in signal production by the signaller, based on an understanding of the social attention of others.

The third case of a facultative multimodal shift to attract attention (Table 2) is unusual in that it describes the use of infrared (IR) heat, used as an antipredator signal by squirrels (Rundus, Owings, Joshi, Chinn, & Giannini, 2007). California ground squirrels, *Spermophilus beecheyi*, regularly flag their tails in an elaborate fashion to ward off snake predators. Rundus et al. (2007) found that these squirrels have the ability to increase heat radiation from their tails and that they do so selectively when they are faced with northern Pacific rattlesnakes, *Crotalus oreganus*, which are sensitive to IR heat, but not when faced with IR-insensitive Pacific gopher snakes, *Pituophis melanoleucus*. This is an example of an individually plastic multimodal shift in production, from visual motion signalling to signalling also with IR heat, in the presence of predators equipped to detect this channel.

Multimodal shifts can also be used to avoid attention by switching from louder or more conspicuous channels to quieter channels. Smith, Taylor, and Evans (2011) observed mixed-sex groups of junglefowl, *Gallus gallus*, in large, naturalistic enclosures. Alpha male chickens attract females using a multimodal, visual/vocal tidbitting display combined with food calling. Subordinate males sometimes attract females in the same way, but when alpha males are paying attention (head up and not vocalizing), subordinate males tend to suppress their vocalizations and switch to visual-only displays. This makes sense because in the natural forested habitat of the junglefowl, birds may be able to hear but not see one another due to intervening vegetation (McBride, Parer, & Foenander, 1969). This example indicates a flexibility in signal production on the part of the subordinate males that is sensitive to social cues.

The final two examples of shifts due to biotic factors (Table 2) are at the population level, in which some taxa may have evolved a reliance on vibratory or acoustic communication over time. Belwood and Morris (1987) found that forest species of katydids (Tettigoniidae) that are sympatric with bat predators (Phyllostominae) have shorter acoustic mate attraction songs than songs of katydid species that do not live near bats, but they also add substrate-borne vibrations that the bats cannot hear. This represents a shift in production of the signal from audio towards vibration, enacted at the population level over evolutionary time due presumably to predation pressure. In most insects, however, vibration is ancestral and continues to be widespread (Cocroft & Rodríguez, 2005; Henry, 1994; Strauß & Stumpner, 2015). In fact, in the singing cicadas, the sound-producing organ, the tymbal, was originally used in ancestral forms for substrate vibration, suggesting that auditory signalling has evolved from vibratory signalling in these insects (Strauß & Lakes-Harlan, 2014).

Cases in Which a Multimodal Shift Does Not Occur

The literature search for multimodal shifts revealed several cases in which researchers explicitly tested for the possibility of a multimodal shift between channels and did not find one (Ríos-Chelén, Lee, & Patricelli, 2015; Secondi, Rodgers, Bayle, Sourice, & Théry, 2015; Troianowski, Melot, & Lengagne, 2014). While negative results are generally difficult to interpret because we do not know whether the animals do not engage in that behaviour (i.e. do not shift between channels) or whether the designs of the studies were simply not able to detect it, we can still glean important insights about signal evolution, meaning and perception as well as experimental design.

In terms of signal evolution, Secondi et al. (2015) suggested that it is possible that the divergence rates of different sensory channels differ. If two channels are used for species identification during mate choice, for example, and one channel has diverged farther than the other over time, the more divergent channel will be more

dependable for species discrimination and the other channel may not be able to act as a backup. As a possible case, [Secondi et al. \(2015\)](#) tested female palmate newts, *Lissotriton helveticus*, on a two-choice test of conspecific males versus males of a closely related species with which they hybridize in nature (*Lissotriton vulgaris*). The experimental design allowed olfactory cues in all conditions but varied across three decreasing degrees of visual cue transmission, intended to simulate the decrease in water clarity from water pollution (see [Environmental Impacts on Signalling Channels That May Lead to Shifts](#), below). The authors predicted that in cloudy water, when visual species recognition was impaired, olfactory cues would compensate, but they found that the females discriminated only in the clear water condition and that olfactory cues did not allow discrimination when vision was occluded. It would be interesting if the olfactory channel was indeed more conserved than the visual channel in the newts; in other organisms such as cichlid fish, olfactory information may be as important as or even more important than visual information for species recognition and assortative mating ([Blais et al. 2009](#)).

Signal meaning plays a role in whether or not a multimodal shift in signal production can occur. If a channel shift involves a change in intensity or structure of a signal, and that in turn changes its meaning, then a shift will not work. As a possible example, [Ríos-Chelén et al. \(2015\)](#) observed the song and visual display of male red-winged blackbirds, *Agelaius phoeniceus*, in varying levels of traffic noise, and predicted that the visual display would become more intense in the presence of noise so as to be more conspicuous and compensate for the masked audio signal. They found, however, that although song changed in noise, the visual display did not. This might be because, as noted by the authors, the intensity of the visual display is indicative of aggressive motivation ([Yasukawa, 1978](#)), so the intensity cannot change without changing meaning. Redundancy in meaning between channels is required for a multimodal shift to work; this will be discussed at length below.

From the point of view of signal perception, it is possible that sensation or perception in some sensory channels is more acutely tuned to the signals in question than in other channels, affecting the success of a channel shift. [Secondi et al. \(2015, page 217\)](#) suggested that the female newts described above may have a 'lower sensory capacity' to make olfactory discriminations than they do to make visual discriminations, rendering it difficult to use olfaction as a backup to the visual channel. This would be interesting to explore further.

It is also possible that experimental design may simply limit our ability to detect a multimodal shift. In studies that use playback methods, the accuracy of the simulation of a signal can affect the animals' response, and it may be difficult to ensure equal accuracy across sensory channels. As a potential example, [Troianowski et al. \(2014\)](#) tested audio/visual mate assessment in European treefrogs, *Hyla arborea*, with and without the presence of added traffic noise. Female frogs chose between two model males, one intended to have high-quality audio but low-quality visual signals, and the other to have high-quality visual but low-quality audio signals. The prediction was that the females would prefer the high-quality audio signal in silence but switch to the high-quality visual signal in traffic noise because of audio masking. However, they found that the female frogs did not switch preferences but consistently preferred the high-quality audio model. The lack of a shift might be explained by experimental design issues. The authors suggest, among other possibilities, that the acoustic simulations may have been more effective or convincing than the visual simulations, explaining the consistent preference shown for the acoustic channel.

Finally, as emphasized above, it is important to clarify whether experimental designs test for a shift in signal production or

perception. It is possible that a production shift might not be found, yet receivers may still shift perceptually between channels. For example, in [Ríos-Chelén et al.'s \(2015\)](#) study described above, the authors concluded that there was no evidence that male blackbirds use the visual display as a backup during signal production since their visual displays did not change in noise. However, it is possible that the visual signals may have still served as a backup to female perceivers without necessitating a change in signal structure. So, from the point of view of perception, it is still plausible that receivers may have done a multimodal shift to rely on visual signals in audio noise. Although their study did not explore receiver perception, future work could be designed to test this question explicitly.

The Role of Redundancy in Multimodal Shifts

For a multimodal shift to work (i.e. continue to convey the same message after the shift), the separate components making up the composite signal need to be redundant in meaning with one another ([Halfwerk & Slabbekoorn, 2015](#); [Partan, 2013](#); [Ríos-Chelén et al. 2015](#)). This leads to the prediction that when animals use redundant multimodal signals, they should be able to make a shift, whereas when using nonredundant multimodal signals, they should not be able to shift.

In this section I explore this prediction in two ways. First, I review the examples introduced above of multimodal shifts as well as cases in which a shift was expected but not found, to see whether the signals could be categorized as redundant or nonredundant. Second, I provide some data on overall occurrences of redundant and nonredundant multimodal signals found in the literature and build some predictions about the expected incidence across channels of multimodal shifting.

If redundancy is required for a multimodal shift to be effective, we would expect the examples of shifts in [Tables 1, 2](#) to be redundant, and the examples in which no shift was found, not as likely to be redundant. Examination of the tables shows this is indeed the case. Of the 16 multimodal shift examples, 10 cases were redundant (in 4 cases stated as such by the authors; in 6 cases surmised as redundant from their text, marked in the tables by 'presumably redundant'). Only one case was nonredundant, and five cases were unknown. So there is support for the prediction that multimodal shifts should have redundant components. Furthermore, in the one case of nonredundancy involving the stickleback fish studied by [Heuschele et al. \(2009\)](#) with nonredundant visual and olfactory components, described above, the females changed their mate preferences when they shifted between sensory channels, demonstrating that shifting channels when the two channels carry different information can lead to alteration of preferred traits, changing the ultimate outcome.

Conversely, there is no expectation of redundancy in cases in which a multimodal shift was not found. If the two sensory channels carry nonredundant information, then shifting between the channels would not work. Supporting this idea, in at least two and maybe all of the three studies that did not find a shift, the signals were suggested to be nonredundant. In the red-winged blackbirds described above ([Ríos-Chelén et al. 2015](#)), the acoustic song could be a long-distance signal given when the threat is low, whereas the visual display provides a short-distance signal when a greater threat is present, suggesting that they function in different contexts. In the newts described above ([Secondi et al. 2015](#)), although both the visual and olfactory channels were presumed to play a role in species recognition, the authors concluded that the channels are 'not entirely redundant' (page 224) because the newts could discriminate between males in clear water but not in cloudy water despite olfactory cues. Finally, in the treefrogs described above ([Troianowski et al. 2014](#)), although

Table 3
Sensory channels used in multimodal signalling, by signal category (redundant or nonredundant)^a

Multimodal sensory channels used	Redundant			Nonredundant		
	Number of cases	Animal	Source	Number of cases	Animal	Source
Acoustic/chemical	2	Fruit fly	Rybak, Sureau, and Aubin (2002)	1	Feral horse	Rubenstein and Hack (1992)
Acoustic/vibrational	1	Moth Honeybee	Conner (1987) Michelsen, Andersen, Storm, Kirchner, and Lindauer (1992)			
Acoustic/visual	3	Chickadee	Baker, Tracy, and Miyasato (1996)	4	Dart-poison frog	Narins, Hödl, and Grabul (2003)
		Chicken	Evans and Marler (1991)		Domestic dog	Bekoff (1972)
		Domestic cattle	Soffie and Zayan (1977)		Human	Motley (1993)
Chemical/vibrational	1	Ant	Markl and Hölldobler (1978)	1	Macaque	Partan (2004)
Chemical/visual				7	Tropical wandering spider	Rovner and Barth (1981)
					Chicken	Rowe and Guilford (1996)
					Crayfish	Acquistapace, Aquiloni, Hazlett, and Gherardi (2002)
					Garter snake	Terrick, Mumme, and Burghardt (1995)
					Gobiid fish	Tavolga (1956)
					Hermit crab	Gherardi and Tiedemann (2004)
Chemical/tactile				2	Ringtailed lemur	Mertl (1976)
					Snapping shrimp	Hughes (1996)
Visual/vibrational				1	Mole-rat	Heth and Todrank (1995)
Total	7			16	Tadpole	Stauffer and Semlitsch (1993)
					Wolf spider	Persons and Uetz (1996)

^a Signals were categorized as redundant or nonredundant by Partan and Marler (2005); more details can be found there.

previous work suggests that audio and visual signals each give information on male quality, suggesting that the two channels are redundant in a general sense, at a more detailed level the channels may represent different information. The authors suggest that audio signals may be more reflective of current energetic state, conveying immediate quality, whereas visual colour signals reflect ability to acquire high-quality food over time, more reflective of long-term quality, although these distinctions are not clear-cut. Whether to consider these redundant or not is therefore affected by the grain of analysis; at a more gross level they are redundant (both dealing with quality), but at a finer level they may not be (see Candolin, 2003, for a similar case).

We have seen that redundancy is common in the cases of multimodal shifts reported above. There are many reasons that we would expect redundancy in communication systems, such as for error reduction in noise (Shannon, 1948; Wiley, 1983), especially under conditions of poor signal transmission (Rand & Williams, 1970). Recent surveys of multimodal communication in general, however, have found that nonredundancy may actually be more common than redundancy, and in fact this was predicted by Candolin (2003) with regard to signals of mate quality. Nonredundancy has other advantages such as increasing information content per unit time (Johnstone, 1996; Partan & Marler, 2005) or targeting different receivers (Candolin, 2003). Otovic and Partan (2009, their Table 6) found that only a minority of general multimodal communication cases were redundant (7 out of 18 cases). Those data are expanded here in Table 3, which shows that even with a slightly larger sample of multimodal signals (23 cases), we still find that a minority (7 cases) were redundant and a majority (16 cases) were nonredundant. That a minority of cases are redundant suggests that the ability to shift channels as a coping strategy for environmental noise may be a somewhat limited option for the majority of animals, although this survey should be expanded now that we have more cases of multimodal communication reported in recent literature.

Table 3 also provides information on which sensory channels are involved in the general redundant and nonredundant examples. The most prevalent modality used in the redundant examples was the acoustic channel (involved in 6 of the 7 cases of redundancy); visual and chemical channels were less commonly used for redundancy (each was involved in 3 cases). Of the nonredundant examples, the most common channels were visual (involved in 12 of 16 cases of nonredundant signals) and chemical (involved in 11 of 16 cases); acoustics were less common (5 cases). Vibration and tactile channels were least common overall.

From the point of view of the sensory channel, signals with acoustic components were equally likely to be redundant (6 out of 11) or nonredundant (5 out of 11), but signals with visual or chemical components were more likely to be nonredundant (12 out of 15 visual signals were nonredundant; 11 out of 14 chemical signals were nonredundant). Therefore, if multimodal shifts require redundancy, it follows that animals that communicate with visual and chemical signals may have a harder time coping with environmental changes that affect signalling channels because visual and chemical channels tend to include nonredundant information that could preclude the ability to shift between channels.

Having seen that it is possible for some animals to shift between sensory channels to avoid environmental degradation or noise, I now turn to the question of whether and how anthropogenic environmental change can affect animal signalling channels, potentially leading to such multimodal shifts.

ENVIRONMENTAL IMPACTS ON SIGNALLING CHANNELS THAT MAY LEAD TO SHIFTS

[C]ommunication methods may be modified by changes in ecology... There is no doubt that many relationships will be discovered in the future between the ecology of animals and the detailed form of their communication signals (Marler, 1959, pp. 196–197)

Signals are tuned to their environment (Endler, 1992), as Marler (1959) predicted. Therefore, when the environment changes, signals need to change. Rapid anthropogenic environmental changes such as urbanization and climate change are increasingly affecting animal signalling channels through the introduction of pollution and other noise sources (Halfwerk & Slabbekoorn, 2015; Partan, 2013; Rosenthal & Stuart-Fox, 2012). Although other effects of urbanization and climate change on animals may be more obvious and pressing, such as population declines due to overcrowding or habitat loss, interference with communication is damaging owing to the centrality of communication to fitness and survival. In this section I examine what types of environmental changes may require animals to shift channels, by examining how sensory channels are affected by HIREC. I discuss these effects sensory channel by channel, but as Halfwerk and Slabbekoorn (2015) noted, environmental disturbances in the form of noise or pollution can also occur simultaneously in multiple channels, with complex effects on animal signalling.

Vision

The visual channel is affected by urbanization and climate change in a number of ways. In terrestrial environments, the rapid development and increase of urban areas not only displace animals from their habitats but, for those that stay in the urbanized areas, also introduce built structures that create visual obstructions to clear sight lines. Although we lack a quantitative comparison of the extent of visual 'noise' in rural versus urban habitats from the point of view of a communicating animal (see Ryan & Partan, 2014), it is likely that the types of visual obstructions in urban areas (buildings, walls, vehicles, etc.) may be more challenging to overcome than the types of visual obstructions in natural areas (trees, vegetation, etc.) because of their relative size and opacity. While natural vegetation can obstruct animal communication particularly when it moves in the breeze, animal signals appear to have evolved over time to adapt to this vegetation movement, such as, for example, lizards using jerky, abrupt motion signals which contrast the smooth, sinusoidal motion of plants (Fleishman, 1992). Built structures, however, are recent enough that there may not yet have been the time required to evolve adequate solutions.

Urbanization also causes a dramatic increase in night-time light, which can interfere with normal communication. This effect is not limited to cities but extends far into natural areas (Swaddle et al. 2015). For example, exposure to artificial light at night can cause a decrease in advertisement calling of frogs and move up the time of dawn song in songbirds (reviewed by: Tuomainen & Candolin, 2011; Swaddle et al., 2015).

In aquatic environments, urbanization, agriculture and climate change are leading to visually polluted waterways via several mechanisms (Partan, 2013; van der Sluijs et al. 2011). Climate change enhances storm activity, leading to more turbulent water and to greater levels of stormwater runoff. Stormwater runoff brings both natural material, such as sediment, and unnatural material, such as pollution from cities and agricultural fertilizers, into the waterways. Increased nitrogen from industrial fertilizers causes eutrophication, or increases in algal growth, which decreases both water clarity and oxygen levels. Suspended particles absorb heat, increasing water temperature. Warmer water cannot hold as much dissolved oxygen as cooler water can (Stramma, Johnson, Sprintall, & Mohrholz, 2008), so oxygen levels continue to decrease as water temperature increases, further clouding the water with decomposing material.

Water clarity is important for successful transmission of visual signals. Seehausen, van Alphen, and Witte (1997) found that African cichlid fish species that were once clearly distinguishable by

colour have lost their distinctiveness in turbid water. The implication is that colour is costly to produce and not worth the cost if it cannot be perceived in water that is cloudy owing, for example, to eutrophication. The consequence is that species lines are being blurred by hybridization, because fish have more difficulty distinguishing conspecifics from heterospecifics. More recent work with stickleback fish by Candolin, Salesto, and Evers (2007) shows that mate choice in turbid water leads to an increase in time and effort on the part of both the females (in choosing) and the males (in courting). Wong, Candolin, and Lindström (2007) found that turbid water interferes with visual communication in sticklebacks and has consequent negative effects on the ability of visual signals to represent honest indicators of quality.

Audition

Urbanization and climate change affect auditory communication by altering the transmission and perception of auditory signals (reviewed in Partan, 2013). Climate change affects sound propagation in both air and water. Urbanization and other human activities cause increases in noise levels, as well as spatial and diurnal variability in noise, and the introduction of large built structures interferes directly with acoustic communication (Warren, Katti, Ermann, & Brazel, 2006).

In air, sound transmission is affected by temperature, humidity and wind (Marten, Quine, & Marler, 1977; Wiley & Richards, 1978), all of which are influenced by climate change (Maslin, 2013). Sound absorption, which affects transmission, varies in a complex fashion with both temperature and humidity and is also dependent on the frequency (pitch) of the sound (Snell-Rood, 2012). Sound absorption has less of an effect on lower-frequency calls. Snell-Rood (2012) found that bats indeed produced echolocation calls of lower frequency in habitats with higher sound absorption and that they varied their call frequency and duration by season, lowering pitch during the rainy season. For bats, lowering pitch helps avoid the strongest effects of sound absorption. Snell-Rood (2012) also found that across a survey of wood warblers, those living in habitats with higher sound absorption sang songs that had a narrower frequency bandwidth. A narrower bandwidth may help improve sound detectability due to concentrating sound and minimizing distortions, potentially compensating for losses due to absorption (Snell-Rood, 2012). These changes with climatic variables suggest that as the climate changes, animals may adjust their signalling behaviour. Potential costs of these adjustments should be assessed.

Wind increases with climate change because of heterogeneous temperature and pressure changes that cause increased air movement between areas. Wind directly affects acoustic transmission of sound (Hayes & Huntly, 2005; Wiley & Richards, 1978). Many animals wait for gaps in the wind to communicate, such as African elephants, *Loxodonta africana* (Garstang, Fitzjarrald, Fristrup, & Brain, 2005), and insects that rely on vegetation for transmitting vibrations (Cocroft & Rodríguez, 2005; McNett, Luan, & Cocroft, 2010). With increased wind, animals may have to find new strategies to be heard.

Sound transmission through water is affected by the acidity of the water. As the water becomes more acidic, low frequencies are absorbed less (Hester, Peltzer, Kirkwood, & Brewer, 2008), and therefore low-frequency sounds travel farther. Anthropogenic activities are contributing to dramatically increasing ocean acidification (Friedrich et al. 2012). Furthermore, the ocean has experienced rapidly increasing levels of high-decibel, low-frequency sound pollution from, for example, seismic surveys of the ocean floor and industrial shipping noises. The increased acidity of the water now allows these low-frequency sounds to pollute vast expanses of ocean.

Whales use low-frequency sound to communicate over long distances, and recent studies have found that their signalling behaviour can change with introduced noise (reviewed in Tuomainen & Candolin, 2011). For example, Miller, Biassoni, Samuels, and Tyack (2000) found that humpback whales sang for longer durations during low-frequency Navy sonar playbacks than at other times, indicating that they expend more energy on communication when competing sounds are present in the environment. Di Iorio and Clark (2010) similarly found that blue whales, *Balaenoptera musculus*, call more often during low-frequency seismic surveys than during quieter periods, however, Melcón et al. (2012) found that during mid-frequency sonar noise, blue whales instead decreased calling behaviour. Moreover, the study mentioned above by Dunlop (2016) found that, although humpback whales were able to shift from vocal to nonvocal surface signals in wind, they did not make this shift in response to vessel noise, suggesting that the ability to cope with natural noise may not always transfer well to anthropogenic noise.

Although effects of underwater acoustic noise have been more commonly studied in marine mammals, noise pollution in the ocean also has many effects on fish. Slabbekoorn et al. (2010) reviewed how acoustic noise affects fish, including impacts on hearing and stress hormones. van der Sluijs et al. (2011) reviewed how anthropogenic environmental change in general affects fish communication and discussed the idea of multimodal shifts to compensate for noise. Radford, Kerridge, and Simpson (2014) proposed possible adjustments that fish can make to their signals in audio noise, including possible multimodal shifts. To date, however, there is only one documented example of such a shift in fish, namely that from vision toward olfaction in sticklebacks discussed above (Heuschele et al. 2009), so at the moment the possibility of a shift away from auditory communication in fish is hypothetical.

Olfaction

Chemical transmission in air is affected by climatic factors such as temperature, wind and humidity. These factors can influence chemical volatility and dispersion, affecting the reach and longevity of pheromonal signals. van Oudenhove, Billoir, Boulay, Bernstein, and Cerdá (2011) tested the stability of ant trails under increasing temperature regimens in the laboratory, and found that high temperatures interrupted the ants' ability to follow a trail. Interestingly, ants living in different environments appear to have different levels of heat tolerance. Urban ants are more heat tolerant than are non-urban ones (Angilletta et al. 2007), which is useful for surviving the urban heat island effect, in which cities have elevated temperatures (Shochat, Warren, Faeth, McIntyre, & Hope, 2006), and shows that in some cases physiology can adapt or accommodate to rapid environmental change.

Chemical communication in aquatic habitats is highly susceptible to interference from anthropogenic pollutants (Rosenthal & Stuart-Fox, 2012). For example, mate choice in fish is mediated by chemical signalling, and can be disrupted by elevation of by-products of agricultural waste such as humic acid (Fisher, Wong, & Rosenthal, 2006) or steroids used for meat production (Tomkins, Saaristo, Allinson, & Wong, 2016). Olfactory cues are used for predator recognition by tadpoles, but even sublethal concentrations of anthropogenic pollutants can impair their predator recognition, potentially contributing to global amphibian decline (Polo-Cavia, Burraco, & Gomez-Mestre, 2016).

Signal Structure

In addition to the aforementioned effects of environmental change on signal transmission, there are also cases of signal

structure itself changing as a direct result of a climatic or anthropogenic factor (Partan, 2013). Ecotherm display behaviour is particularly affected by ambient temperature (Prestwich, 1994). In the case of acoustic and vibrational signals, higher temperatures increase insect metabolism and cause crickets to chirp faster (Hedrick, Perez, Lichti, & Yew, 2002; Walker, 1962) and lacewings to increase the frequency and decrease the duration of their vibrations (Henry, 1983). Frogs alter both pitch and rate of calling with temperature (Gerhardt, 1994), although Wong, Cowling, Cunningham, and Donnelly (2004) found this effect to be modulated by the social environment. In the visual realm, lizards perform displays more slowly when the temperature drops (Phillips, 1995). Electric and olfactory signals can be affected by temperature as well, whereby rising temperatures cause electric fish to increase their rate of electric organ discharge (Silva, Perrone, & Macadar, 2007) and moths both to increase their rate of pheromone emission (Liu & Haynes, 1994) and to alter the circadian periodicity of their emissions (Haynes & Birch, 1984). Because reproductive isolation among sympatric moth species is maintained by the circadian periodicity of their emissions (Haynes & Birch, 1986), these temperature-induced changes can have fitness consequences.

Anthropogenic pollutants, such as industrial chemicals and other endocrine disruptors, can have many other effects on animal signal production by causing developmental stress and affecting hormone-driven display behaviour (reviewed in: Shenoy & Crowley, 2010; Rosenthal & Stuart-Fox, 2012; also see Clotfelter, Bell, & Levering, 2004, for a general discussion of the many effects of endocrine-disrupting chemicals on behaviour, including communication).

CONCLUSION

[For a] detailed review of the evolution of the communication systems of animals ... [w]e would need to present comparative data, on a much larger scale ... together with discussion of the special problems which arise with the different sensory modes (Marler, 1961, pp. 315–316)

In this essay I developed and explored the argument that the ability to switch signalling across channels, from a noisy channel to a relatively quiet one, may be key for the ability of an animal to cope with rapid anthropogenic environmental change. I surveyed examples of multimodal shifts and what channels were used in these shifts, and assessed the prediction that redundancy is required for a shift to be successful. I then reviewed how anthropogenic environmental change (or HIREC, Sih et al., 2011) affects communication channels and suggested that animals that can shift channels will have an advantage in coping with HIREC. Since choice of signal channel is tied to the environment (Marler, 1967), and environmental change alters the costs and benefits of using a particular channel, then environmental change should lead to channel changes (see van der Sluijs et al. 2011).

If redundancy is required for a multimodal shift to work, and if multimodal shifts help animals to cope with HIREC, then it follows that animals that use redundant signals should be more successful. As noted above, many animal communication systems include redundancy for error correction (Rand & Williams, 1970; Wiley, 1983). It is interesting therefore that many multimodal communication examples appear to be nonredundant rather than redundant (see Table 3). We need more complete surveys in this area to see if this holds more widely. It would be helpful for researchers studying multimodal communication to identify whether the signals they are studying are redundant or nonredundant, so as to add more data to the survey of sensory channel and signal category shown in

Table 3 and help build on these predictions. Including information on the environment would help predict how the environment influences these variables (Endler, 1992). Noisy environments should be associated with redundancy; it would be useful to come up with standards for noise measurement across sensory channels to test this prediction.

A point relevant to this work is that some composite signals are made of obligate or fixed components that always occur together (see Tables 1, 2), such as mouth shape and corresponding vocalization in macaques (Partan, 2002), whereas the components of other composite signals are free to vary, such as vocalization combined with a visual gesture unrelated to the mouth (Partan, 2002; also see: Partan & Marler, 2005; Smith, 1977). Sensory channels may differ in the extent to which each is a fixed or variable component of a signal (Wilson, Dean, & Higham, 2013). Furthermore, it may be that obligate partners are more likely to be redundant than are flexible components. For example, vocal sac expansion in a frog produces visual and acoustic components that are obligate partners, whereas combinations of, for instance, visual and olfactory components may be flexible. Perhaps the use of different physiological systems to produce the signal components may allow decoupling of meaning. This is worth exploration.

In continued work on multimodal shifts it will be important to determine clearly whether the shift occurs in signal production or is evident only during signal perception (see examples in Tables 1, 2). Of course, if a channel shift in production occurs, then perceivers also must shift channels during perception. However, a shift in perception does not require a production shift. This point is related to the issue of whether we classify the meaning of a communication signal from the point of view of the sender or the receiver. For example, a signal may be considered redundant in terms of its information content (e.g. in wolf spiders, *Schizocosa floridana*, where both leg colour and rate of seismic signalling reflect a high-quality diet; Rundus, Sullivan-Beckers, Wilgers, & Hebets, 2011) but nonredundant in terms of receiver response (female wolf spiders pay attention to seismic, but not visual, signals for mate choice; Rundus et al. 2011). This complicates the communication system as well as our attempts to categorize signals. To achieve clarity, it will help if researchers do their best to identify which point of view a study addresses: sender/production or receiver/perception.

Future work on multimodal shifts should also strive to distinguish individually facultative (behaviourally plastic) context-dependent shifts from evolved or population-level shifts. For example, during a noisy conversation, we may shift as needed between relying solely on vocal cues and augmenting these with visual cues of articulation. This is a different sort of shift than one that evolved over time in a population owing to, for example, living near a noisy area (further examples are given in Tables 1, 2). Keeping in mind that there is a continuum between plasticity and canalization, see Ord et al. (2010) for a discussion of the role of plastic and evolved changes in response to naturally fluctuating environments, and Sih et al. (2011), Tuomainen and Candolin (2011), and Wong and Candolin (2015) for discussions of the relative roles of behavioural plasticity and evolutionary history in coping with HIREC in particular. Note that in addition to context-dependent, individual facultative shifts and population-level evolved shifts, it is also possible in some species for individuals to shift reliance between sensory modalities during ontogeny. For example, guppies reared in low-light conditions compensate later in life by relying more heavily on chemoreception than on vision (Chapman, Morrell, Tosh, & Krause, 2010).

I hope that connecting the recent work on multimodal communication involving shifts between sensory channels with the work on behavioural responses to rapid environmental change may lead to a greater understanding of some of the 'special

problems' (Marler, 1961) of communication, as well as help to predict how animals will fare with environmental change.

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