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REVIEW

# Receiver psychology and the evolution of multicomponent signals

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Many animals produce and respond to signals made up of multiple components. For example, many avian sexual displays are highly extravagant combinations of visual and acoustic elements, and are described as being 'multicomponent'. One possible reason for the evolution of such complex signals is that they provide more reliable information for receivers. However, receivers also influence signal evolution in another important way, by how they perceive and process signals: signallers will be selected to produce signals that are more easily received. The potential role of receiver psychology in the evolution of multicomponent signals has not previously been considered; in this review I present psychological results that support the notion that two components are better received than one alone. Detection can be improved by producing two components together, thus reducing the reaction time, increasing the probability of detection and lowering the intensity at which detection occurs. Discriminability of multicomponent stimuli is also made easier through better recognition, faster discrimination learning and multidimensional generalization. In addition, multicomponent stimuli also improve associative learning. I show that multicomponency does indeed improve signal reception in receivers, although the benefits of producing components in two sensory modalities (bimodal multicomponent signals) may be larger and more robust than producing them in just one (unimodal multicomponent signals). This highlights the need for consideration of receiver psychology in the evolution of multicomponent signals, and suggests that where signal components do not appear to be informative, they may instead be performing an important psychological function.

Many animals produce and respond to displays made up of multiple components. These signals have been described as being 'multicomponent' (Hölldobler 1995; Johnstone 1995), or 'multimodal' where components occur in more than one sensory modality (Guilford & Dawkins 1991; Rowe & Guilford 1999). Examples include many sexual displays (e.g. Frith 1981; Petrie et al. 1991; Zuk et al. 1992), warning signals (e.g. Cott 1940; Rothschild 1964; Edmunds 1974; Marples et al. 1994), aggressive displays (e.g. Paton 1986; Deag & Scott 1999), and begging signals (e.g. Davies et al. 1998; Kilner et al. 1999).

Despite this widespread occurrence across communication systems, most theoretical interest has focused upon explaining multicomponent sexual displays, exploring the conditions under which multiple handicaps or Fisherian traits might evolve (e.g. Møller & Pomiankowski 1993; Pomiankowski & Iwasa 1993; Iwasa & Pomiankowski 1994; Johnstone 1995, 1996). However, although multiple reliable indicators have now been demonstrated in a nonsexual signalling system (chick begging: Kilner et al. 1999), focusing purely on the honesty of signals, or their 'strategic' design, omits other selection pressures that enhance message transfer, that is, the 'tactical' design features of signals (Guilford & Dawkins 1991, 1993).

In this review I aim to redress this apparent imbalance by presenting data from laboratory studies demonstrating that two stimuli are more effective than one in eliciting responses from experimental subjects. Some of these studies present two stimuli that require the same response, mimicking the evolutionary scenario where a signaller sends redundant signals containing the same information (Zuk et al. 1992; Möller & Pomiankowski 1993). Others show that an accessory noninformative stimulus can enhance performance to a focal informative

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stimulus, in parallel with signallers improving their signal efficiency by producing an extra, potentially less costly component (Hasson 1989; Guilford & Dawkins 1991). In this review I uphold the idea that 'receiver psychology' (Guilford & Dawkins 1991) is important in the evolution of complex displays, because multicomponent signalling can enhance the detection, recognition, discrimination and memorability of signals by receivers. Using illustrative data from psychological experiments investigating interactions between cues in the laboratory, my aim is to show how these could benefit signallers and receivers in nature. An additional section considers some perceptual issues of multicomponency and the possible implications for signal design.

## DETECTABILITY

Guilford & Dawkins (1991) defined a signal's detectability as 'how easily it can be perceived as distinct from its background'. Although Guilford & Dawkins used the term in a way that suggested information accuracy was involved, I assume that once the receiver has started gathering information about a stimulus the detection process has finished. Obviously some level of processing must occur for the signal to be identified as being of relevance to the receiver, but I restrict detection merely to reacting to the presence or absence of a stimulus. Three measures of detectability are affected by multicomponency: (1) reaction times; (2) the probability of detection; and (3) detection thresholds. Experimental evidence in all three areas shows the benefits of producing two signal components in comparison to either component alone (see Welch & Warren 1986 for a review).

### Reaction Time

Reaction time is the amount of time that it takes an observer to respond to the onset of a given stimulus. Typically, when asked to respond to the presence of either an auditory stimulus, a visual stimulus or the bimodal audiovisual compound, subjects detect the compound stimulus faster than the fastest detection time for either isolated component (Hershenson 1962; Miller 1982; Gielen et al. 1983). From statistical theory, it is possible to make predictions about what the reaction time to the compound of two components should be, given the distribution of reaction times to each component (known as 'statistical summation': Raab 1962). However, statistical models often overestimate the reaction time to bimodal compounds, with the reaction times being significantly shorter than predicted. This has been termed 'intersensory facilitation', in that a psychological interaction between the auditory and visual components causes an additional improvement in detection speed (Todd 1912; Nickerson 1973; Miller 1982; Gielen et al. 1983). In contrast, statistical summation models do seem able to explain the reaction times to unimodal compounds (Miller 1982; Grice et al. 1984), suggesting that unimodal and bimodal compounds are processed differently. However, the distinction between the responses to unimodal and bimodal compounds is not necessarily so clear cut, and may depend upon the 'separability' of the components forming the compound (see below; Cohen 1997).

Reaction time to a single cue can also be enhanced by the simultaneous presentation of a neutral stimulus, even where this second stimulus does not require a response and is merely an accessory. Thus the reaction time of humans to a visual stimulus is faster when it is accompanied by an accessory acoustic stimulus than when presented alone (Simon & Craft 1970). Facilitation in reaction time to the visual stimulus occurs even when the accessory acoustic cue follows up to 120 ms afterwards (Morrell 1968a; Bernstein et al. 1969, 1970, 1973), although when the roles of the cues are swapped, an accessory visual stimulus does not improve the reaction time to an acoustic stimulus to the same degree (Morrell 1968b; Miller 1986). This asymmetry is likely to be due to the differences in processing time between the two sensory modalities (Stein & Meredith 1993), a factor also likely to be important in multicomponent signal evolution.

Reaction times have consistently been shown to be faster to compounds than to either component stimulus. This is true whether an additional component contains the same information and requires the same response, or is simply an arbitrary component presented alongside the stimulus requiring detection. Therefore, signallers would benefit from producing even a relatively cheap accessory component in their signal when detection speed is important, perhaps in a contest or as a warning to predators.

### Detection Probability

Detection probability is the likelihood that a given stimulus is detected against background noise. Howarth & Treisman (1958) investigated the effect of a synchronous flash on the probability of sound detection in humans at near threshold levels (i.e. where the amplitude is detectable just over 50% of the time); they found that the detection probability of the sound rose by ca. 30% when the flash was also present. In this experiment, the maximal increase in detection probability occurred when the light was flashed 1–3 s before the sound.

Extensions of signal detection theory also propose that detection probability is improved when the number of components is increased (e.g. Green 1964; Mulligan & Shaw 1980). Signal detection theory allows for both environmental noise and within-subject variability in signal detection, such as attentional and motivational changes (Tanner & Swets 1954; Green & Swets 1966). Green (1964) combined tones of various frequencies and found that the detection probabilities to compound stimuli were higher than to either constituent component alone. In this case, the improvement was predicted by a statistical summation model, although in other experiments where components have been combined from two sensory modalities, the improvement in detection probability exceeds that predicted by the summation model (Mulligan & Shaw 1980; Fidell 1982; Shaw & Mulligan 1982; Bonnel & Prinzmetal 1998).

In addition, detection can be improved when an accessory (neutral) cue occurs several seconds before the stimulus that requires a response, suggestive of an alerting role for accessory cues (Watkins & Feehrer 1965). Therefore, movement at the start of a signal display draws attention to the ensuing informative signal components (Wiley 1983; Fleishman 1988), and one would predict that signal components emitted first would be less likely to be informative than those that followed. Furthermore, if an initial component acts as an alerting stimulus, the second component need not be as detectable. Movement can increase the detectability of visual traits (e.g. Hansen & Rohwer 1986; Fleishman 1988; Endler & Théry 1996), and similarly other behavioural traits, such as calling, could also amplify fixed morphological traits as and when required.

Instead of extra components acting as alerting stimuli, their intensities or energies could combine to enhance detection (Nickerson 1973). However, this is perhaps less likely than that they act as an alerting stimulus, since there is evidence that the onset and ending of a continuous tone are equally good at increasing the detection of a visual cue (Watkins & Feehrer 1965; Bernstein & Eason 1970). Therefore, altering a stimulus by decreasing or increasing its overall intensity will increase compound detection, making increased attention a more likely explanation.

A final example of how cues can interact to enhance detection is called the face detection effect (Purcell & Stewart 1988). When simple line drawings of faces were given to human observers, either in the correct configuration (i.e. facial features in the correct position), or containing the same but rearranged elements, configurations that looked like faces were detected more often than those that were a random arrangement of facial features. Signal receivers are almost certainly predisposed to recognize specific configurations of cues, as in the case of warning colours being avoided more when a warning odour is also present (Rowe & Guilford 1996). Whether such a configural effect enhances signal detection is not known.

### Detection Threshold

Detection threshold is defined as the intensity at which a subject detects the stimulus ca. 50% of the time. When thresholds of compound stimuli and their components are compared, thresholds are lower to compounds than to either stimulus alone, whether these are in the same or in different modalities (Howarth & Treisman 1958; Treisman & Howarth 1959; Green 1964). Howarth & Triesman's experiments also showed that detection thresholds could be lowered when a neutral accessory stimulus was presented prior to the onset of a focal stimulus requiring a response. Again, it would seem that one signal component can increase the detection of another signal component even when produced in succession.

### Conclusion

The initial detection of a signal is crucial. All these experiments using stimulus compounds show that detection is enhanced whether components are produced together, or in quick succession. Detection is faster to a compound compared to either of its constituent elements, and when the components are in separate sensory modalities, detection is faster than predicted (intersensory facilitation). In addition, the presence of a simple accessory stimulus increases the detection of a focal imperative stimulus, probably by eliciting the receiver's attention. Therefore, interactions between signal components could aid detectability, either when two components require the same response, or where a simple component alerts the receiver to ensuing information. Of course, even without components interacting, increasing the number of components increases detection by chance alone. Scheffer et al. (1996) suggested that the vibratory components of the displays of male wolf spiders (Araneae, Lycosidae) might have evolved to increase detection by females at greater distances than was possible by using visual components alone. However, I have shown in this section that interactions between components can increase detection beyond that predicted by individual responses to each component.

## DISCRIMINABILITY

Discrimination occurs where animals have to respond differently to a variety of stimuli, either through learned association or through innate predispositions. It is not a simple phenomenon, and involves psychological processes such as stimulus recognition, learning and generalization.

### Stimulus Recognition

There is evidence that stimulus recognition can be improved through having two simultaneous stimuli produced in different modalities, either both conveying the same information or where a neutral accessory stimulus accompanies a component bearing the message (the imperative stimulus: Loveless et al. 1970; Heller 1982; Stein et al. 1988). For example, the intelligibility of speech by a human observer is greater when the speaker's lips can be seen speaking the words (Sumby & Pollack 1954; Massaro & Stark 1998), whilst cats, *Felis cattus*, perceive light intensity more accurately when sound is presented than in the absence of any accompanying stimulus (Stein et al. 1988). There is also evidence in sheep, *Ovis aries*, that although acoustic cues do not improve facial recognition, they are used in some kind of confirmatory role in facial discriminations (Kendrick et al. 1995). Perhaps more curiously, perceptual changes can occur: sounds can change the way moving objects are perceived (Sekuler et al. 1997), whilst sex pheromones increase the visual attractiveness of the opposite sex in humans (Kirk-Smith et al. 1978). Although it is not immediately obvious how such perceptual interactions will guide signal evolution generally, it is perhaps important to be aware of potentially unpredictable effects between components.

Whether such interactions occur within a single sensory modality is unclear. Components occurring within a modality are often perceived as a single configural stimulus rather than as interacting component stimuli (Honey & Hall 1989), for example two tones become a single noise, whilst a mixture of two colours becomes a unified pattern. It is, therefore, unlikely that noninformative accessory components from the same modality will enhance the perception of the message in the same way as a component in a different modality. Although different processes are probably occurring within and between sensory modalities to aid recognition, additional cues in the same modality could improve stimulus specificity, and consequently make them more recognizable.

For components that oppose each other (i.e. when each requires a different response), reaction to compounds can be slower and responses less accurate (Tulving & Lindsay 1967; Miller 1982). This is predicted if attention is divided between sensory modalities, causing the animal to respond less well to at least one of the stimuli (Broadbent 1958; Kahneman 1973). Therefore, signalling different messages is disadvantageous unless there is enough time for them to be assessed sequentially. This argues against animals signalling simultaneous messages (Wedekind 1992, 1994; Zuk et al. 1992; Møller & Pomiankowski 1993), instead supporting the idea of signal redundancy where both signals contain similar information (Zuk et al. 1992; Møller & Pomiankowski 1993; Kilner et al. 1999).

## Discrimination Learning

Discrimination learning is the process by which animals learn to distinguish between recognizable stimuli. Compound stimuli that differ in two dimensions are more easily discriminated than those that differ in only one. In a classic experiment, Eninger (1952) trained three groups of rats, *Rattus norvegicus*, in a Y maze: one was trained using colour alone, another using only sound and the last group with sound and colour. Rats in the bimodal discrimination group took fewer trials to learn the task than either of the groups using only a single stimulus. In signalling terms, this could mean that it is easier for receivers to distinguish between signallers on the basis of differences in two or three signal components rather than a single one.

However, when multicomponent stimuli vary in a single sensory channel, such an improvement in discrimination is not apparent. Rhesus macaques, *Macaca mulatta*, and bonnet macaques, *M. radiata*, given a discrimination task between objects that differ in either colour alone, shape alone, or in both dimensions simultaneously, base their assessment on colour alone (Harlow 1945). In this purely visual task, macaques relied solely on colour whenever it was available; rhesus monkeys also discriminated using only colour differences when two other cues (shape and size) differed between objects (Warren 1952). These results suggest that discrimination learning is improved only if the signals that animals receive are bimodal.

## Generalization

An important phenomenon associated with discrimination learning, and indeed all learning, is generalization (Guttman & Kalish 1956; Honig & Urcuioli 1981). When an animal learns about a rewarded stimulus and a nonrewarded stimulus that differ along a given dimension, a gradient of excitatory and inhibitory responses is evident around each stimulus. These gradients are known as generalization curves, and are predicted because animals are responding to similar stimuli, either in an adaptive fashion or mistakenly confusing them to varying degrees with the original stimulus.

When animals that have been trained to associate a multicomponent stimulus with a reward are given novel stimuli that differ from the training stimulus, their response to the novel cues diminishes as more components are altered (Fink & Patton 1952; White 1958; Hara & Warren 1961; Butter 1963; McGonigle 1967; Heineman & Chase 1970; Blough 1972). This is true whether the components are in different sensory modalities (visual, auditory and tactile in the case of Fink & Patton 1952), or within a single modality (usually varying visual cues in brightness, form and size: White 1958; Hara & Warren 1961; McGonigle 1967). Often one cue is generalized more than others (Fink & Patton 1952; Hara & Warren 1961; Butter 1963; McGonigle 1967; see Honig & Urcuioli 1981 for other examples), suggesting specificity in some signal stimulus dimensions and not in others.

How extra signals in one dimension affect generalization gradients in others has yet to be investigated. However, London (1954) reviewed Russian studies that showed that auditory and olfactory stimuli change colour perception in humans. Although these experiments were not rigorously scientific, they suggest that when an accessory stimulus is presented in a different modality, visual perception can change along a given dimension, in this case colour. Therefore, it can be advantageous for signallers to produce extra signal components in order that receivers have a more accurate representation of another component. A good example might be warning displays, where odours and sounds might combine to enhance predator learning of a particular colour pattern. This will provide an interesting line of research in the future, and a possible mechanism by which discrimination is more effective with an accessory component than without.

## Conclusion

This section has shown that signals are recognized more readily and that discrimination is easier for signals that differ along multiple dimensions. It could be that once efficacious components evolve, they can become important in revealing signaller quality, perhaps by 'amplifying' the original trait (Hasson 1989, 1990, 1991). Brooks (1996) showed experimentally in guppies, *Poecilia reticulata*, that black coloration around carotenoid pigment acts to amplify these areas of orange, without being a focus of female choice itself (Brooks & Caithness 1995). Where discrimination among signallers is important, as in mate choice, signallers will be selected to produce signals that enable receivers to distinguish between them (Grafen 1990; Buchanan & Catchpole 1997; Marchetti 1998).

Of course, some signallers, such as Batesian mimics (Bates 1862; Dittrich et al. 1993) or female mimics (e.g. Lloyd 1981; Gross 1982), aim not to be discriminable. Mimicry can damage the effectiveness of a model's signal since receivers are unable to distinguish between palatable and unpalatable prey. It is in the models' interests to appear different from the mimic, whilst the mimics are selected to do exactly the opposite. Such an arms race between models and mimics might have led to the complex warning signals that we see today. If predators confused models and mimics on the basis of a single component, it would be advantageous for the models to evolve another distinguishing component which the predator would learn in addition to the original component. This would then put pressure on the mimics to copy this new component to ensure that they are not eaten, and indeed such multicomponent mimicry is commonplace (Gaul 1952; Moore et al. 1990).

Whether discrimination is enhanced in a similar way between multicomponent signals within a single modality is unclear. However, extra components within or between modalities allow finer discriminations between signals, for example, patterns distinguishing different signals of similar colours. Hölldobler (1995) suggested that ants achieve more information content and more appropriate responses, perhaps more than would be achieved if each odour was used alone, by varying the relative concentrations of chemicals in an odour mixture. Discrimination can be improved by the addition of an extra component to improve message specificity, to make it more readily identifiable, and also learned more quickly. In the next section I consider how extra components can improve learning outside the context of discrimination.

## MEMORABILITY

Guilford & Dawkins (1991) equated memorability with learning, in that wherever learning is involved, memory is also important. However, psychologists see learning as the process by which an association is made, whilst memory is mainly concerned with how that association is maintained in the longer term (e.g. Pearce 1994, 1997). In fact, very little is known about the role of different stimuli in memory storage and retrieval (Fetterman 1996), and consequently in this section I focus on learning.

### Learning

There are two ways in which compound stimuli can be acquired more quickly than either of their component stimuli. The first is called 'stimulus compounding', or 'within-group summation' (Kehoe & Gormezano 1980; Kehoe 1982): animals are trained separately to individual component stimuli that are then presented simultaneously as a compound stimulus; results consistently show a higher response to the compound stimulus than to either component alone (Wolf 1963; Miller & Ackley 1970; Kehoe & Gormezano 1980; Kehoe 1986; Kehoe & Graham 1988; Kehoe et al. 1994). Although called 'summation', the term is used purely to describe the phenomenon rather than any mechanism behind it, and the response to the compound is not simply additive as the term suggests.

The second experimental method is 'compound conditioning', or 'between-groups summation' (Kehoe & Gormezano 1980; Kehoe 1982), where animals in separate groups are trained with either a single component or a compound stimulus; for example, one group is trained with a sound, another a light, and a final group with the light and sound combined. The association with the compound proceeds much faster than with either component stimulus alone (Miller 1939; Sutherland & Mackintosh 1971; Kehoe 1982, 1986).

Nearly all of these experiments have been conducted with lights and sounds, although Sutherland & Mackintosh (1971) reported between-groups summation using orientation and brightness of a visual stimulus. However, Kehoe et al. (1994) looked for within-group summation in unimodal and bimodal compounds, and found it only when component stimuli were from different modalities (a light and a tone), and not when they were from the same ones (a click and a tone). Aydin & Pearce (1997) proposed that it is the degree of difference between compounded stimuli that determines whether summation will occur (as did Cohen 1997 to explain differences in reaction times). In a series of experiments, they showed that summation can occur in unimodal and bimodal compounds, although when it fails to materialize it is always in unimodal compounds and never in bimodal ones.

Learning about signals is important. Even in mate choice where decision making has a predominantly genetic basis (e.g. Fisher 1930; Hamilton & Zuk 1982; Bakker & Pomiankowski 1995), females survey potential mates before making a choice, and this may involve learning about the relative attractiveness of males in a population and where to find them (e.g. Real 1990; Bensch & Hasselquist 1992; Dale & Slagsvold 1996). Not only do females need to remember males within a breeding season, they may also have to be continually assessing traits within the population, involving considerable learning and memory. To be remembered easily, males should signal multicomponently.

When signals themselves have to be learned, the presence of an additional efficacious component can aid learning. For example, during song tutoring of hand-reared male nightingales, *Luscinia megarhynchos*, a synchronous strobe light pulsating alongside tutoring songs leads to their being learned and repeated more than songs played without the accompanying light (Hultsch et al. 1999). Furthermore, additional cues can bias learning: hen calls played to domestic chicks, *Gallus gallus domesticus*, induce an imprinting bias for a stuffed junglefowl in preference to a more neutral stimulus (a preference that is absent without acoustic stimulation; Hampton et al. 1995). It is likely that unnatural cues in the laboratory will, if anything, underestimate the complexity of the situation in the wild.

Perhaps the best studied communication system involving learning is aposematism, when signal components may interact to improve predators' abilities to learn the link between the display and the unpalatability (Rothschild et al. 1984; Guilford & Dawkins 1991). Both types of summation may be important in this case, since insect warning signals can consist of odour, sound, colour, movement or any combination of these (e.g. Cott 1940; Edmunds 1974). Combining components could be favoured if predators either learned about each component separately before meeting an insect with more than one display component (within-group summation), or if they learned both components upon their first encounter (between-groups summation).

One final issue is that during compound learning, components within a compound have the opportunity to interact, either competing with or promoting each other (Kehoe & Gormezano 1980; Pearce 1997). Despite the evidence for increased learning when two components are combined, there is one case when this does not always occur: when one component is much more intense than another. In this situation, the acquisition speed of two components combined can be the same as that when the animal is given only the stronger of the two components, a phenomenon known as 'overshadowing' (Kehoe 1982; Couvillon & Bitterman 1982, 1989). Because no advantage is conferred on the signaller, overshadowing will probably not exist in natural communication systems. However, 'potentiation', where one stimulus promotes the learning of a second stimulus, evokes a stronger reaction than if it had been learned on its own (Mackintosh 1974; Couvillon & Bitterman 1982). Guilford & Dawkins (1991) suggested that multicomponent displays might be 'potentiating displays', with extra components evolving to enhance the learning of a key component that contains the information required by the receiver. Potentiation results in a stronger association between the signal and its message than would be possible from signalling only the informative component (e.g. Kaye et al. 1989; van Kampen & Bolhuis 1991, 1993).

## Conclusion

Compounds can be learned more quickly than either component alone in those situations where there are no large differences in intensity between components. There are three situations where learning can be improved: where components are learned separately by an animal and then presented together (within-group summation); where animals learn the compound more quickly than either constituent component (between-groups summation); and where the presence of one stimulus promotes the learning of another (potentiation). However, it should be emphasized that summation in unimodal compounds is supported by inconsistent results, and potentiation has been shown only in bimodal situations.

Between-groups summation and potentiation are robust psychological processes in signal receivers that means they could accrue and remember information more accurately from multicomponent signals than with just a single component. Rarely would signal components be learned separately and combined (within-group summation), since individuals within a species will have the same signals and receivers will not experience components in isolation. However, where a receiver responds to the signals of more than one species, such as a predator attending to warning signals that could be olfactory, acoustic or visual, signallers that combine these elements will be at an immediate selective advantage.

# PERCEPTION OF MULTICOMPONENT SIGNALS

The way that animals perceive compound stimuli will have affected the evolution of multicomponent signals. Perhaps the most important issue is that what human receivers treat as a signal component may not be differentiated by the intended nonhuman receiver. There has been little attempt to define 'component': theoreticians have not needed to do so and empirically it is obvious only where components are from two sensory modalities (e.g. Marples et al. 1994; Hughes 1996; Rowe & Guilford 1996, 1999; Kilner et al. 1999). This problem of definition is a difficult one, since it is possible to break complex displays down into an almost infinite number of components for our own study. In this section I do not provide an answer to this question, but I provide a new angle of attack by considering how animals perceive and break down complex stimuli. There are two main issues: (1) are compound cues seen as a single stimulus or as their component parts; and (2) are unimodal compounds perceived differently from bimodal ones?

## 'Configuration' versus 'Atomization'

There is a continuum of how animals could perceive compound stimuli, from the extremes of being a single stimulus to that of being separate components added together. 'Configural' theories promote the idea that a compound stimulus is not the sum of its parts, but is a separate stimulus of its own, gaining associative strength independently from its component stimuli. Conversely, 'atomistic' theory proposes that it is possible to predict the response to a compound stimulus by knowing how an animal reacts to each component individually. Neither view alone can fully account for the results of experiments investigating this question, although by far the most evidence exists for configural rather than atomistic hypotheses (Couvillon & Bitterman 1982; Pearce & Wilson 1991; Pearce et al. 1992, 1997; Aydin & Pearce 1994; Redhead & Pearce 1995, 1998; Nakajima 1997). Kehoe's work (Kehoe 1986; Kehoe & Graham 1988; Kehoe et al. 1994) supports the 'unique stimulus hypothesis' (Rescorla 1973), where responding to a compound is governed by coexisting representations of both compound and components. Consequently, the compound is represented by a unique compound stimulus as well as its components (i.e. a compromise of configural and atomistic views), and is capable of eliciting a completely different response from that of either component (e.g. Kehoe & Graham 1988).

Because a compound can be viewed as a unique stimulus, multicomponent signals could relay a different message independently from that of their constituent components. Signallers could evolve extra components to elicit more specific responses in receivers, whilst receivers evolve responses and biases for specific signal component combinations (e.g. Hampton et al. 1995; Hughes 1996; Rowe & Guilford 1996). Consequently, by studying signal components in isolation, we may miss the synergistic function of the entire signal. The psychological studies discussed above show that compounds are unlikely to be merely the sum of their parts, and only by studying multicomponent signals in their entirety are we likely to understand their full function.

### Unimodal versus Bimodal Compounds

In this review I have suggested that there is a difference in the way that animals perceive unimodal and bimodal compounds, although the distinction is not clear-cut. Experiments have shown that unimodal compounds are viewed as a single unified stimulus whilst bimodal stimuli are more readily dissociated into their components (e.g. Brown 1987; Honey & Hall 1989; Pearce & Wilson 1991; Kehoe et al. 1994). However, more recent evidence has shown that the components of unimodal compounds can interact in a similar manner to those in bimodal compounds, both in reducing reaction times (Cohen 1997) and enhancing acquisition speeds (Aydin & Pearce 1997). This difference between experiments has been attributed to the 'separability' of components, that is whether stimuli can exist independently of each other (e.g. sound and shape), or whether they are inextricably linked (e.g. every object must have a shape and colour). The separability of dimensions within a sensory modality is currently difficult to define and so far there has been little experimental interest in this question (Aydin & Pearce 1997; Cohen 1997). Although it is currently difficult to apply this distinction to the evolution of multicomponent signals, the effects are probably more substantial and more robust for bimodal displays than for unimodal ones, and signallers will therefore benefit more consistently from producing components in multiple modalities rather than just one. If future work shows consistent differences in the perception of and behaviour to different compounds, it may be necessary to divide multicomponent signals into those that are 'unimodal', and those that are 'bimodal' or 'multimodal', in order to distinguish between the possible psychological forces acting in them.

## THE EVOLUTION OF MULTICOMPONENT SIGNALS

In this review I have looked at the benefits to signallers of communicating multicomponently through receivers being more likely to detect, discriminate between and remember their signals. However, an important issue remains: did multicomponent signals evolve because of psychological processes already present in receivers, or did the evolution of multiple components lead to more efficient perceptual systems? This is a difficult question to answer, and in all probability, both processes will have been involved in the evolution of signals and receiving mechanisms that we see today. Indeed, specific responses to specific component combinations (e.g. Hughes 1996; Rowe & Guilford 1996) underline the importance of the coevolutionary dynamic between signallers and receivers.

At this stage, it is impossible to know whether multicomponent signals arose through the need for more accurate information with receivers adapting to process them more efficiently, or whether psychological mechanisms already existed to process an array of environmental information, prior to the evolution of multicomponent signals that used them. However, there are some data that suggest that intersensory integration could have led to the evolution of multimodal signals. A wide range of taxa show integrative intermodal sensory processes that enhance the accurate perception of their environment, including taxa outside those that we know to signal multimodally (Stein & Meredith 1993; Rowe 1998). Such neural connectivity exists between sensory channels that are not used for communication, for example, between infrared and visual sources of information in rattlesnakes, *Crotalus viridis* (Hartline et al. 1978; Newman & Hartline 1981), or visual and magnetic inputs in pigeons, *Columba livia* (Semm & Demaine 1986). Adaptive sensory integration appears to be a general feature across taxa and sensory channels, and could have been an important selection pressure in the evolution of multimodal signals. Whether psychological mechanisms have driven the evolution of multicomponent signals in general is, however, open to debate.

## GENERAL CONCLUSIONS

Multicomponency improves the detectability, discriminability and memorability of signals by receivers. This is true whether signallers produce two complementary components requiring the same response from receivers, or produce a noninformative accessory stimulus alongside their original message. However, once an accessory component has initially evolved, it may then be selected by receivers to be more informative. Where signal components are produced together, specific responses to particular component combinations are free to evolve in receivers. Psychological interactions between components mean that we cannot expect to understand multicomponent signals fully by studying their components independently of one another.

The perception of unimodal and bimodal compounds appears to differ. Intersensory facilitation favours bimodal signals where separable components interact to enhance signal performance consistently beyond that produced by unimodal signals. Unimodal multicomponent signals do improve signal reception, but, perhaps more importantly, they can improve the specificity of the information received along a single sensory channel. Which is more important to a signaller will depend upon its environment and the message that it is trying to relay.

In this review I have shown that receiver psychology is important for multicomponent signal design, and presented an abundance of evidence that shows that receiver psychology could have been an important selection pressure in the evolution of multicomponent signals. Consequently, it is not necessary to rely purely upon signal reliability for explaining the widespread occurrence of complex displays. Receiver psychology is inevitably involved in signal design, and is important for our full understanding of multicomponent signals.

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