Optimal multisensory integration

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INTRODUCTION

Animals are often confronted with potentially informative stimuli from a variety of sensory modalities. Although there is a large proximate literature demonstrating multisensory integration, no general framework explains why animals integrate. We developed and tested a quantitative model that explains why multisensory integration is not always adaptive and explains why unimodal decision-making might be favored over multisensory integration. We present our model in terms of a prey that must determine the presence or absence of a predator. A greater chance of encountering a predator, a greater benefit of correctly responding to a predator, a lower benefit of correctly foraging, or a greater uncertainty of the second stimulus favors integration. Uncertainty of the first stimulus may either increase or decrease the favorability of integration. In three field studies, we demonstrate how our model can be empirically tested. We evaluated the model with field studies of yellow-bellied marmots (Marmota flaviventris) by presenting marmots with an olfactory-acoustic predator stimulus at a feed station. We found some support for the model’s prediction that integration is favored when the second stimulus is less noisy. We hope additional predictions of the model will guide future empirical work that seeks to understand the extent to which multimodal integration might be situation dependent. We suggest that the model is generalizable beyond antipredator contexts and can be applied within or between individuals, populations, or species.

Key words: antipredator, decision-making, information, integration, multimodal, multisensory, risk assessment, unified percept, yellow-bellied marmots.
can change depending on the animal's situation or environment. For example, a population of birds near a stream will receive conspecific vocalizations with greater uncertainty due to the noise of flowing water. If an animal is starving mistakenly missing a foraging opportunity may greatly outweigh the cost of a missed reproductive opportunity; if the animal is well fed, then the opposite might be true.

Here, we formalize a framework outlined by Munoz and Blumstein (2012) by developing a quantitative model to 1) explain why unimodal decision-making might be favored over multimodal decision-making, 2) identify key factors that favor multimodal integration, and 3) make clear predictions regarding the extent to which various factors influence integration with the aim of providing testable hypotheses to guide future research. Finally, to illustrate that the model makes testable predictions that can be evaluated with animals, we ask whether three parameters (the benefit of alert behavior when a predator is present, the benefit of relaxed behavior when no predator is present, and the uncertainty of the second of two predator stimuli) influence multimodal integration in free-living yellow-bellied marmots (Marmota flaviventris).

**PART I: THEORETICAL MODEL**

**Methods**

**Modeling framework**

When the world is uncertain, sometimes it might not pay for an individual to attend to a stimulus (Bradbury and Vehrencamp 1998, 2000). Here, we formally expand on this idea by modeling a situation where an animal receives two sequential stimuli in different sensory modalities (see Table 1 for definitions and Table 2 for a complete summary of assumptions). In our model, different sensory modalities are represented in our model through the uncertainty parameter $U_1$ and $U_2$. This is because different modalities are generally independent from one another. For example, wind may diffuse chemical odors but leave a visual stimulus unchanged. Furthermore, an individual likely perceives stimuli in different modalities with different accuracies. To a terrestrial animal, vision may be the most accurate of modalities and, therefore, have a relatively low uncertainty compared with other modalities. We also recognize that different stimuli in a single sensory modality can indicate events with different accuracies. For example, the sound of rustling vegetation could correspond to a predator, but something innocuous such as wind is also likely to produce a similar sound. Therefore, rustling vegetation may have high uncertainty compared with, for example, a vocalization even though both are acoustic stimuli.

The model examines the extent to which stimulus uncertainties, prior probability of a given state, and the costs of mistakes influence whether or not a prey will integrate two stimuli in different sensory modalities. We also include a physiological cost to integration. For the purposes of developing our model, we use an example of a foraging prey (notation descriptions in Table 3). We refer readers to Supplementary Material for an application of the model to mate recognition.

The world is in one of two possible states, predator present (PRED) or no predator present (NONE). The prey has an estimate for the prior probability of the presence of a predator, $P_{PRED}$, which could have been gathered over evolutionary time or within the lifetime of the prey. The prey can engage in one of two behaviors, either forage (F) or hide (H). Because the prey is not certain as to the presence of a predator, the prey will sometimes make mistakes. The
prey always manages to escape the predator, but the predator will injure the prey if the prey fails to hide. Depending on the state of the world and whether the prey is foraging or hiding, the prey can receive one of four payoffs, \( W_{\text{PRED}} \), \( W_{\text{NONE}} \), \( W_{\text{PRED}} \), and \( W_{\text{NONE}} \) are the payoffs of behaving appropriately either when a predator is absent or present, respectively. \( W_{\text{PRED}} \) and \( W_{\text{NONE}} \) are the payoffs of mistakes either when a predator is absent or present, respectively. Foraging receives the greatest benefit when a predator is not present, and hiding receives the greatest benefit when a predator is present. We assumed these payoffs do not change in between the first and second stimuli.

In the absence of a stimulus or when the prey “ignores” a stimulus, the prey sets a cutoff probability \( P_c \), which is optimal when the following condition holds (Bradbury and Vehrencamp 1998):

\[
P_c = \frac{W_{\text{PRED}} - W_{\text{NONE}}}{W_{\text{PRED}} - W_{\text{NONE}}}
\]

The payoff the prey receives when ignoring a stimulus depends on the value of \( P_i \), relative to \( P_{\text{PRED}} \). When \( P_{\text{PRED}} \leq P_i \), the prey always forages with low vigilance and receives the average payoff:

\[
P_{\text{ignore}} = (1 - P_{\text{PRED}}) W_{\text{PRED}} + P_{\text{PRED}} W_{\text{NONE}}
\]

When \( P_{\text{PRED}} > P_i \), the prey will always hide and receives the average payoff:

\[
P_{\text{ignore}} = P_{\text{PRED}} W_{\text{PRED}} + (1 - P_{\text{PRED}}) W_{\text{NONE}}
\]

Throughout, we use “stimulus” to refer to a feature within a sensory modality which can assume a set of magnitudes \( S_i \). We have used the subscript \( i \) to index the order of stimuli. For the purposes of introducing our model, we use “body size” as an example of a stimulus. If the prey uses the stimulus, then it incorporates information about body size into its decision to forage or hide. When using a stimulus, the prey receives an average payoff \( P_{\text{ignore}} \). The animal should use stimulus \( i \) only when \( P_{\text{ignore}} \geq P_{\text{ignore}} \). The difference between these two average payoffs is also known as the value of information \( V_i \) (Stephens 1989; Bradbury and Vehrencamp 1998), which must be positive for the prey to use the stimulus.

The prey correctly decides to forage with some probability \( P_{\text{correct reject}} \). The animal also makes a correct decision if it hides, which occurs with probability \( P_{\text{false alarm}} \). The probabilities of mistakes are the probability of foraging when a predator is present, \( P_{\text{max}} \), and the probability of hiding when in fact a nonthreat is present, \( P_{\text{false alarm}} \). The average payoff of using a stimulus equals the average payoff of doing each behavior in each state weighted by the probability that the world is in that state minus the processing costs in the form of energy expenditure and/or physiological investment in sensory systems (Niven and Laughlin 2008), \( K_i \), of attending to the stimulus. Thus,

\[
P_{\text{ignore}} = (1 - P_{\text{PRED}}) P_{\text{correct reject}} W_{\text{PRED}} + P_{\text{true alarm}} W_{\text{NONE}} + (1 - P_{\text{PRED}}) P_{\text{PRED}} W_{\text{NONE}}
\]

Because \( P_{\text{correct reject}} = 1 - P_{\text{false alarm}} \) and \( P_{\text{true max}} = 1 - P_{\text{false alarm}} \), the preceding can be rewritten as

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
</tr>
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<tbody>
<tr>
<td>Stimulus</td>
<td>A feature within a sensory modality such as body size, auditory frequency or odor concentration. A stimulus encompasses the spectrum of magnitudes ( S_i ) that said feature can assume.</td>
</tr>
<tr>
<td>Uncertainty, ( U_i )</td>
<td>Difference in means of the distributions of ( S_i ) (Figure 1). When the difference in means is smaller, the stimulus is more uncertain and the state of the world (e.g., predator vs. nonthreat) is less distinguishable. We model different sensory modalities by specifying different ( U_i ) for each stimulus.</td>
</tr>
<tr>
<td>Receiver environment</td>
<td>Properties of the receiver (e.g., predator vs. nonthreat) and/or the receiver’s environment that influence how a receiver might respond to the world.</td>
</tr>
<tr>
<td>Using/attending to a stimulus</td>
<td>The change in the animal’s expectation of the state of the world [after Bradbury and Vehrencamp (1998), p. 389]. If it is optimal for an animal to ignore a stimulus, then the stimulus does not have information.</td>
</tr>
<tr>
<td>Ignoring a stimulus</td>
<td>The animal does not incorporate any ( S_i ) into its behavioral decision. Its estimate of the state of is not improved.</td>
</tr>
<tr>
<td>Information</td>
<td>The change in the animal’s expectation of the state of the world [after Bradbury and Vehrencamp (1998), p. 389]. If it is optimal for an animal to ignore a stimulus, then the stimulus does not have information.</td>
</tr>
<tr>
<td>Multimodal integration</td>
<td>When the animal incorporates information from ( n ) stimuli from more than one sensory modality in order to improve the accuracy of its expectation of the world. Optimal when ( V_i \geq 0 ).</td>
</tr>
<tr>
<td>Noise</td>
<td>A property of the world that generates stimulus uncertainty.</td>
</tr>
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Table 3
Notation definitions

<table>
<thead>
<tr>
<th>Notation</th>
<th>Definition</th>
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<tbody>
<tr>
<td>PRED</td>
<td>State of the world when a predator is present</td>
</tr>
<tr>
<td>NONE</td>
<td>State of the world when a nonthreat is present</td>
</tr>
<tr>
<td>F</td>
<td>Foraging. Optimal when a nonthreat is present</td>
</tr>
<tr>
<td>H</td>
<td>Hiding. Optimal when a predator is present</td>
</tr>
<tr>
<td>$P_{\text{PRED}}$</td>
<td>Prey's estimate of the prior probability that a predator is present</td>
</tr>
<tr>
<td>$B_{\text{PRED}}$</td>
<td>Net benefit of correctly hiding when a predator is present</td>
</tr>
<tr>
<td>$B_{\text{NONE}}$</td>
<td>Net benefit of correctly foraging when a nonthreat is present</td>
</tr>
<tr>
<td>$PO_{\text{ignore}}$</td>
<td>Average payoff of not using a stimulus when making an antipredator decision</td>
</tr>
<tr>
<td>$PO_{\text{use}}$</td>
<td>Average payoff of using the $i$th stimulus when making an antipredator decision</td>
</tr>
<tr>
<td>$K_i$</td>
<td>Cost of using the $i$th stimulus</td>
</tr>
<tr>
<td>$\mu_{\text{PRED}}$</td>
<td>Mean $S_i$ when a predator is present</td>
</tr>
<tr>
<td>$\mu_{\text{NONE}}$</td>
<td>Mean $S_i$ when no predator is present</td>
</tr>
<tr>
<td>$U_i$</td>
<td>A unitless index of uncertainty of the $i$th stimulus equal to the proportion of overlap between the NONE and PRED distributions of $S_i$, and is a function of $\mu_{\text{PRED}}$ and $\mu_{\text{NONE}}$</td>
</tr>
<tr>
<td>$S_i$</td>
<td>Magnitude of the $i$th stimulus</td>
</tr>
<tr>
<td>$V_i$</td>
<td>The value of information is the output variable of model. Equals the difference $PO_{\text{use}} - PO_{\text{ignore}}$. When $V_i &gt; 0$, the animal will use the $i$th stimulus in improving the accuracy of its estimate of the state of the world</td>
</tr>
<tr>
<td>$A$</td>
<td>Favorability of integration. Equals the proportion of a parameter area while holding all other parameters constant, in which integration is favored (Supplementary Figure S1)</td>
</tr>
</tbody>
</table>

The value of information, $PO_{\text{use}} - PO_{\text{ignore}}$, for using a stimulus when $P_{\text{PRED}} \geq P_{\text{hit}}$ is then

$$V_i = P_{\text{PRED}}P_{\text{hit}}B_{\text{PRED}} - (1 - P_{\text{PRED}})P_{\text{false alarm}}B_{\text{NONE}} + P_{\text{PRED}}W_fB_{\text{PRED}} + (1 - P_{\text{PRED}})W_fB_{\text{NONE}} - K_i$$

and when $P_{\text{PRED}} < P_{\text{hit}}$ is

$$V_i = P_{\text{PRED}}P_{\text{hit}}B_{\text{PRED}} - (1 - P_{\text{PRED}})P_{\text{false alarm}}B_{\text{NONE}} - K_i$$

$B_{\text{PRED}} = W_{H\text{PRED}} - W_{F\text{PRED}}$ is the net benefit of hiding when a predator is present. $B_{\text{NONE}} = (W_fB_{\text{NONE}} - W_fB_{\text{NONE}})$ is the benefit of foraging when a nonthreat is present.

An object with a body size $S_i$ corresponds to a predator with a certain probability $P(S_i|\text{PRED})$ and to a nonpredator with a certain probability $P(S_i|\text{NONE})$. We assumed these probability distributions are continuous and normal with a standard deviation (SD) equal to 1 unit on an arbitrary scale (Table 2). We assumed that the prey has knowledge of these distributions

![Figure 1](https://academic.oup.com/beheco/advance-article-abstract/doi/10.1093/beheco/arz175/5601418)

Body size indicates if the object is more likely a predator or nonpredator because the average body size of predators, $\mu_{\text{PRED}}$, and nonpredators, $\mu_{\text{NONE}}$, are different (Figure 1). Here, we have assumed that, on average, predators are larger than nonpredators: $\mu_{\text{PRED}} > \mu_{\text{NONE}}$ (Figure 1). However, sometimes predators are smaller than nonpredators and vice versa. On our arbitrary scale for $S_i$ the grand mean of body sizes equals 0 (as will be shown below; only the difference in means between predators and nonpredators is important). The extent to which the world is uncertain depends on $\mu_{\text{PRED}}$ and $\mu_{\text{NONE}}$. As $\mu_{\text{PRED}}$ and $\mu_{\text{NONE}}$ become more similar, the overlap between the NONE and PRED distributions increases, thereby increasing the probability of making mistakes.

We assumed that when the prey uses a stimulus, it makes foraging decisions following signal detection theory in which the prey receives the maximum average payoff when it sets a cutoff at some stimulus magnitude $S_{c}$. (Green and Swets 1966; Oaten et al. 1975; Brilot et al. 2012). If the prey receives a stimulus with magnitude $S_i \geq S_{c}$, the prey will always hide. If the prey receives a stimulus with magnitude $S_i < S_{c}$, the prey will forage. Consequently, we calculated $S_{c}$ from the relationship that, at the optimal $S_{c}$, the average payoff of foraging $PO(F)$, equals the average payoff of high vigilance $PO(H)$. The average payoff of a given behavior is the payoff of the behavior in each state weighted by the probability that the world is in a given state. Therefore,

$$PO(F) = P(\text{PRED} | S_{c}) W_{F\text{PRED}} + P(\text{NONE} | S_{c}) W_{F\text{NONE}}$$ and
Alternatively, at $S_{\alpha}$, the following is true:

$$B_{\text{PRED}}P(\text{PRED}|S_{\alpha}) = B_{\text{NONE}}P(\text{NONE}|S_{\alpha})$$

where $P(\text{PRED}|S_{\alpha})$ and $P(\text{NONE}|S_{\alpha})$ are the probabilities of the presence of a predator and a non-predator given a stimulus of magnitude $S_{\alpha}$, respectively. From Bayes' Theorem,

$$P(\text{PRED} | S_{\alpha}) = \frac{P(\text{PRED}|S_{\alpha})P(S_{\alpha})}{P(S_{\alpha})}$$

and similarly for $P(\text{NONE} | S_{\alpha})$. $P(S_{\alpha})$ is the sum of the probability of $S_{\alpha}$ in each state, weighted by the probability that the world is in that state.

$$P(S_{\alpha}) = P(\text{PRED})P(S_{\alpha}|\text{PRED}) + (1 - P(\text{PRED}))P(S_{\alpha}|\text{NONE})$$

Therefore, on specifying $B_{\text{PRED}}$, $B_{\text{NONE}}$, $\mu_{\text{PRED}}$, and $\mu_{\text{NONE}}$, the value of $S_{\alpha}$ is known (see Supplementary Material for the explicit equation for $S_{\alpha}$). $P_{\text{hit}}$ and $P_{\text{false alarm}}$, which are the areas under the PRED distribution above $S_{\alpha}$ and under the NONE distribution above $S_{\alpha}$, respectively, are given by

$$P_{\text{hit}} = 1 - 0.5 \left[1 + \text{erf} \left( \frac{S_{\alpha} - \mu_{\text{PRED}}}{\sqrt{2}} \right) \right]$$

and

$$P_{\text{false alarm}} = 1 - 0.5 \left[1 + \text{erf} \left( \frac{S_{\alpha} - \mu_{\text{NONE}}}{\sqrt{2}} \right) \right]$$

where $\text{erf}(x)$ is the error function of $x$.

Using the preceding equations and on specifying $P_{\text{PRED}}$, $B_{\text{NONE}}$, $\mu_{\text{PRED}}$, $\mu_{\text{NONE}}$, and $K_i$, the value of information of the first stimulus can be calculated (see Supplementary Material for the explicit equation for $V_i$ when $P_{\text{PRED}} \geq P_i$, or when $P_{\text{PRED}} < P_i$).

If the prey uses the first stimulus (i.e., $V_i \geq 0$), we can calculate $P_{\text{PRED}}'$ from $S_i$, $\mu_{i, \text{STATE}}$, and $P_{\text{PRED}}$ using Bayes' Theorem:

$$P_{\text{PRED}}' = \frac{P_{\text{PRED}}P(S_i|\text{PRED})}{P(S_i)}$$

where $P(S_i|\text{PRED})$ is the probability of receiving a stimulus with magnitude $S_i$ when a predator is present. Because we have assumed that the probability of receiving $S_i$ in each state is a normal distribution with unit SD,

$$P(S_i | \text{PRED}) = \frac{1}{\sqrt{2\pi}} \exp \left[ -0.5(S_i - \mu_{i, \text{PRED}})^2 \right]$$

$P(S_i)$ is the probability of a stimulus with magnitude $S_i$ occurring in the world, which is the sum of the probabilities of $S_i$ in each state weighted by the probability that the world is in that state:

$$P(S_i) = P_{\text{PRED}}P(S_i|\text{PRED}) + (1 - P_{\text{PRED}})P(S_i|\text{NONE}).$$

The animal then receives a second stimulus having properties $\mu_{\text{NONE}}$ and $\mu_{i, \text{PRED}}$. Because processing costs are likely to be greater with increasing number of stimuli, we assumed that $K_i \leq K$. Setting $P_{\text{PRED}} = P_{\text{PRED}}'$, $V_i$ is then calculated.

When $V_1 \geq 0$ and $V_2 \geq 0$, it is optimal for the prey to use information from both modalities in making a foraging decision, a situation we call integration. Thus, the criterion $V_1 \geq 0$ and $V_2 \geq 0$ is a formal definition of multimodal integration. The situation can be specific to multiple modalities by specifying different levels of uncertainty for each stimulus. As is typically the case, different sensory modalities are independently disturbed by environmental noise (acoustic noise will not affect a visual stimulus) and/or by the fact that an individual is generally better at discriminating the world based on stimuli in certain modalities. Two instances of unimodal information use can occur. The first instance is when $V_1 \geq 0$ and $V_2 < 0$, which is when the prey only uses the first stimulus. The second instance of unimodal information use occurs when $V_1 < 0$ and $V_2 \geq 0$. In the latter example, the prey evaluates the second stimulus without updating $P_{\text{PRED}}$. When $V_1 < 0$ and $V_2 < 0$, the prey does not obtain information from either stimulus to inform its perception regarding the presence/absence of a predator.

When discussing uncertainty, we are referring to a unitless parameter $U_i$, which is the proportion of overlap between the NONE and PRED distributions of the $i$th stimulus. By doing so, uncertainty, which is the difference in means of PRED and NONE distributions, is on a unitless scale.

### Sensitivity analysis

We assessed the sensitivity of $V_2$ to $P_{\text{PRED}}$, $B_{\text{NONE}}$, $B_{\text{PRED}}$, $U_1$, $U_2$, $K_2$, and $S_i$ by calculating Spearman partial rank correlation coefficients (PRCC) between input parameters and $V_2$. We ran 500 simulations with parameters sampled using Latin Hypercube Sampling (LHS). LHS is commonly used to explore the behavior of models by, effectively, simultaneously varying all the values of all input parameters (McKay et al. 1979; see Blower and Dowlatabadi 1994 for an example). Because we were interested in an exploratory LHS analysis, we assigned uniform Supplementary Material (Helton 1993) to all parameters. We varied $U_1$ and $U_2$ from 0 to 1; $S_i$ from $-1$ to 1; $P_{\text{PRED}}$ from 0 to 1; $B_{\text{NONE}}$ and $B_{\text{PRED}}$ from 0 to 5; and $K_i$ from 0 to 5 (because $V_2$ is only calculated when $V_1 \geq 0$, we assumed $K_i = 0$ as a simplification. By doing so, $V_i \geq 0$ for all parameter combinations).

### Graphical methods

We examined different situations where information use switches from unimodal to bimodal. In presenting our results graphically we frame our results in terms of the “favorability of integration” $A$, which we define as the proportion of a 2D parameter area in which $V_2$ is positive while the other parameters are held constant (see Supplementary Figure S1). Each area consisted of $40 \times 40$ simulations and each plot consists of 20 values of $A$. All simulations and analyses were done using R, version 3.0.2 (R Core Team 2016).

### Model results

We developed a general model that determines whether or not an animal should integrate two stimuli in different sensory modalities given a set of environmental conditions when deciding to engage in one of two behaviors. Two different modalities were modeled by specifying different $U_i$ and $U_2$. When integrating additional stimuli, an animal increases the accuracy of its perception of the world, thereby increasing the likelihood that the animal makes a correct decision. However, our model demonstrates that, in some situations, due to the costs of mistakes and the costs of attending to stimuli, the benefit from making more accurate decisions is not sufficient to warrant integration.

Spearman PRCC between model parameters and $V_2$ sampled using LHS are given in Table 4. Because $K_2$ is a cost of attending to the second stimulus, a greater $K_2$ decreases $V_2$ (PRCC = −0.80, $P = 9.87 \times 10^{-141}$, Est. = −25.26).
A larger $P_{\text{PRED}}$ increases the favorability of integration ($\text{PRCC} = 0.74, P = 4.87 \times 10^{-94}, \text{Est.} = 20.57$; Figure 2). Larger $U_2$ decreases the favorability of integration ($\text{PRCC} = -0.25, P = 1.41 \times 10^{-6}, \text{Est.} = -4.82$). The magnitude of the first stimulus $S_1$ influences integration through its action in the prey's updated prior after receiving the first stimulus $P_{\text{PRED}}'$. An $S_1$ that is more like a predator (i.e., $S_1 > 0$) generates $P_{\text{PRED}} > P_{\text{PRED}}$, indicating an increased likelihood of encountering a predator. An $S_1$ that is more like a nonthreat (i.e., $S_1 < 0$) decreases a decreased likelihood of encountering a predator ($P_{\text{PRED}}' < P_{\text{PRED}}$). Therefore, greater $S_1$ increases the importance of distinguishing predators from nonpredators ($\text{PRCC} = 0.65, P = 5.18 \times 10^{10}, \text{Est.} = 16.34$). This effect is also seen by, for a given $U_1$ and $P_{\text{PRED}}$, a smaller $A$ when $S_1$ is more likely to have originated from a nonthreat (Figure 2a) than predator (Figure 2b).

The relationship between $U_1$ and favorability of integration is nuanced. Sensitivity analysis shows a negligible correlation between $U_1$ and $V_2$ ($\text{PRCC} = 0.004, P = 0.93, \text{Est.} = 0.09$). This result emerges because the directional effect of $U_1$ on $V_2$ depends on $S_1$; thus, on average, the effect of $U_1$ is negligible. For $S_1$, highly indicative of a nonthreat (i.e., $S_1 < 0$), greater $U_1$ increases the favorability of integration (Figure 2a). For $S_1$, highly indicative of a predator (i.e., $S_1 > 0$), smaller $U_1$ increases the favorability of integration (Figure 2b). When $S_1$ is equally likely to have originated from a predator and nonthreat (i.e., $S_1 = 0$), $U_1$ has no effect on integration and the effect of $U_1$ is most strongly observed for smaller $P_{\text{PRED}}$ (Figure 2c top vs. bottom).

$B_{\text{NONE}}$ is the benefit for correctly hiding (i.e., hiding when a predator is present). As $B_{\text{PRED}}$ increases, the prey's perception should tend toward integration ($\text{PRCC} = 0.70, P = 1.31 \times 10^{-77}, \text{Est.} = 18.65$). A larger $B_{\text{NONE}}$ means that the prey receives a greater benefit for correctly foraging (i.e., foraging when a nonthreat is present). As the need for accuracy in detecting a predator decreases, as might arise when the prey's energy reserves run low and a missed foraging opportunity could compromise the prey's health, the prey does better to ignore the second stimulus and always forages even if it means increasing the rate at which the prey misses detecting a predator. Consequently, higher $B_{\text{NONE}}$ tends to decrease the favorability of integration ($\text{PRCC} = -0.25, P = 9.79 \times 10^{-77}, \text{Est.} = 20.57$). However, $B_{\text{NONE}}$ has more than three times the effect on integration compared with $B_{\text{NONE}}$ (Est = 18.65 compared with $-4.90$).

### PART II: EMPIRICAL TESTS

#### Methods

Through three separate field studies, we illustrate how three predictions of our model can be empirically tested. We examined the effects of $B_{\text{PRED}}$, $U_2$, and $B_{\text{NONE}}$ on integration in free-living yellow-bellied marmots. We measured marmot responses to coyote olfactory and/or acoustic stimuli while foraging at a feed station (we refer readers to Supplementary Material for details of the feed station and playback setup). Individuals received four treatments, water-$X_1$, urine-$X_2$, water-$X_3$, or urine-$X_4$, where $X_1$ and $X_2$ are different levels of the model parameter we were testing in the given experiment (i.e., $B_{\text{PRED}}$, $U_2$, or $B_{\text{NONE}}$). We assigned treatments according to a predefined Latin square.

The study testing the model prediction that higher $B_{\text{PRED}}$ favors integration was conducted in 2011. Within the framework of our model, $B_{\text{PRED}}$ is the benefit to marmots of correctly increasing alert behavior when a predator is present. We manipulated $B_{\text{PRED}}$ based on the distance of the feed station to the burrow. Assuming a greater severity of injury when failing to appropriately respond to a predator when farther from the burrow, the higher-$B_{\text{PRED}}$ condition is associated with marmots foraging further from the burrow. In the lower-$B_{\text{PRED}}$ situation, the feed station was set up 1 m from the burrow. In the higher-$B_{\text{PRED}}$ situation, the feed station was set up 3.5 m away from the burrow.

The study testing the model prediction that higher $U_2$ decreases the favorability of integration was conducted in 2012. $U_2$ is the uncertainty of the second stimulus, which in our setup is vocalizations. We established two levels of $U_2$ based on the level of white noise embedded (using Sound Studio V. 4) in the audio files of coyote vocalizations, high (~5 dB) or low (~20 dB) noise (see Supplementary Material for spectrograms and waveforms). The overall amplitude of the playback was not adjusted after embedding in noise. The feed station was set up 3.5 m from burrow.

The study testing the model prediction that greater $B_{\text{NONE}}$ decreases the favorability of integration was conducted in 2013. Within the framework of our model, $B_{\text{NONE}}$ is the benefit to marmots of foraging in the absence of a predator. We manipulated $B_{\text{NONE}}$ through handling time of the bait by mixing the bait with pebbles approximately 7 mm in diameter (“Pea Pebbles,” Pavestone, Tyrone, GA). The ratio of bait to pebbles was either 6:1 or 4:3. A lower ratio of bait to pebbles (4:3) establishes a longer handling time such that, in a given amount of time, marmots obtained a lower foraging return compared to a higher ratio of bait to pebbles (6:1). Therefore, the low- and high-$B_{\text{NONE}}$ conditions are associated with the 4:3 mixture and 6:1 mixtures, respectively. The feed station was set up 3.5 m from burrow.

All analyses were done using R (V. 3.3.2) (R Core Team 2016). We fitted linear mixed-effects models by maximizing the log-likelihood using the function lme in the R package nlme (Pinheiro et al. 2013). We specified “individual” as the random factor and the arcsine square root transformation of proportion of time spent foraging as the dependent variable. Fixed factors were odor:acoustic stimulus [water:none, water:vocalizations, urine:none, and urine:vocalizations], age (yearling, adult), sex, audio exemplar (1–3), trial number (1–4), model parameter ($X_1$, $X_2$), and the interaction between stimulus and model parameter. We tested the significance of fixed effects through Wald tests using the function anova in the package multcomp (Hothorn et al. 2008).

Marmots were studied under protocols approved by the Animal Use and Care Committees of the University of California Los...
Angeles and the RMBL (UCLA Protocol No. 2001-191-01, RMBL protocol No. 1, both renewed annually) and under permits from the Colorado Division of Wildlife (TR917 issued annually). By design, animals were not harmed by routine live trapping or by these brief experiments.

**Results**

We found that marmots’ \( N = 21 \) pattern of responses to predator stimuli was influenced by noise level of vocalizations \( U_2 \), shown by a significant noise \( \times \) stimulus interaction \( (F = 3.887, P = 0.011; \text{Table 5}) \). Post hoc comparisons (Figure 3) of responses to stimuli show a different pattern of responses to low-noise (Table 6) and high-noise (Table 7) situations. In the low-noise condition, the multimodal response was different from urine \( (\text{Est.} = -0.355, \text{SE} = 0.69, Z = -5.142, P < 0.001) \) and vocals \( (\text{Est.} = -0.207, \text{SE} = 0.066, Z = -3.130, P = 0.009) \). In the high-noise condition, the multimodal response was different from urine \( (\text{Est.} = -0.399, \text{SE} = 0.049, Z = -8.142, P < 0.001) \) but not different from vocals.

We did not find a significant parameter \( \times \) stimulus interaction in the studies testing \( B_{\text{PRED}} \) \( (N = 24) \) or \( B_{\text{NONE}} \) \( (N = 21) \) on marmots’ pattern of responses to predator stimuli. We refer readers to Supplementary Material for tables summarizing these results.

**DISCUSSION**

Understanding the factors responsible for the diverse types of multimodal integration responses and the evolution or loss of integration abilities is challenging. Through a mathematical model, we suggested that multimodal integration may be situation dependent as has been reported in previous studies (e.g., population-specific differences in multimodal integration in squirrels: Partan et al. [2010]; reproductive state influenced multimodal integration in...
We demonstrated in three field experiments how an animal's environment may be parameterized in our model and by doing so hope to stimulate future empirical tests. Our model defines “multimodal integration” as occurring when the values of information for sequential stimuli are >0. We modeled different sensory modalities by defining differing uncertainties for each stimulus. The following parameters were found to increase the favorability of integration: greater prior probability of a predator present, greater probability that the first stimulus came from a predator, lower uncertainty of the second stimulus, lower benefit of foraging in the absence of a predator (B_{NONE}), greater benefit of increased antipredator behavior in the presence of a predator (B_{PRED}), and lower cost of attending to a stimulus. The directional effect of uncertainty of the first stimulus on the favorability of integration depends on whether S_1 is more indicative of a nonthreat or a predator. For S_1 more like a nonthreat, the favorability of integration increases with increasing U_1. For S_1 more like a predator, the favorability of integration decreases with increasing U_1. For S_1 equally likely to have been produced by a predator or nonthreat, U_1 has no effect on integration.

In the field, we tested the effect of uncertainty of the second stimulus (U_2) on olfactory-acoustic integration by playing back coyote vocalizations embedded in one of two different noise levels. We found that noise influences multimodal integration in marmots. Under low noise, marmots’ multimodal response was different from the unimodal responses, consistent with the formation of a

Figure 3
Mean proportion of time marmots spent foraging when coyote vocalizations were (a) less noisy or (b) more noisy. Brackets indicate significantly different pairwise comparisons. Error bars show 95% confidence intervals. N = 21.

Table 6
Pairwise comparisons of stimulus types for low-noise vocalizations

<table>
<thead>
<tr>
<th>Stimulus comparison</th>
<th>Est.</th>
<th>SE</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Urine + vocals</td>
<td>−0.355</td>
<td>0.069</td>
<td>−5.142</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Water</td>
<td>−0.105</td>
<td>0.066</td>
<td>−1.591</td>
<td>0.383</td>
</tr>
<tr>
<td>Water + vocals</td>
<td>−0.561</td>
<td>0.066</td>
<td>−8.500</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Water + vocals</td>
<td>0.250</td>
<td>0.066</td>
<td>3.779</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Water</td>
<td>−0.207</td>
<td>0.066</td>
<td>−3.130</td>
<td>0.009</td>
</tr>
<tr>
<td>Water + vocals</td>
<td>−0.456</td>
<td>0.060</td>
<td>−7.639</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Proportion of time spent foraging is the dependent variable (N = 21). Significant P-values are in bold.

Table 7
Pairwise comparisons of stimulus types for low-noise vocalizations

<table>
<thead>
<tr>
<th>Stimulus comparison</th>
<th>Est.</th>
<th>SE</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Urine + vocals</td>
<td>−0.399</td>
<td>0.049</td>
<td>−8.142</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Water</td>
<td>0.117</td>
<td>0.056</td>
<td>2.089</td>
<td>0.156</td>
</tr>
<tr>
<td>Water + vocals</td>
<td>−0.343</td>
<td>0.056</td>
<td>−6.106</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Water + vocals</td>
<td>0.516</td>
<td>0.056</td>
<td>9.202</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Water</td>
<td>0.057</td>
<td>0.057</td>
<td>1.007</td>
<td>0.744</td>
</tr>
<tr>
<td>Water + vocals</td>
<td>−0.460</td>
<td>0.057</td>
<td>−8.124</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Proportion of time spent foraging is the dependent variable (N = 21). Significant P-values are in bold.
multimodal percept (sensu Partan and Marler 1999; Stein et al. 2009; Halfwerk et al. 2019). The multimodal foraging response was less compared with urine alone but greater compared with vocals alone. For an interpretation of foraging levels on marmots’ perception of risk, we refer readers to Supplementary Materials. Under high-noise marmots, we did not find evidence of multimodal integration. The result dovetails with predictions from our model that integration is favored under lower $U_2$. Furthermore, this result is an example of how noise can cause a shift in multimodal perception at the level of the individual and demonstrates how changes in perception could ultimately impact changes in signaling (Partan 2017).

In the field, we manipulated $B_{\text{RED}}$ and $B_{\text{NONE}}$ through distance at which marmots foraged from the burrow and bait handling time, respectively. We did not find an effect of $B_{\text{RED}}$ or $B_{\text{NONE}}$ on olfactory-acoustic integration in marmots. This result could be because the influence of a given parameter depends on the values of other parameters. It is possible that the region in parameter space in which we tested marmots was such that the favorability of integration does not strongly respond to $B_{\text{RED}}$ or $B_{\text{NONE}}$. It is possible that, if we had chosen more disparate levels of these parameters, we could have detected a change in integration response.

Although we have developed and tested our model within the context of a prey making antipredator decisions, our model can predict integration in a variety of ecological contexts (see Supplementary Materials for an example of mate recognition). Furthermore, our model can be modified to capture more complex situations. In nature, objects often have several attributes (e.g., size, color, and vocalization frequency); each of these attributes can be incorporated by defining $S_i$ as a vector on several axes. Furthermore, more than two stimuli can be examined simply by iteratively applying the algorithm with the new updated probability and stimulus’ uncertainty. So far, we have assumed stimuli are received on a time scale such that the benefits of correct decisions are constant. However, these benefits may change in rapidly changing environments or when the time lag between receiving a stimulus is relatively large. Our model can also be extended to represent a world that can be in three or more states. For example, a prey’s response may depend on whether an aerial predator is present, a terrestrial predator is present, or a nonthreat is present (e.g., Brilot et al. 2012). Furthermore, behavior decisions may not be bimodal as we have assumed. A prey’s decision may be with regards to the level of vigilance it should display, which can vary on a continuous scale depending on the level of threat posed (Lima and Dill 1990). This can be incorporated by specifying a “response function”, for example, that varies from 0 (no vigilance) to 1 (constant vigilance) that varies from 0 (no vigilance) to 1 (constant vigilance) which can be incorporated by defining $S_i$ with some function through $S_i$. These readily modeled situations should be further explored.

Given a changing set of environmental conditions, an individual’s decision to switch from unimodal to multimodal integration (or vice versa) will follow our model’s predictions only if the individual has knowledge of the extent to which the environment changed. Sih et al. (2011) provide a thorough review of how animals might have this knowledge in order to adaptively respond to changing environments. Given the premise that multimodal integration is an adaptive response to an individual’s environment (Partan 2017), knowledge of a changing environment assumed by our model may be obtained by animals through mechanisms identified by Sih et al. (2011).

In conclusion, we have developed and tested a model that predicts the extent to which animals should integrate multisensory stimuli given a set of environmental conditions. Uncertainty and the value of information (Stephens 1989; Koops 2004) have previously been applied to several problems involving a single stimulus. Our model is relevant to multimodal situations because of differing degrees of uncertainty specified for each stimulus. We hope the model will inspire future empirical tests of the model, which are necessary to further understand the extent to which integration is an adaptation and the environmental situations that may preclude integration at the level of the individual, population, or species.

SUPPLEMENTARY MATERIAL

Supplementary data will be available online after publication.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Munoz and Blumstein (2019).

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REFERENCES


