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Issues in the Classification of Multimodal Communication Signals

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ABSTRACT: Communication involves complex behavior in multiple sensory channels, or “modalities.” We provide an overview of multimodal communication and its costs and benefits, place examples of signals and displays from an array of taxa, sensory systems, and functions into our signal classification system, and consider issues surrounding the categorization of multimodal signals. The broadest level of classification is between signals with redundant and nonredundant components, with finer distinctions in each category. We recommend that researchers gather information on responses to each component of a multimodal signal as well as the response to the signal as a whole. We discuss the choice of categories, whether to categorize signals on the basis of the signal or the response, and how to classify signals if data are missing. The choice of behavioral assay may influence the outcome, as may the context of the communicative event. We also consider similarities and differences between multimodal and unimodal composite signals and signals that are sequentially, rather than simultaneously, multimodal.

Keywords: animal communication, multisensory, multichannel, composite signal, redundancy.

Animals communicate with their entire bodies and perceive signals with all available faculties (vision, audition, chemoreception, etc.). To best understand communication, therefore, we must consider the whole animal and all of its sensory emissions and percepts. Although it has

been known for years that multiple sensory systems are important for communication (Darwin [1872] 1965; Beach 1951; Tinbergen 1959; Marler 1965), there has been little study of the relationships among and the integration of components from different sensory channels until recently. New advances in experimental facilities, and in computer interfaces for audio and video analysis systems in particular, have allowed us to gather empirical evidence of the interactions of multiple sensory channels (e.g., Cragon de Caprona and Ryan 1990; Evans and Marler 1991; Stauffer and Semlitsch 1993; Marples et al. 1994; Heth and Todrank 1995; Terrick et al. 1995; Baker et al. 1996; Hughes 1996; Persons and Uetz 1996; Rowe and Guilford 1996; Scheffer et al. 1996; Fusani et al. 1997; Roper and Marples 1997; Massaro 1998; Hassler and Brockmann 2001; Partan 2002). To bring cohesion to these new data, we previously proposed a classification system with which to categorize different types of multimodal signals (Partan and Marler 1999; Partan 2004). Here we discuss issues, complexities, and difficulties to consider when classifying multimodal signals.

This article begins with an introduction to multimodal communication, including functional considerations such as costs and benefits of multimodal signaling, and a brief review of our classification system for categorizing multimodal signals, with illustrative examples in tables 2 and A1 in the online edition of the *American Naturalist*, followed by a discussion of issues in the categorization of multimodal signals, including how to classify signals if data are missing, the choice of categories and of behavioral assay, issues of meaning and context, similarities and differences between multimodal and unimodal composite signals, and signals that are serially versus simultaneously multimodal. We conclude with suggestions for further work.

Multimodal Communication

Multimodal (or multisensory) communication is defined as communication via composite signals received through more than one sensory channel. We use the word “signal”

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(or “composite signal”) to refer to the entire set of communicative features (“components”) of an animal’s behavior that occur simultaneously. Our examples of composite signals include both those that Smith (1977) called “fixed,” in which the signal components are always emitted together as obligatory partners, and those that he called “fluid,” in which the signal components do not always occur together or are “free” (Wickler 1978; see Marler 1961).

Multimodal signals differ from unimodal composite signals in that the additional channels afford new constraints and opportunities for communication. In this section, we describe multimodal signals using humans as an example, then discuss the function and evolution of multimodal signals and their costs and benefits in comparison to unimodal ones.

Multimodal signals are important in human communication. McGurk and MacDonald (1976) demonstrated that the perception of speech sounds by adults is modulated by observation of the accompanying articulatory gesture (now dubbed the “McGurk effect”); Kuhl and Meltzoff (1982) showed that even in infancy, humans can recognize the correspondence between visual and auditory aspects of speech and are able to detect discrepancies. Massaro (1998) has elaborated on this work by creating a virtual animated talking face and conducting perceptual experiments by manipulating the degree of conflicting audio and visual speech information. He has proposed that we rely on both channels to understand the signal, giving more weight to the channel with the most reliable information. Support for this perceptual model was found in multisensory perception of emotion as well (Massaro and Egan 1996), although there may be other explanations for the data (de Gelder and Vroomen 2000).

Vocalizations of nonhuman primates can also have unique visual accompaniments. Following the leads provided by Huber (1931) and Andrew (1963), several researchers have described distinct, externally visible articulatory gestures that accompany nonhuman primate vocalizations (in chimpanzees: Marler and Tenaza 1977 and Bauer 1987; in rhesus monkeys: Hauser et al. 1993 and Partan 2002). This work suggests that nonhuman animals also have the raw material necessary for detecting visual and vocal correspondences. Ghazanfar and Logothetis (2003) replicated a “McGurk-like” effect in macaque monkeys, showing that the subjects matched vocalizations with the corresponding facial gesture that originally accompanied the sound, and Parr (2004) found the same in chimpanzees.

The phenomenon of multimodal communication is important in many disciplines, from zoology, ethology, and behavioral ecology to psychology, perception, and cognitive neuroscience. Next, we review the function and evolution of multimodality.

Neural multisensory integration is reviewed by, e.g., Horn (1983b), Stein and Meredith (1993), Stein et al. (1995), King and Calvert (2001), and Calvert et al. (2004).

Function of Multimodal Signals

Some functions of multimodal signaling are unique to the coincidence of multiple channels. For example, detection and localization can be improved by using more than one channel. Attention can be attracted with one channel while a second channel carries the message. Quality can be indicated by carefully coordinating disparate signal components, as with male jumping spiders (*Habronattus dos-senus*) coordinating visual displays with complex seismic signals as an indicator of quality for mate attraction (Elias et al. 2003). Ambiguous messages sent in one channel can be clarified by adding a more specific component in another channel, such as when male Cuban grassquits (*Tiaris canora*; Baptista 1978) or female red-winged blackbirds (*Agelaius phoeniceus*; Beletsky 1983) use the same visual display for aggression and courtship but add vocalizations to distinguish the two contexts. Distance estimates between sender and receiver can be made by comparing arrival times of signals in different channels, as when morning warblers (*Cichladusa guttata*) estimate distance based on the phase mismatch of simultaneously produced audio and visual components (Todt and Fiebelkorn 1979) or when white-lipped frogs (*Leptodactylus albilabris*) compare arrival times of airborne and seismic components of male advertisement calls (Lewis et al. 2001).

Other functions of multimodal signaling could potentially apply to any composite, multicomponent signal. For example, habituation can be decreased by using more than one component (Todt and Fiebelkorn 1979). One component can prime or modulate readiness to respond to another, as with ants or bees using vibration to activate other individuals in the colony (Markl and Hölldobler 1978; Visscher et al. 1999; Schneider and Lewis 2004). One component can enhance the “memorability” of partner components (Guilford and Dawkins 1991), as may occur in compound learning (Rowe 1999b, 2002). Additional signal components can amplify a message to increase, for example, male mating success (Hasson 1989).

Evolution of Multimodal Signals

Game theorists have built elegant models for predicting when multicomponent, and occasionally multimodal, signaling should evolve, particularly in the context of sexual selection (e.g., Møller and Pomiankowski 1993; Schluter and Price 1993; Iwasa and Pomiankowski 1994; Johnstone 1995, 1996; Møller et al. 1998). These models are reviewed

Table 1: Benefits and costs of multimodal communication

Benefits	Costs
Multiple redundant signal components provide insurance that the message will be received, and they correct for possible errors of signal detection and identification	Production, coordination, reception, and cognitive and neural integration of multiple signals may have high energy costs and require extensive anatomical and physiological equipment
Multiple nonredundant signal components provide increased information content; nonredundant components may each play a different functional role (e.g., one may attract attention, and another may transmit more specific information)	The use of multiple channels can increase risk of predation: senders may be more conspicuous to eavesdroppers because of signaling in more channels, or they may attract a new predator by signaling in an additional channel; receivers may be more vulnerable to predation by devoting more senses to detecting conspecific signals and leaving fewer free to detect predators

elsewhere (Bradbury and Vehrencamp 1998; Grether et al. 2004). Here we discuss basic requirements for the evolution of multimodal signaling and costs and benefits of multimodal communication. While the evolution of multimodal signals is to a large extent specific to the function of the signal (e.g., courtship, aggression, affiliation, territoriality, antipredator behavior), there are some general commonalities: the signaler must produce signals simultaneously in more than one sensory channel, and the receiver must have the ability to detect and integrate signals from multiple channels. Given that these conditions exist in many cases, we next examine environmental factors, both biotic and abiotic, that favor multimodal signaling.

Biotic factors include the type of noise made by sympatric species: excessive acoustic noise, for example, may encourage the evolution of visual signals and vice versa. Simultaneous use of multiple channels is facilitated if the interacting animals are spatially close enough to see, hear, smell, and/or touch one another. For this reason, multimodal signals may be particularly appropriate for short-distance communication and may facilitate the use of graded rather than discrete signals, as occurs in group-living species (Marler 1965). Additional influences of receivers on signaler behavior were discussed by West and King (1988), Guilford and Dawkins (1991), and Rowe (1999b).

Abiotic factors also can influence the evolution of the signal channel used in both multimodal and unimodal situations, although they may not be as important as biotic factors for the multimodal case. Abiotic factors include habitat density (less dense areas facilitate visual signaling as part of the suite of signals) and substrate composition (some substrates transmit seismic signals better than others, encouraging the evolution of vibrational components). The evolution of multimodal signaling will depend further on the benefits and costs of communicating in multiple channels.

Benefits and Costs of Multimodal Communication

Benefits. Signaling in multiple channels proffers benefits and costs to both the signaler and the receiver (table 1; see Marler 1959, Endler 1992, and Rosenthal and Ryan 2000 for further discussion). Here we focus on the unique benefits of simultaneous communication in multiple channels. The use of more than one channel allows the signaler to contact receivers in more than one way, with implications for signal range, locatability, temporal coding, and the size of the potential signal repertoire.

The amount of information available in signals that include multiple sensory components is potentially greater than that available in a single-channel signal. The type of benefit gained from this potential increase in information capacity depends, in part, on whether the signal components in the various channels contain redundant or non-redundant information.

Redundant multimodal signals provide insurances against noisy channels (Rand and Williams 1970; Wilson 1975; Krebs and Dawkins 1984). For example, if the auditory channel is jammed by signals from other animals, a redundant visual signal may give some insurance that the message will still be received and recognized accurately. This benefit is shared by receivers as well as senders because it is in the receiver's best interest to identify a signal correctly, no matter how this may then be acted upon. A common example is the "cocktail party" phenomenon with human speech: it is easier, in noisy situations such as a crowded room, to understand a speaker who can be both seen and heard (see Cherry 1953 and Sumbly and Pollack 1954; Partan 2004 discusses this further).

Very important signals are likely to be redundant because of the great costs of missing or misidentifying signals given to potential mates or predators. Noncooperative contexts, in particular, may favor the evolution of loud, conspicuous, redundant signals (Krebs and Dawkins 1984). Bradbury and Vehrencamp (1998) suggest that mul-

timodal signals may evolve through ritualization such that vocalizations are added to visual or tactile signals to make a display more conspicuous.

There have been fewer reports of nonredundant multimodal signals. Nonredundant signals provide the benefit, shared by senders and receivers, of increased information content per unit time. Endler (1993) suggested that animals using multiple sensory channels will send different information in each channel. For example, two channels may play different roles in communication: a signal component in one channel may attract the receiver's attention, while signal components in other channels carry more subtle information requiring an attentive receiver (Wiley and Richards 1982). A displaying blue-black grassquit (*Volatinia jacarina*), for example, leaps 30–45 cm straight up out of the grass while vocalizing (Wilczynski et al. 1989). The leap allows receivers to better localize the acoustic signal.

Costs. Costs of producing and receiving multimodal signals are less well studied. Potential costs to the signaler could include increased energy required to send multiple signal components, although it is also possible that multimodal signals might use the same amount of energy but divide it among the channels in such a way that lower quality signals were sent in each channel, combining to be effective. The dramatic multimodal visual and acoustic courtship display of male sage grouse is known to be energetically expensive (Vehrencamp et al. 1989), although we do not have comparison figures for the energetic expense of each channel alone. Adding signal channels may also carry the survivorship cost of preempting body parts used for signaling from other functions that they may serve or increasing the risk of detection by eavesdroppers, such as predators or parasites. Some channels may be more vulnerable to exploitation than others. Most examples of exploitation of mate attraction signals are in the acoustic or chemical channels (Zuk and Kolluru 1998).

Potential costs to the receiver include increased energy requirements of receiving and processing multiple signals, neural and cognitive costs of signal integration, and survivorship costs if dedicating more sensory equipment to detecting and analyzing the signal distracts the receiver from other tasks, such as predator detection. Vehrencamp (2000) discusses how the type of cost incurred (production or reception, etc.) allows us to distinguish between signal categories common in the modeling literature (handicap, conventional, index, etc.).

Classification of Multimodal Signals

To organize research on the co-occurrence of multiple signal components and the effects of multimodal signals

on others, we have proposed a comprehensive classificatory framework (fig. 1; Partan and Marler 1999). We present this classification system in the hope that it will encourage others to gather more complete information about the effects of both multimodal signals and their component parts. Here we briefly review the categories with reference to cases that exemplify each category (table 2). A longer online table contains more examples, and Partan (2004) provides details on many of these. The classification fits all signals, regardless of message conveyed, including signaler status or condition, intentions, and information about the environment (Krebs and Dawkins 1984). Signals can be classified even if they are viewed as not transmitting information at all but are instead thought to manipulate or persuade (Dawkins and Krebs 1978) or manage the behavior of others (Owings and Morton 1997).

Figure 1 presents the receiver's point of view in a communication interaction: geometric shapes symbolize responses to signals. We take this approach because the response of receivers is the primary means of deciphering the meaning of a nonhuman animal signal (Marler 1959, 1961; Wilson 1975). Furthermore, receiver assessment plays an important role in the evolution of communication signals (Ryan and Rand 1990; Guilford and Dawkins 1991; Owings and Morton 1997; Rowe 1999b). Note that the "response" of the recipient can be a physical action, an internal physiological response, or even no response (information theory analyses of crayfish behavior show that doing nothing can have informative value; Gherardi and Pieraccini 2004).

Levels of Classification: Redundant versus Nonredundant Signals

There are two types of multimodal signal composites: those whose components are redundant, or mean the same thing, and those whose components are nonredundant, meaning different things. Redundant signals have also been labeled "backup signals" (Johnstone 1996) and nonredundant ones "multiple messages" (Møller and Pomiankowski 1993; Johnstone 1996).

Empirically, the difference between the two types can be determined by the behavior that the signal components elicit from a recipient (Partan and Marler 1999; Partan 2004). When presented individually, redundant signal components should have equivalent effects on a receiver, while nonredundant components should have different effects. The effect of redundant signal components presented together can be identical to that of either component on its own (equivalence; see fig. 1), or the response can be increased (enhancement). Nonredundant signal components in combination can each continue to have an effect (independence), or one can overshadow or change the

SEPARATE COMPONENTS		MULTIMODAL COMPOSITE SIGNAL		
	signal response	signal	response	
Redundancy	a → □	a + b →	□	Equivalence (intensity unchanged)
	b → □	a + b →	□	Enhancement (intensity increased)
Nonredundancy	a → □	a + b →	□ and ○	Independence
	b → ○	a + b →	□	Dominance
		a + b →	□ (or □)	Modulation
		a + b →	△	Emergence

Figure 1: Classification of multimodal signals (after Partan and Marler 1999; Science 283:1272–1273. Copyright AAAS). Redundant signals are depicted above and nonredundant ones below. In the first column, the responses to the separate components of multimodal signals are represented by geometric shapes. Only two components are included (*a* and *b*), but more components could be added. The components of redundant signals are followed by equivalent responses (the same geometric shape indicates the same qualitative response). The responses to nonredundant components are not equivalent (a new shape represents a qualitatively different response or, in some cases, no response). On the right is the response to the combined multimodal signal. In the case of redundancy, the response can be equivalent to the responses to individual components, or it can be qualitatively similar but increased by degree (enhanced). The relationship between nonredundant signal components can be one of dominance, independence, modulation, or emergence. See tables 2 and A1 in the online edition of the *American Naturalist* for examples.

effect of the other (dominance or modulation, respectively; see Markl 1985 and Hölldobler 1999 for discussion of modulation), or their combination may elicit an entirely new result (emergence). In the latter case, there may be no response at all to the individual unimodal components until they are combined. Nonredundant multimodal signals may present examples of combinatorial syntax, if the change in response is a logical product of their meanings when used alone or in other combinations (Mitani and Marler 1989).

Note that when we speak of a signal “affecting receiver behavior,” we intend it as a shorthand and do not discount other influences that bear on receiver behavior, such as individual differences in genetic makeup and experience, current social situation, and motivational states or environmental conditions (see Endler 1992). We are aware that signal *x* does not always elicit response *y*, but we use words like “elicit” or “affect” to convey the idea that response *y* is more likely to occur after signal *x* is received than it would be otherwise. We will return to a discussion of context below.

Issues in the Classification of Multimodal Signals

We have laid out a general framework with which to understand the large variety of combinations of signal components possible in animal communication systems. Like all representations of natural systems, this one is, by necessity, simplified. The classification involves unidirectional communication via a simple bimodal signal between only one sender and one receiver. In real life, communication events are often much more complex; below, we address some of the issues that arise.

Terminology

We have attempted to be consistent with terms used in previous ethological literature. Related work on applications of insect pheromone blends uses the term “redundant” to mean that multiple components elicit the same response, so that one component could be replaced or removed without any consequence to the signal efficacy (e.g., Borden et al. 1990; D. P. W. Huber and J. H. Borden, unpublished manuscript). This usage is identical to our

Table 2: Multimodal signal examples

Taxa	Behavior	Component <i>a</i> ; response to <i>a</i>	Component <i>b</i> ; response to <i>b</i>	Response to multimo- dal signal <i>ab</i>	Proposed signal category	Reference
Honeybee <i>Apis mellifera</i>	Mechanical model bee recruits live bees to food source	Acoustic (buzzing component of waggle dance); response = recruitment	Vibration (vibratory component of waggle dance); response = recruitment	Recruit same number of bees as <i>a</i> and <i>b</i>	Equivalence	Michelsen et al. 1992
Fruit fly <i>Drosophila melanogaster</i>	Courtship	Acoustic (playback of wing vibration song); response = 37% mated	Chemical (hydrocarbons on male cuticle); response = 10% mated	More successful matings (61%)	Enhancement	Rybak et al. 2002
Tropical wandering spider <i>Cupiennius salei</i>	Courtship	Chemical (pheromone); response = undirected male courtship behavior	Vibration (from abdomen and leg movement); response = males move in female's direction	Males court in the female's direction	Independence	Rovner and Barth 1981
Dog <i>Canis familiaris</i>	Play solicitation	Visual (paw lift, presumed play); not tested alone	Acoustic (growl, presumed aggression); not tested alone	Play behavior elicited	Dominance	Bekoff 1972
Dart-poison frog <i>Epipedobates femoralis</i>	Aggression toward intruding robotic frog	Visual (mechanical frog model with stationary or pulsing vocal sac); response = none	Acoustic (audio playback of frog vocalizations); response = some males approached	Almost all males approached; some were aggressive (depending on motion of sac)	Modulation	Narins et al. 2003
Chicken <i>Gallus domesticus</i>	Aversion to unpalatable prey items	Visual (red or yellow coloration on artificial prey items); response = none	Chemical (pyrazine odor); response = none	Strong aversive response	Emergence	Rowe and Guilford 1996

Note: Signals are made of two components, *a* and *b*. An example is provided for each category from figure 1. Further examples are found in table A1 in the online edition of the *American Naturalist*.

subcategory of redundancy called “equivalence.” We believe that it is appropriate to also consider redundancy more broadly to include all cases in which the single components elicit the same response, regardless of whether the combination of components may elicit a greater response.

We divided redundancy into two types, “equivalence” and “enhancement.” Leger (1993) labeled the first case “additive” and the second “synergistic.” We believe that our labels are less ambiguous and more fitting, since in the first case there is no increase in intensity of response, while in the second case an increase occurs. We avoided the terms “additive” and “synergistic” because they have been variably defined in the past, from a mathematical summation to any increase of response to a multiplicative increase (Köster 1969, Aydin and Pearce 1997, D. P. W. Huber and J. H. Borden, unpublished manuscript, respectively). Our term “enhancement” includes any increase in response over the unimodal cases, whether a mathematical sum or multiplicative increase (Partan 2004).

Entirely different terms were used by Horn (1983a), who classified motor responses to multisensory stimulation, focusing particularly on orientation behavior shown to light and gravity in flies. He suggested that a response could, for example, be controlled by different modalities successively (“trigger effect”) or simultaneously (“coupling”) or that the response could be a blend between the two, if they give competing information (“compromise”).

Choice of Categories Used and Issues of Prevalence

A division of multimodal signals into the two main categories of redundant and nonredundant composites is supported by both empirical research (see tables 2, A1) and theoretical models (Møller and Pomiankowski 1993; Johnstone 1995, 1996). In an early review of composite signals, Wilson (1975) wrote that “signals transmitted through different sensory channels are often combined in ways that increase information. In some instances the signals are simply redundant Components in different modalities can be added as part of the graded intensification of a signal. ... Other animals use more or less orthogonal gradients of display” (p. 189). Here Wilson has indicated that signal components can be redundant or orthogonal, such as a combination of threat and fear displays. Redundancy is common: Rowe (1999b) suggests an explanation for this, in that simultaneous conflicting signals would lead to decrements in reaction time and response accuracy. Between the two subcategories of redundancy discussed here, enhancement appears to be more common than equivalence (Seitz 1940; see discussion of Seitz’s law of heterogeneous summation in Partan 2004).

Among the four subcategories of nonredundancy, mod-

ulation appears to be most common, and dominance and emergence appear to be rare (tables 2, A1). Dominance of one component over another is a concept commonly found in expository writings. For example, Loizos (1966) suggested that if two conflicting signals are given simultaneously, one communicating play and the other aggression, the play signal will take precedence, and Bekoff (1972) provided an anecdotal example of this in dogs (table 2). Empirical studies are needed, however, as Marler (1976) reached the opposite conclusion concerning play and aggression in a study of graded and discrete vocal signals in chimpanzees. The context of the multimodal signal may influence which component of a display is dominant. In the human ethological literature, the primacy of visual signals for detection of deception has been debated extensively (see Noller 1985 for review). In compound learning, a component that is much more intense than another can overshadow the secondary component, a phenomenon similar to our “dominance” category. Rowe (1999b) suggested that overshadowing probably does not exist in natural communication systems because it would not benefit the signaler. This may explain why we have found so few examples of dominance in our review of the literature.

Issue of Missing Data

To categorize signals, ideally we need data on responses both to the multimodal composite signal and to each unimodal component. In practice, however, our ability to categorize these signals definitively is often limited because researchers have not tested the unimodal condition or have tried but found it difficult to test (Leger 1993). Knowing the response to each unimodal component separately is necessary in order to determine whether the components have the same or different effects. Without this information, therefore, we cannot begin the classification at the broadest level into redundant or nonredundant categories. In many cases (lower section of table A1), we have information on only one of the unimodal components as well as on the bimodal composite. With this type of information, we can begin to judge subcategory adequately, but since we cannot determine whether the signal is redundant or nonredundant, we cannot make the final classification. An example of an experiment that needs one more condition tested before the signal can be completely classified is an elegant study of the effects of chemical and visual cues on sex recognition in male crayfish by Acquistapace et al. (2002). Males did not respond to chemical cues alone but required both chemical and visual cues to significantly change their behavior. The visual-alone condition was not tested. The authors suggest, rightly, that the study would have to be expanded to test the visual

condition before we can classify the signal into our categorization scheme. However, according to our definitions, the signal can already be classified as nonredundant because the chemical cues alone produced no response, and by definition, redundant components alone must produce some kind of response. The subclassification of the signal into, in this case, emergence or modification will be possible only with more information on the visual condition alone.

Issues of Meaning and Context

Rowe (1999a) assumed that we (Partan and Marler 1999) categorized signals only by "information content" or "meaning." While this may have been implied by our emphasis on receiver responses, we believe that all signals and displays can be classified into the proposed categories, regardless of whether one subscribes to the perspective that signals carry information. A related assumption that signals must be adaptive to be classified in our system is equally unintended. Nonadaptive behaviors can be as well classified as adaptive ones.

Some authors have considered behaviors that occur concurrently with signaling behavior to be "contextual" to the signal (Smith 1965; Leger 1993). Here, rather than regard one component as the "signal" and another as "context," we prefer to regard all components of a display that are accessible to the receiver to be potential contributors to the signal.

Context, in the sense of the external events preceding and surrounding the signal, however, can matter a great deal. Responses to communication signals can differ depending on who gave the signal, the relationship and the history of the relationship between the individuals, when and where the signal was given, and so on (Leger 1993; Rundus and Hart 2002). Categorizations using the scheme discussed here are, therefore, context dependent. For example, Tavolga (1956) studied visual, chemical, and acoustic communication in teleost fish (*Bathygobius soporator*). He found that some males needed only olfactory cues from a female to elicit full courtship behavior but that other males needed visual information along with olfactory cues before they would court. In the same system, the females did not respond to either olfactory or visual cues alone from males but needed to hear male grunts before they would respond. The categorization of these signals must therefore be informed by the context: who gives the signal and who responds.

Animals may use flexibility in their immediate choice of signal components and channels, depending on the context or in order to solve problems such as attracting mates without attracting predators (Ryan and Rand 1990; Endler 1992). For example, to avoid predation some insects switch

from using airborne songs for mate attraction to using substrate-borne vibrations (Belwood and Morris 1987; Henry 1994). Wolf spiders (*Schizocosa* spp.) can switch to reliance on visual components of visual-vibratory courtship signals if the substrate is not conducive to vibration (Scheffer et al. 1996).

Choice of Method and of Behavioral Assay

The responses measured in the studies reviewed here vary widely by taxa, method, and question studied. An excellent review by Uetz and Roberts (2002) covers techniques for studying multimodal communication in spiders, but the methods are widely applicable to other taxa. They discuss cue isolation studies, cue conflict studies, and playback methods. Cue isolation studies involve allowing receivers access to one signal component at a time and also to the compound signal as a whole, using a live signaler to produce the signal. Playback methods involve using audio or video recordings, with the stimulus either faithful to the original or manipulated in any of numerous ways. Manipulations have included changing the visual, acoustic, or vibratory features of the signal, or, in cue conflict studies in spiders, mismatching one component from a conspecific and another from a heterospecific (Uetz and Roberts 2002). In other taxa, cue conflict can also include mismatching signal components across emotional categories (e.g., playing threat vocalizations mismatched with submissive postures in primates; S. R. Partan, unpublished manuscript). Another method for multimodal presentations makes use of mechanical robots with multiple behaviors (Michelsen et al. 1992; Narins et al. 2003; S. R. Partan, unpublished data; table 2).

The number of behavioral responses measured in a study is important. If only one behavior is measured, then the conclusion reached will pertain, of course, to that behavior only. For example, say a female responds with behaviors x and y to multimodal stimuli of a courting male (stimulus ab , using terminology of fig. 1). With playback methods isolating each component of the male signal, it is discovered that the number of female x -responses is low to each unimodal presentation on its own (components a or b) but higher to the multimodal signal (ab). We would conclude that this is an example of enhancement, a subcategory of redundancy. However, if response y is also measured and it turns out that the females do not show response y at all to component a of the male's display but show a great deal of response y to component b , then with this fuller picture of the female's response we would have to classify the male's signal components as nonredundant rather than redundant (because the unimodal components a and b each evoked a different response when the female's behavior was assessed more broadly). Among the subcat-

egories of nonredundancy, we would then classify this example as modulation, in that response x to the multimodal signal ab was increased by the combination of the two modalities. The conclusion to draw from this example is not that the study of one isolated response behavior is invalid but that we must carefully limit the generalizability of such a study and strive to obtain a fuller understanding of the response.

One potential limitation of the use of playback studies for studying multimodal communication is that the different channels may not reproduce equally well. If acoustic components of a playback are more true to the original than, for example, visual components of a video playback, then the two channels may appear differentially efficacious when in fact their disparate effects are due to the quality of the simulation. Since the response of the animal is the only metric we have, this point deserves careful consideration when designing studies. Playback experiments should always begin with verification that the behavior elicited resembles that evoked by live animals and that the behaviors displayed in captivity closely resemble their natural counterparts.

Inferences from Studying the Signal

Quantitative analyses of the structure of animal displays, as opposed to analyses of the responses, only indirectly allow us to classify the signals according to figure 1. For example, Fusani et al. (1997) studied in detail the bow-coo display of the male Barbary dove (*Streptopelia risoria*). They found that the coo component differed individually among males but that the visual aspects of the bowing did not. On the basis of these data, Fusani et al. suggested that the coo may function in individual recognition, whereas the bow serves the more general cause of gender recognition. If so, then the bow-coo display would be an example of independence, in which each component has a different meaning that is retained when emitted in synchrony. The responses to the bow and coo need to be documented to confirm this proposition (see Partan et al., 2005). In another example, Elias et al. (2003) described elaborate seismic signals that accompany various visual displays of male jumping spiders (*Habronattus dosseus*). On the basis of when and where the signals occur, they argue that the signals are unlikely to be redundant. To be certain of this classification we will need data on responses to the two components.

Other Types of Composite Signals

In this section, we discuss categorization of other types of composite signals not described above, such as unimodal composites and trimodal or even more complex signals.

Unimodal signals. Composite signals can be complex even when they are only unimodal (i.e., all components are in the same sensory channel). Here we list some examples, followed by a discussion of how to categorize unimodal composites.

Visual signals. Visual signals of facial expressions and body postures in primates, for example, can involve many co-occurring signal components (Marler 1965, 1967; Zeller 1986; Partan 2002). One body part alone can have several visual features that vary independently, such as hue, brightness, and speed or direction of movement (Vine 1970; Endler 1993), and these different features may even be processed along independent routes in the brain. Taken to a micro level, even a single color patch on a fish can be considered a composite trait with multiple pigment types (Grether et al. 2004).

Acoustic signals. Multiple simultaneous auditory signals can be produced, as when a chimpanzee pant-hoots and drums on tree trunks with hands and feet (Goodall 1986). Some organisms can produce multiple synchronous vocalizations using different parts of the vocal apparatus (birds: Nowicki and Marler 1988, Suthers 1990; cetaceans: Cranford and Amundin 1989; primates: Brown and Canino 1995). In any complex sound, some features can be varied separately within the vocal channel (Marler 1992; Vehrencamp 2000). In human speech, frequency, amplitude, and temporal pattern can vary independently and carry different information (Scherer 1985).

Olfactory signals. Multiple chemical signals can be produced simultaneously by separate glands on the body (e.g., in ants; Hölldobler 1995), and pheromones even from one gland are often made of a complex blend of chemicals (moths: Cardé and Baker 1984; hamsters: Johnston 1990). The reception of multiple chemical signals has been studied in crayfish, where it was found that three different chemical signals produced different behavioral responses, depending on how they were combined (Hazlett 1999).

Tactile signals. Multiple tactile signals can be produced by using several body parts at the same time, as may occur during grooming or copulation (fruit flies: Ewing 1983).

The framework we propose for multichannel signals may also be applicable to some unimodal, multicomponent signals, so that each signal component could influence other components as described in figure 1. For example, Rand and Williams (1970) suggested that the color, pattern, and size of the dewlaps of anole lizards (*Anolis* sp.) are redundant visual characteristics used for species identification. Nelson (1988) found that song frequency, number of phrases, trill-note duration, and internote interval are at least partially redundant acoustic features used for species recognition in field sparrows (*Spizella pusilla*). Zuk et al. (1992) studied mate choice in red jungle fowl (*Gallus gallus*) by manipulating comb size, color, and tail

length, and they concluded that females judge male quality with a suite of redundant visual characters. Zucker (1994) found that tree lizards (*Urosaurus ornatus*) have two different visual coloration signals (throat color and dorsal color) that function in independent roles.

Trimodal and more complex signals. Multimodal composite signals can of course be more complex than those discussed so far: animals can combine signal components from more than two sensory channels. The schema that we have described should still be applicable when more than two channels are used in concert. For example, if an animal gives a signal with visual, vocal, and tactile components (such as a grooming interaction between two monkeys where the groomer lip-smacks, vocalizes, and touches the groomee), the three signal components might be redundant, or each might carry unique information. The components may modify each other, or they may amplify or even contradict each other, as described in figure 1. Bielert (1982) studied the importance of cues from three sensory channels (visual, olfactory, and vocal) given by sexually receptive females to male chacma baboons (*Papio ursinus*). He found that visual cues, especially those provided by the female's sexual swelling, were dominant, eliciting sexual responses in the males more effectively than olfactory or vocal cues.

Fruit flies (*Drosophila*) use at least four channels during courtship: visual, acoustic, olfactory, and tactile (Ewing 1983). In fact, what may appear to be a simple acoustic signal, song produced by wing vibration, may actually be a complex composite signal: the vibrating wings may also be detected via air movement or visual cues (although Bastock 1956 wrote that the visual component is not important, because the flies court just as well in the dark), and wing movement may even help to disperse pheromones (Rybak et al. 2002). These additional components appear to enhance the efficacy of the male's courtship display beyond that achieved by just the bimodal audio and chemical signal reported in table 2 (Rybak et al. 2002).

Temporal Characteristics of Composite Signals

In this article, we have addressed simultaneously produced multimodal signals. Others have discussed sequences of unimodal signals given in different channels. For example, Goldfoot (1982) developed a "sequential multichannel model" in which sexual behavior in rhesus monkeys (*Macaca mulatta*) is mediated by a series of visual, olfactory, and behavioral cues. Tavolga (1956) described a sequence of visual, audio, and olfactory signals used in courtship between fish, and Zimmerman (1990) similarly reported a sequence of visual, audio, and tactile signals in courtship between frogs.

Even multiple components that are emitted simultaneously, however, might in some cases be perceived sequentially. This can occur when physical properties of each sensory channel differ. Since light travels more quickly than sound, a distant receiver detects the visual part of an audiovisual composite stimulus before the audio part (Wickler 1978). Some degree of internal compensation may help to synchronize audio and visual stimuli, however: auditory information is transmitted to multisensory processing areas in the cat brain, for example, more quickly than is visual information (Stein and Meredith 1990).

When the components of a multimodal signal are perceived sequentially, the first component received can potentially have a greater effect on responsiveness to subsequent components than if it were received simultaneously with the rest of the signal. For example, if an acoustic component serves to attract attention and subsequent visual components convey specific information, the efficacy of the acoustic component could have a strong influence on the success or failure of the entire communication event. Crapon de Caprona and Ryan (1990) suggest that olfactory cues in swordtails (*Xiphophorus nigrensis* and *Xiphophorus pygmaeus*) might be perceived at a distance and used for localization of males by females, while concomitant visual cues are perceived at short range and used for assessment of male quality by females. Myrberg (1975) suggested that chemical cues are dominant over concomitant visual ones in parental recognition of young cichlid fish in the wriggler stage but that as the young mature and enter the free-swimming stage, visual cues become dominant.

Visible and chemical components of scent marking may act on different timescales and ranges, the visible being immediate and long distance, whereas the chemical component is longer lasting but of shorter range. Bekoff (1979) found that visible ground scratching accompanies urination and marking in dogs more often when another dog is in sight than when the dog is alone, suggesting that the visual component functions as a display. Several authors have found that the visual cues from lizard markings are responded to first (they attract attention) and that the chemical signals are investigated later (Duvall et al. 1987; Alberts 1989).

The effect of combining sequential multimodal cues can depend on the order in which they are presented or encountered. For example, Hazlett and McLay (2000) presented alarm odors and threatening visual stimuli to crabs (*Heterozius rotundifrons*) either before or after tactile stimulation, causing a difference in how much time the crabs spent catatonic (a defensive posture).

*Audience: Can Individual Components
Target Different Recipients?*

When the components of multicomponent signals are independent, each part may have its own target audience. The flexibility proffered by neural control of numerous skin chromatophores, for example, allows the male Caribbean reef squid (*Sepioteuthis sepioidea*) to simultaneously produce a dark display on one side to attract females and a silver display on the other side to ward off competing males (Messenger 2001). Different components of the courtship display of the male satin bowerbird (*Ptilonorhynchus violaceus*) might be directed at different female audiences, because younger and older females tend to prefer different levels of male courtship behavior (Coleman et al. 2004; Ryan 2004). Duetting birds often give visual signals while they are producing territorial vocalizations; these visual components may be short-distance signals directed at mates, while the simultaneous vocalizations are long-distance signals directed at neighbors (von Seibt and Wickler 1977; see Partan 2004).

Questions to Pursue in Future Work

We encourage others to gather complete information about the effects of multimodal signals and their component parts. Although we consider Myrberg (1980) too pessimistic in referring to intersensory interactions as a Gordian knot, we agree that “each worker has the responsibility, at least, to consider how the ‘knot’ of the sensory gestalt might be effectively unraveled” (p. 165). As Acquistapace et al. (2002) and Gherardi and Pieraccini (2004) indicate, if we can collect data on responses to single components, then we can discover into which category a particular signaling system belongs.

Most of the examples found in the literature are of enhancement or modulation (see table A1). Reasons for this should be explored further. The unequal distribution of examples across categories may be due to the rarity of some categories or may reflect our not having discovered enough appropriate examples. It would be interesting to explore whether there are asymmetries in the importance of different categories and different modalities across taxonomic groups.

A theoretician could work on determining quantitative thresholds for levels of response that define each category. For example, the dividing line between equivalence (in which the response to the multimodal signal is the same as the response to each of the components) and enhancement (in which the response to the multimodal signal is greater than the response to each of the components) could be identified by the point at which the response to the multimodal stimulus is statistically greater than the re-

sponse to either of the components. Similar thresholds should be defined for each of the nonredundant categories as well.

Several of the issues raised earlier lead naturally to further work. The target audience for multimodal signals that appear to be directed at different recipients should be tested with playback studies. Experiments are needed to determine whether visual signals can be used to designate the intended addressee of an acoustic signal. The alerting function of one component of a multimodal signal could be examined further, particularly as to whether one modality is better suited for attracting attention than another. For example, do visual cues enhance localizability of acoustic cues or vice versa? The costs of signaling in multiple modalities need to be assessed and compared to the cost of signaling in single modalities to better understand pressures driving the evolution of multimodality. Although it is challenging to grapple simultaneously with questions of mechanism, function, and evolution, we firmly believe that an interdisciplinary, comparative approach to studying multimodal communication will be most fruitful.

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