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Forum: Invited Review

Multisensory perception in uncertain environments

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Animals must use cues from smells, sounds, and sights to reduce uncertainty about the environment. Despite the ecological relevance of multisensory perception in helping animals cope with uncertainty, empirical support from natural systems is rarely placed within an adaptive framework. The field of psychophysics provides a model for the study of cognitive processes by studying behavior. Using this as a foundation, we develop a framework that can be used to understand the evolutionary significance of multimodal perception. We develop predictions about the conditions under which multiple stimuli combine differently. A key outcome of our analysis is that the ecological context can influence the processes by which animals perceive multisensory stimuli. In addition to its theoretical importance, this framework predicts that anthropogenic activities can affect how animals perceive their environment, which may have profound ecological consequences. *[Behav Ecol 23:457–462 (2012)]*

INTRODUCTION

Animals must use information transmitted by smells, sounds, and sights to make decisions that reduce their uncertainty about the environment (Sih 1992; Dall and Johnstone 2002; Dall et al. 2005). The field of psychophysics analyzes perception by measuring changes in behavior with changes in stimulation (Shettleworth 2010). Under such an approach, changes in behavior indirectly indicate changes in cognitive processing and integration (Curio 1975; Meredith and Stein 1983; Leger 1993). An advantage of psychophysics is that we gain an understanding of which stimuli have behavioral consequences. However, multisensory perception is rarely placed within an adaptive framework. Here, we present a framework that predicts the conditions under which we expect different mechanisms of multisensory perception. For example, multiple predator stimuli lead prey to increase, decrease, or not change their antipredator effort (Table 1).

Borrowing heavily from terminology used to understand the function of multimodal signals (Partan and Marler 1999), we develop a framework to explain the various ways in which animals combine multiple stimuli. We frame multimodal perception as a solution to the problem of making decisions with some degree of uncertainty (Dall and Johnstone 2002). Given that supplemental cues across modalities reduce uncertainty, we expect enhancement when the costs of missed opportunities are high and antagonism when the costs of wasted time and energy are high. We expect dominance and equivalence when the cost of acquiring more information is high.

Three key points emerge from our analysis. First, we suggest that to study the adaptive utility of multisensory perception, we must consider environmental uncertainty. Second, despite the potential for a multicomponent stimulus to reduce uncertainty relative to a single-component cue, animals may not necessarily utilize all components of a multisensory cue. Third, multiple stimuli may combine differently under different ecological contexts, thus the study of animal perception will benefit by examining the effect of multiple stimuli under various cost–benefit landscapes.

We hope that as future studies on a variety of taxa are placed within this framework that we will develop a better understanding of the evolution of multisensory perception. We will use many examples from the antipredator literature (Table 1) because avoiding predation risk is something that virtually every species must do (Nonacs and Blumstein 2010) and because the balance between managing predation risk and engaging in other activities such as foraging and reproduction sets the stage for different cost–benefit conditions (Lima and Bednekoff 1999), which is the foundation of our framework. However, our framework should also apply to any ecological situation, such as communication, other predator–prey interactions (Roberts et al. 2007; Cross and Jackson 2009; Bassett and Montgomery 2011), interactions with abiotic aspects of the environment (Johnson and Borgo 1976), or cued phenotypic plasticity (Kasumovic and Brooks 2011). Our review will begin with a clarification of terms and conclude with a discussion of conservation applications.

CLARIFYING DEFINITIONS

Multisensory perception: a psychophysics approach

We define "perception" as the product of reception, integration, and processing of stimuli. Under a psychophysics approach, observed behavior is the product of these processes (Meredith and Stein 1983; Shettleworth 2010). Thus, if we observe different stimuli generating different behaviors, we can conclude that the different stimuli were perceived differently (Proops et al. 2009; Shettleworth 2010). For our purposes, we use the term "multisensory stimulus" to define stimuli that are contextually similar and are aligned temporally and spatially as found in nature. For instance, when doves take

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Table 1

Experimental studies of antipredator behavior employing multimodal cues classified according to a taxonomy modified from Partan and Marler (1999)

Taxa	Component A; response(s) to A	Component B; response(s) to B	Response(s) to composite A + B	Stimulus category	Reference
Mosquito fish (*Gambusia affinis*)	Chemical (water conditioned with predators); response: increased inspection distance	Visual (movement patterns of predator); response: same as A	Further increase in inspection distance	Enhancement	Smith and Belk (2001)
Mosquito fish (*Gambusia holbrooki*)	Chemical (water conditioned with predators); response: no change in avoiding stimulus	Visual (predator fish); increased avoidance behavior	Avoidance behavior equal to B response	Dominance of visual cue	Ward and Mehner (2010)
Roach (*Rutilus rutilus*)	Chemical (water conditioned with either pike or perch); response: 1) Pike—increase in open-water refuge; 2) Perch—increase in covered refuge	Visual (pike or perch predator); response: 1) Pike—increase in covered refuge; 2) Perch—increase in open-water refuge	For congruent stimulus combinations: 1) Pike—increase in covered refuge; 2) Perch—increase in covered refuge	1) Pike—dominance of visual cue; 2) Perch—dominance of olfactory cue	Martin et al. (2010)
Crabs (*Heterozius rotundifrons*)	Chemical (crushed conspecifics); response: increase in alarm behaviors (decreased leg extension and increased time spent motionless)	Visual (shadow); response: same as A	Decrease in alarm behaviors (increased leg extension and decreased time spent motionless)	Antagonistic	Hazlett and McLay (2005)
Gray squirrels (*Sciurus carolinensis*)	Visual (conspecific tail flicks); response: elevated threat-sensitive behavior	Auditory (conspecific alarm calls); response: same as A	Further increase in antipredator behavior equal to the sum of response A and B	Enhancement	Partan et al. (2009)

flight quickly, their wings flap and the wings may produce a whistle (Barrera et al. 2011), and individuals may respond to either the movement, the whistle, or both stimuli.

We speak of stimuli as conveying information, thereby changing perception, to the extent that stimuli influence behavior (Guilford and Dawkins 1993). Although stimuli are often correlated with physical characteristics in the environment, we do not presume that behavior is based on knowledge of a specific aspect of the environment. For example, California ground squirrels (*Spermophilus beecheyi*) respond more strongly to the rattling sounds from larger rattlesnakes (Swaisgood et al. 1999). Whether squirrels are responding to body size per se or to the acoustic properties of the rattle, a different response to different rattles indicates that the rattles are perceived differently.

The costs of uncertainty

We define environmental uncertainty as ambiguity due to imperfect information about the state of the environment (e.g., Sih 1992; Dall and Johnstone 2002; Esber and Haselgrove 2011). Uncertainty may be characterized by stimulus intensity and/or the signal-to-noise ratio (Dall et al. 2005) or by variation in the predictiveness of a stimulus (Esber and Haselgrove 2011). All stimuli are associated with some inherent degree of uncertainty due to their physical properties and characteristics of the environment (Brown and Cowan 2000). Environmental uncertainty can lead to costly errors in decision making, which suggests that cognitive systems should be adapted to cope with uncertainty (Stephens 1989). Imperfect information about an event can lead to errors, in that animals will engage in activities that are not matched to the probability of an event (Sih 1986). Errors include underestimating the likelihood of an event, which may lead to missed opportunities, and overestimating the likelihood of an event, which may lead to wasted time and energy.

The benefits and costs of multisensory perception

Multisensory perception can assuage the consequences of uncertainty. Two characteristics of multimodal stimuli illustrate this point.

First, each modality has its own set of limitations. For example, chemical cues from a predator are difficult to localize but are often difficult for a predator to manipulate. Therefore, chemical cues may be better suited for gaining information about a predator's hunger state and recent prey preferences (Brown and Cowan 2000). Visual cues may be particularly useful for locating a predator, however, predators can easily manipulate their intention by changing their posture or behavior patterns, for example (Brown and Cowan 2000). By combining 2 chemical cues, only uncertainty about a predator's hunger state is reduced. By combining chemical and visual cues, prey gain knowledge about the predator's hunger state and intention.

Second, a unique property of multimodal stimuli compared with multiple unimodal stimuli is that each sensory channel can offer independent estimates of events or objects (Møller and Pomiankowski 1993; Ernst and Banks 2002). For example, a noisy audio stimulus is one with a low signal to noise ratio and hence includes some degree of uncertainty. Noise in one modality may be unrelated to the noise in another modality. Indeed, psychological research has demonstrated that cognitive systems integrate stimuli according to the signal-to-noise ratio of each modality (Ernst and Banks 2002; Ghazanfar et al. 2005; Fetsch et al. 2009). Ernst and Banks (2002) conducted an experiment where humans estimated the height of an object based on visual and tactile stimuli. Tactile stimuli became more important in height estimation as the noise in visual images increased (Ernst and Banks 2002). Further evidence suggests that biasing perception away from uncertain modalities may be common. California ground squirrels living in areas with higher levels of anthropogenic auditory noise displayed elevated levels of vigilance to the playback of auditory alarm cues, suggesting an increase reliance on visual cues (Rabin et al. 2006). In another study, gray squirrels (*Sciurus carolinensis*) living in areas with higher urban auditory noise responded more to the visual component of an auditory–visual alarm signal from conspecifics compared with squirrels in rural environments, indicating an increased reliance on visual cues (Partan et al. 2010).

Together, these examples explain why we are particularly interested in examining multimodal stimuli as opposed multiple stimuli within a single modality as a mechanism to reduce uncertainty. However, our framework can also be applied to multiple unimodal stimuli.

Uncertainty reduction through stimulus acquisition and processing requires time and energy (Sih 1992; Dall and Johnstone 2002; Dall 2010) and can be distracting (reviews in Dukas 2002; Chan and Blumstein 2011). Wolf spiders (*Schizocosa uetzi*) presented with bimodal courtship signals were more likely to be captured by human "predators" compared with spiders that were presented with a single stimulus (Hebets 2005). Thus, in addition to the costs of uncertainty, we must also consider the costs of multisensory perception.

MULTISENSORY PERCEPTION AS A MECHANISM

Throughout our analysis, we use terms from the framework of Partan and Marler (1999, 2005) to describe perception of multimodal stimuli (Figure 1). Partan and Marler's framework provides a foundation to study the evolution and function of multimodal signals by categorizing multimodal stimuli based on the behavior evoked by signal components in isolation and in combination (Møller and Pomiankowski 1993; Partan and Marler 1999, 2005; Candolin 2003; Hebets and Papaj 2005). If separate components evoke the same response, the components are said to be redundant. Redundant stimuli can evoke a more intense response (enhancement), the same response (equivalence), or a response of lower intensity (antagonistic). Antagonism, a distinct category not made explicit by Partan and Marler (1999), is supported by a body of literature that has focused on antipredator behavior (Zuberbühler et al. 1999; Hazlett and McLay 2005; Thompson et al. 2008), and we include it in Figure 1. In the case of nonredundant stimuli, each component of a bimodal stimulus evokes different responses. Nonredundant stimuli can elicit both unimodal responses simultaneously (independence) or only one of the unimodal responses at equal (dominance) or different (modulation) intensity. Nonredundant stimuli may also lead to a completely new behavior (emergence).

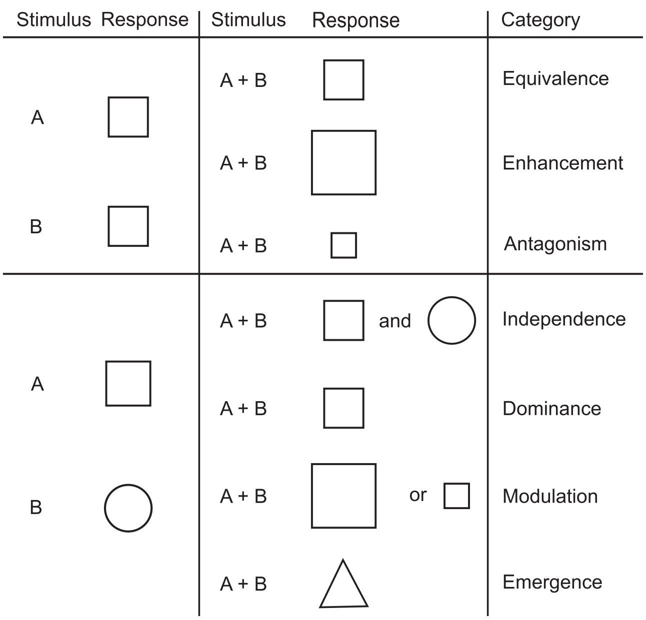

Figure 1
Classification system of multisensory stimuli based on behavior responses to stimulus components in isolation and in combination (Partan and Marler 1999).

In our framework, perceiver's cognitive processes are subject to change over evolutionary and ecological time. Instead of asking why signals contain multiple components across modalities, we ask why receivers combine multisensory stimuli in different ways. The categorization of receiver responses in Figure 1 can be thought of as mechanisms that enable animals to make adaptive decisions. Consider the California ground squirrels that increased antipredator behavior in response to rattles from larger snakes (Swaisgood et al. 1999). Though we do not know if squirrels respond to body size per se, a sensitivity to rattles from different sized snakes is the mechanism that allows squirrels to reserve intense antipredator effort for those snakes capable of striking further and faster. Similarly, a perceiver whose response increases when presented with a multimodal versus unimodal stimulus could be increasing its response to one of the signal components in the presence of the second or could be combining the stimuli in an additive fashion. Regardless of the specific psychophysiological processes, we view the increase in perceiver response as a mechanism.

In the next section, we predict the conditions under which we expect to see enhancement, antagonism, equivalence, and dominance. We focus on these 4 categories as they have the greatest representation among the nascent field of multisensory perception.

PREDICTIONS FROM A COST–BENEFIT ANALYSIS OF MULTISENSORY INTEGRATION

Enhancement: minimizing missed opportunities

The problem of uncertainty can lead animals to miss opportunities such as finding a mate or evading a predator. Animals can reduce uncertainty by gathering information from cues in the environment (Dall and Johnstone 2002). An elevated response to multiple cues is adaptive when the number of cues corresponds to the likelihood of an event.

Within the predatory–prey literature, the sensory complement hypothesis states that multiple cues relating to predation risk combine in an additive manner, evoking increased alarm responses (Lima and Steury 2005). Within the context of the sensory complement hypothesis, enhancement is the mechanism that minimizes mortality when predators are nearby. We found 2 studies where a cross-modal predator stimulus evoked enhanced antipredator behavior (Smith and Belk 2001; Partan et al. 2009) such that 2 simultaneous predator cues were perceived as more risky than either cue alone.

Antagonism: minimizing wasted time and energy

In some cases, we see antagonism, a diminished response to a composite stimulus compared with either unimodal component in isolation. Antagonism is expected when multimodal cues indicate a decreased likelihood of an event, thereby allowing time and energy to be redirected toward other fitness-enhancing activities.

Antagonism with respect to exploratory behaviors was found in sagebrush lizards (*Sceloporus graciosus*). Sniffing, a chemical exploratory behavior, and head-bobbing, which also increases information because it in turn engages an opponent in head-bobbing, are behaviors that reduce uncertainty about a rival (Thompson et al. 2008). When visual and olfactory cues from a rival male were presented simultaneously, resident males decreased the intensity of these behaviors (Thompson et al. 2008). This implies that the time and energy engaged in exploratory behaviors are costly and by being able to acquire more complete information about their rival lizards saved energy.

Crabs (*Heterozius rotundifrons*) showed no response to predator chemical cues but decreased the length of time spent in a catatonic defensive position relative to predator tactile cues when presented with both cues simultaneously (Hazlett and McLay 2005). The simultaneous presentation of both cues may have indicated another type of predation risk such that crabs should change their antipredator tactic by spending less time in a defensive posture and seek refuge (Hazlett and McLay 2005).

Alternately, the pattern of responses could be explained if multiple cues indicated an overall reduction in the likelihood of predation. Because prey should perceive uncertain situations as riskier (Sih 1992; Blumstein et al. 2004), a decrease in antipredator effort is expected when multiple predator cues are available if the cues indicate reduced risk. Under this reducible uncertainty hypothesis, multiple cues may constrain the location or motivation of a predator and indicate that the predator does not pose an immediate threat.

The distinction between the reducible uncertainty hypothesis (antagonism) and the sensory compliment hypothesis (enhancement) can be explained by how multiple cues specify aspects of the environment (e.g., information about risk) compared with a single cue (Figure 2). The sensory compliment hypothesis is expected when multiple cues indicate elevated risk relative to a single cue. The reducible uncertainty hypothesis is expected when multiple cues indicate reduced risk relative a single cue.

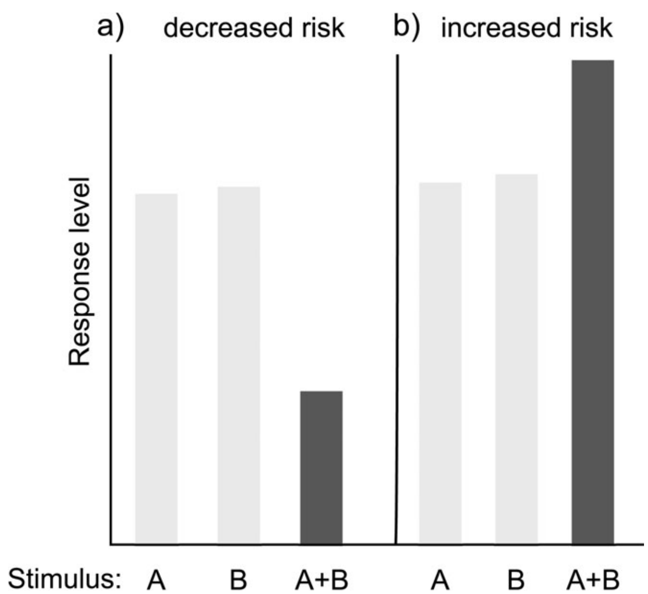

Figure 2
A bimodal predator stimulus (A + B) reduces uncertainty about the risk of predation compared with either isolated unimodal cue.
(a) Antagonism is expected when a bimodal stimulus informs prey that a predator does not pose an immediate danger (see Hazlett and McLay 2005; Thompson et al. 2008). (b) Enhancement is expected when a bimodal stimulus informs prey that a predator poses an immediate danger (see Smith and Belk 2001; Partan et al. 2010).

Equivalence and dominance: a solution when reducing uncertainty is too costly

As in the case of enhancement and antagonism, animals can reduce uncertainty by sampling the multisensory environment (Dall and Johnstone 2002). However, when the costs are particularly high, combining multisensory stimuli may not be favored (Bernays and Wcislo 1994; McNamara and Houston 2009; Marewski et al. 2010; Santangelo et al. 2010). Under such conditions, we predict that a bimodal response will equal the response to one of the unimodal components in isolation. In terms of the framework of Partan and Marler (1999), such a pattern of responses is called either dominance or equivalence depending on whether isolated components evoke the same (equivalence) or different (dominance) responses. These responses may be adjusted over evolutionary time, as seen when a species specializes on a particular resource type (Bernays and Wcislo 1994), or over ecological time, as seen when predators pay attention to features of only a single prey type when prey are cryptic (Dukas and Ellner 1993).

FUTURE DIRECTIONS

Our framework predicts the conditions under which we should expect different mechanisms of multisensory perception based on the relative costs of uncertainty and multisensory perception. Uncertainty can lead to the costs missed opportunities and wasted time and energy (Sih 1992). To test the predictions resulting from our framework, we need to examine systems where the relative costs of uncertainty differ. For example, under some conditions, missed opportunities may be more costly than wasted time and energy. Predation risk presents an ideal context within which to test predictions from our framework. Predation risk, and therefore the system of costs and benefits, is wonderfully amenable to experimental manipulation (e.g., Lendrem 1983; Brown 1988; Holbrook and Schmitt 1988), and it is possible to study populations with different histories of exposure to predators (Blumstein 2006; Ferrari et al. 2007; Lahti et al. 2009). In a predation context, underestimating risk leads to the "missed opportunity" of failing to respond to a predator. Overestimating risk leads to wasted time and energy on antipredator effort that could be spent on other fitness-enhancing activities.

Thus, to begin to understand the adaptive significance of multisensory perception, we urge future studies to move beyond simply categorizing multisensory perception. Instead, we suggest that researchers should design studies that examine how the relative costs of missed opportunities and wasted time and energy influence the dynamics of multimodal perception.

CONSERVATION APPLICATIONS OF RESEARCH ON MULTISENSORY PERCEPTION

Urbanization is often characterized by the introduction of chemical pollutants, novel structures, and the sounds of both humans and traffic, which can affect species' survival (Chan and Blumstein 2011). Studies by Rabin et al. (2006) and Partan et al. (2010) examined the influence of anthropogenic activities on behavior from a multisensory perspective and illustrate the applied significance of understanding the interplay between uncertainty and multimodal perception. In situations with anthropogenic auditory noise, auditory predator cues contributed less to a prey's perception of risk as indicated by an increased effort to obtain visual cues (Rabin et al. 2006) and elevated responses to visual cues (Partan et al. 2010). Impact studies often precede a planned anthropologic action that may change the environment. Incorporating into these studies investigations on how noise introduced by human actions impacts a population by measuring shifts in multisensory perception will be crucial for a more comprehensive measurement of environmental impact.

The management of threatened or endangered species may also benefit from studies that directly test how multisensory perception differs in different ecological contexts. Multisensory stimuli are important for habitat selection, prey recognition, predator avoidance, and mate selection. The inability of animals to recognize these stimuli on their release has been attributed to a low success in translocations and reintroductions despite implementing prerelease training programs (Stamps and Swaisgood 2007). The success of translocations and reintroductions can be enhanced by understanding how uncertainty influences multisensory learning and retention of stimulus recognition.

CONCLUSIONS

We emphasize that uncertainty is an important consideration to the study of multisensory perception. Within our framework, the costs of uncertainty (missed opportunities and wasted time and energy) and the costs of uncertainty reduction may account for different perceptive mechanisms. The current state of multisensory studies within behavioral biology is to characterize perceiver responses. In taking the next step toward a greater understanding of the evolution of multisensory perception, a challenge for future research will be to measure the pattern of responses across different cost–benefit landscapes to test these predictions. Furthermore, the development of quantitative models could significantly improve predictions of when we expect various mechanisms of perception.

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