

## Review

The Cognitive Ecology of Stimulus Ambiguity:  
A Predator–Prey PerspectiveBrian C. Leavell <sup>1,\*,@</sup> and Ximena E. Bernal<sup>1,2,@</sup>

**Organisms face the cognitive challenge of making decisions based on imperfect information. Predators and prey, in particular, are confronted with ambiguous stimuli when foraging and avoiding attacks. These challenges are accentuated by variation imposed by environmental, physiological, and cognitive factors. While the cognitive factors influencing perceived ambiguity are often assumed to be fixed, contemporary findings reveal that perceived ambiguity is instead the dynamic outcome of interactive cognitive processes. Here, we present a framework that integrates recent advances in neurophysiology and sensory ecology with a classic decision-making model, signal detection theory (SDT), to understand the cognitive mechanisms that shape perceived stimulus ambiguity in predators and prey. Since stimulus ambiguity is pervasive, the framework discussed here provides insights that extend into nonforaging contexts.**

**Decision-Making and Stimulus Ambiguity**

Organisms continuously make **decisions** (see [Glossary](#)), some of great consequence, in response to sensory information from their environments. Often, however, sensory stimuli from vastly different sources are difficult to parse not only due to their similar physical properties, but also how organisms translate and process stimuli [1,2]. This forces organisms to make decisions based on imperfect information. Indeed, **detection** and **discrimination** of ambiguous stimuli drive the outcomes of myriad ecological decisions, such as in predator–prey interactions (e.g., [3–5]), kin recognition (e.g., [6–8]), and mate choice (e.g., [9–11]). While not all decisions result in such extreme fitness payoffs as being a predator's next meal, **stimulus ambiguity** is nonetheless pervasive and has the potential to greatly impact the ecology and evolution of organisms [12].

To examine how stimulus ambiguity shapes decisions, behavioral and evolutionary ecologists often employ principles of **signal detection theory (SDT; Box 1)**. Though alternative decision-making models have been useful in many cases (e.g., [13–16]), signal detection models are especially suitable for the study of stimulus ambiguity, given their explicit and quantitative accounts of stimulus ambiguity and capacity to be modified to suit specific ecological and cognitive contexts (e.g., [17–20]). While signal detection models have been widely used in evolutionary ecology, their predictions can be highly sensitive to underlying assumptions of receiver **cognition** and ecology [18,20]. Here, we lean on contemporary advances in the study of animal cognition to critically evaluate largely overlooked assumptions of sensory processing, which are at the core of all signal detection models. The generality of stimulus ambiguity in decision-making makes concepts reviewed here relevant across ecological contexts. We focus our discussion, however, on predator–prey interactions, given that decision-making by both predators and prey has been studied using signal detection approaches for over 50 years [21]. Such emphasis on these systems is not surprising considering the high fitness payoffs associated with detection and discrimination errors in foraging and defense. Indeed, the ecological challenge of stimulus ambiguity has led to a diversity of antipredator strategies employed by prey (e.g., mimicry), as well as counteracting predator foraging strategies (e.g., attacking or avoiding potentially costly mimics). By examining

## Highlights

Advances in neurophysiology and sensory ecology are unraveling the mechanisms that shape an organism's perception of ambiguous stimuli.

Sensory filters, neural noise, iterative sampling, attention, and integration of multiple stimulus components and modalities, and their interactions with state-dependent effects, collectively modify perceived stimulus ambiguity.

Decisions made by predators (foraging) and prey (defense and escape) provide fertile ground to integrate recent advancements on the neural mechanism underlying decision-making.

Placing these advances in an ecological context reveals that modifiers of stimulus ambiguity, both internal and external to an organism, interact dynamically to affect decision-making and can potentially alter ecological and evolutionary processes.

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**Box 1. Signal Detection Theory Overview**

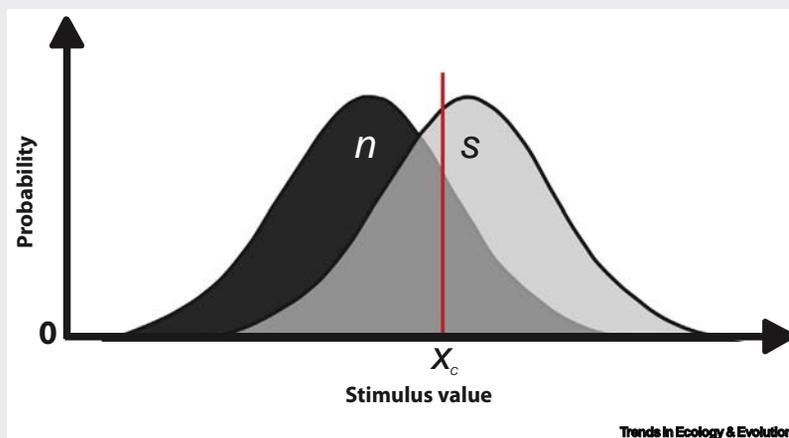
Signal detection theory (SDT) provides a framework for understanding decision-making that separately accounts for stimulus ambiguity and an organism's threshold for response. It can be applied to empirical and theoretical assessments of detection and discrimination [22]. A simple, common application of SDT is to model the detection of a signal against background noise. Consider that two stimuli in the environment, background noise and a signal, vary from each other only in a single sensory dimension. Here we assume that due to a host of factors, such as the physical properties of the sound producers and environment, the intensity of the background noise ( $n$ ) at a given moment is a probability density function (PDF) along a continuous range ( $x$ ) (Figure 1). This PDF is inherently quantifiable in terms of variance and distribution type (e.g., Gaussian). The signal ( $s$ ) has a unique PDF that overlaps with  $n$  (Figure 1).

Assuming both PDFs are normally distributed and of equal variance, the difference between the means of each PDF, divided by their standard deviation, can be used as an index of the signal's detectability ( $d'$ ) [23]:

$$d' = \frac{\mu_s - \mu_n}{\sigma} \quad [1]$$

Greater separation between the PDFs results in greater detectability. Detectability is thus the antithesis of 'ambiguity.' For PDFs with normal distributions but unequal variances, or those with different distribution types, detectability can be expressed with modified mathematical formulas ( $d'_e$  or  $D$ ) [23].

Detectability ultimately interacts with the decision criterion, another critical feature of SDT, which is a response threshold of some value ( $X_c$ ) within the stimulus dimension's boundaries (Figure 1). Here, values  $>X_c$  generate a response in the receiver as if  $s$  occurred, while values  $<X_c$  do not elicit a response. The relationship between the PDFs of the stimulus and the decision criterion generate four possible outcomes of the decision process. Responding to values  $>X_c$  given that  $s$  actually occurred is considered a 'hit', whereas responding to the same values given  $n$  is considered a 'false alarm.' By contrast, not responding to values  $<X_c$  given that  $s$  occurred is a 'miss', while not responding to the same values given  $n$  is a 'correct rejection.' Since each outcome is associated with a payoff (positive or negative), the position of the decision criterion along the stimulus dimension determines the receiver's cost-benefit tradeoff.



**Figure 1. Probability Density Functions (PDFs) of Overlapping Noise ( $n$ ) and Signal ( $s$ ) Along a Stimulus Dimension.** Here, both PDFs are normally distributed with equal variance. The decision criterion is symbolized by the vertical line at  $X_c$ . The organism responds to all values greater than  $X_c$  and does not respond to values less than  $X_c$ .

the importance of cognition in predator-prey interactions, we put forth an integrative framework for investigating how stimulus ambiguity affects ecological and evolutionary processes.

**Internal Modifiers of Stimulus Ambiguity**

When an external stimulus reaches a receiver, it is encoded and modified by internal processes beginning with transduction at the sensory system's periphery to downstream central processing, such as the formation of short- and long-term memory (Figure 1, Key Figure). Neural coding of a stimulus is, in part, a product of the variability inherent in cognitive processes and can therefore be expressed as a **probability density function (PDF)**. The overall effect of internal modifiers of an organism's perception of a stimulus is often referred to as

**Glossary**

**Active sensing:** the process by which an organism dynamically modifies its behavior or sensory system to reduce stimulus ambiguity.

**Attention:** the allocation of cognitive resources to a subset of potential cognitive processes.

**Batesian mimicry:** form of mimicry in which profitable organisms produce a stimulus or stimuli with characteristics that predators have difficulty discriminating from unprofitable model organisms.

**Bayesian updating:** the process by which a prior probability estimate is updated by a likelihood distribution to form a posterior probability distribution.

**Cognition:** processes involved in information use by organisms, including transduction, processing, and storing of such information.

**Decision:** one of two or more possible behavioral or physiological responses to stimuli, in the form of action or inaction, following stimulus transduction. Can be made with or without conscious intent and in the short-term or long-term.

**Detection:** a process in which an organism responds to a stimulus of interest embedded in background noise.

**Discrimination:** a process in which an organism differentially responds to each of two stimuli of interest.

**Multidimensional integration:** the neural integration of multiple stimuli dimensions that can alter an organism's perception of stimulus ambiguity.

**Neural noise:** differential neural responses to a given stimulus due to variation in the starting state of neural circuitry, stochastic synaptic release mechanisms, and random processes within neurons and neural networks.

**Probability density function (PDF):** the distribution for a given stimulus that specifies how probable each value is across a stimulus dimension.

**Sampling:** the process by which an organism processes stimuli transduced over a given time interval, either independently or by integrating the encoded information with previous samples.

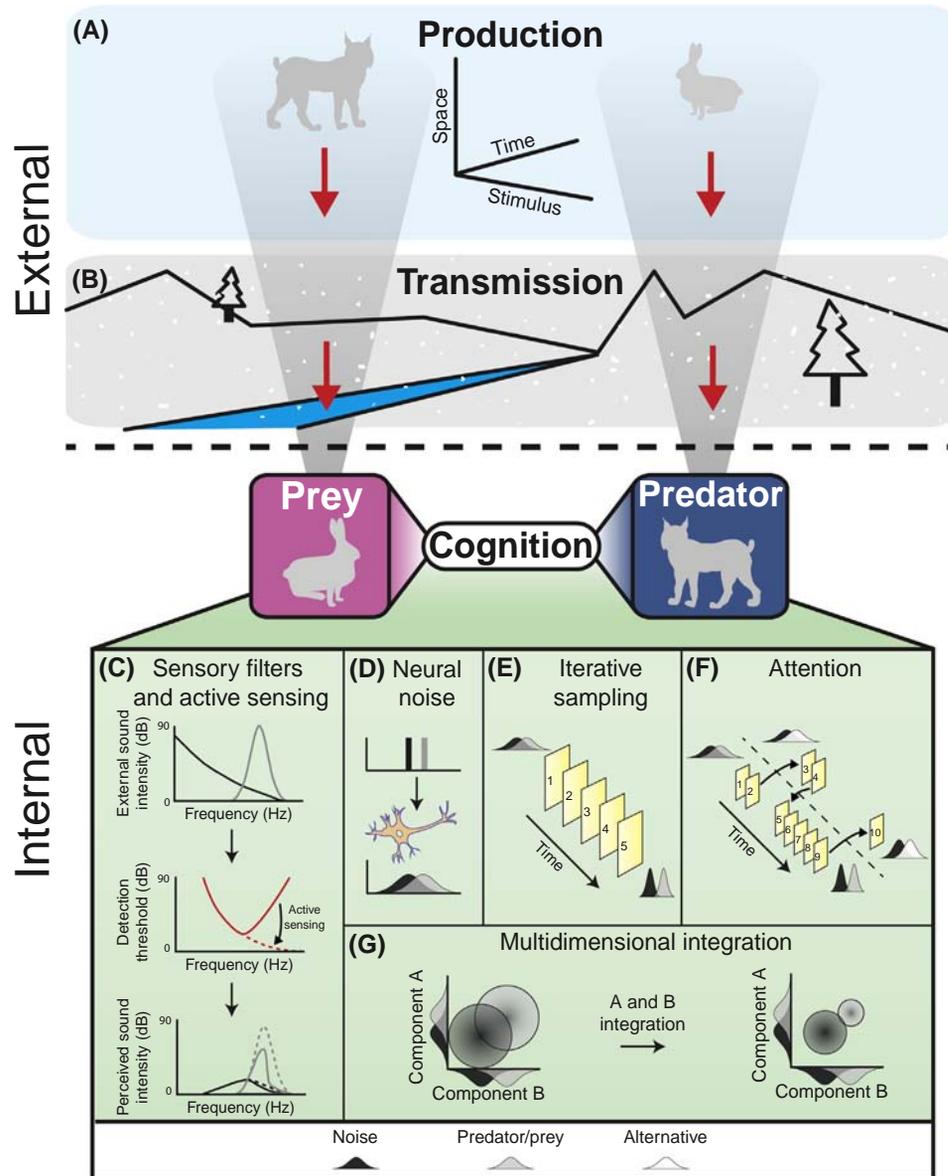
**Sensory filters:** mechanisms involved in initial processing of external stimuli as it is transduced to the nervous system, resulting in nonlinear encoding of the properties of the stimuli.

Key Figure

Factors That Affect Perceived Stimulus Ambiguity

**Signal detection theory (SDT):** a theory of receiver performance that distinguishes between the detectability of stimuli and the receiver's decision criterion.

**Stimulus ambiguity:** reduced detection and/or discrimination ability that results from stimuli with high degree of perceived similarity due to overlapping physical properties and/or internal representations.



Trends in Ecology & Evolution

**Figure 1.** Both external and internal processes shape the perceived stimulus ambiguity from which prey and predators base decisions. Red arrows indicate the progression of stimulus ambiguity from production to transmission and finally cognition. (A) Variation in the spatiotemporal distributions and stimulus characteristics at the point of production is subsequently modified by (B) an ever-changing, heterogeneous sensory environment. (C) At reception, stimuli are further modified by sensory filters, which in turn can be affected by active sensing that alters the overlap between a stimulus of interest and background noise. In a hypothetical scenario, the top graph depicts two sounds just prior to transduction that have distinct but overlapping power spectra (i.e., intensity per frequency; background noise, black line; predator/prey stimulus, grey line).

(Figure legend continued at the bottom of the next page.)

'perceptual error' [17,24–26] or 'noise' [27]. Here, we refer to 'perceived ambiguity' as the overlap in PDFs of stimuli after they are neurally encoded and shaped by internal modifiers, such as those described later. Using a signal detection framework, we discuss effects of internal modifiers of stimulus ambiguity on decision-making for predators and prey.

### Sensory Filters

Transducers and peripheral afferent neurons act as initial filters that encode a subset of the external stimuli, thus setting the stage for an organism's biased perception of the world (i.e., its 'umwelt' [28] or 'perceptual space' [29]). That is, upon reception, organisms are restricted to only a portion of the potentially available sensory properties of external stimuli (Figure 1C). Signal detection models, however, rarely incorporate such limits to stimulus parameters [26]. An insightful exception in predator–prey interactions is an evolutionary mimicry model developed to examine imperfect **Batesian mimicry** [26]. In this model, truncating traditional Gaussian PDFs to reflect natural limits of prey phenotypes (e.g., there is no phenotype 'blackier than black' in the visual domain) altered the stability of prey phenotypic variation and degree of model–mimic resemblance. An intuitive extension of this prediction is that a predator's **sensory filters**, which inherently limit the perception of natural phenotypic variation, may also have significant ecological and evolutionary consequences. Considering the variation in perceptual spaces within and between individuals and among species [30], the ecology and evolution of predator–prey dynamics are likely highly sensitive to variation in sensory filters. In support of this hypothesis is recent work that suggests predator–prey communities can be structured by sensory-based niche partitioning [31–35].

An organism's sensory filters can also play a dynamic role in the ambiguity it perceives. In visually-guided prey, for instance, the degree of visual acuity and depth perception can be greatly impacted by the orientation of the prey's eyes relative to an approaching predator [36]. State-dependent factors traditionally known to modulate behavioral responses also dynamically alter sensory filters: temperature affects auditory tuning in tree crickets (*Oecanthus nigricornis*) [37], hormones enhance temporal encoding of acoustic frequencies in the plainfin midshipman (*Porichthys notatus*) [38], and diet and immune response alter retinal carotenoid levels associated with spectral sensitivity in house finches (*Carpodacus mexicanus*) [39,40]. Active movement can also affect perceived ambiguity of auditory stimuli in humans and other animals via inhibition from motor pathways [41]. If, and to what extent movement affects the stimulus ambiguity perceived by immobile versus fleeing prey and ambush versus mobile predators are exciting questions for cognitive ecologists to pursue. Collectively, these state-dependent effects demonstrate that predator and prey perception is subject to sensory filter plasticity. It is therefore prudent to explore how predictions of signal detection models might change when the distributions of PDFs reflect ecologically relevant plasticity in a predator or prey's sensory filters.

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The properties of the receiver's transduction mechanism and peripheral afferent neurons filter which characteristics of the stimuli will be encoded (unbroken red line in middle graph). Through active sensing, the organism increases its sensitivity to higher frequencies (broken red line in middle graph). The encoded properties of each stimulus are then shown in the bottom graph (unbroken lines, no active sensing; broken lines, active sensing). Once stimuli are transduced, (D) neural noise continues to shape the degree of variation. Both (E) iterative sampling and (F) the allocation of attention are processes that update prior representations of perceived stimulus ambiguity. The yellow, numbered rectangles represent samples over time. The arrows crossing the broken line represent shifts in attention between two stimuli of interest. (G) Higher-level processing of multidimensional stimulus components also shapes the perceived ambiguity. Here, the perceived ambiguity of the multidimensional noise (darker circle) and predator/prey stimulus (lighter circle) is reduced via multidimensional integration. While most of the cognitive processes depicted here show the reduction of ambiguity, these processes may also lead to increased ambiguity.

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Reexamining assumptions of PDF distributions may be especially important for modeling predator–prey dynamics, given that organisms often employ mechanisms to actively shape their sensory filters in ways that reduce stimulus ambiguity. **Active sensing**, which we define here as the process in which an organism dynamically modifies its behavior or sensory system to reduce stimulus ambiguity, is well known across diverse taxonomic groups (vertebrates [42–46] and insects [37,47–49]). In the context of predator and prey interactions, investigations have largely focused on more overt forms of active sensing, in which organisms use self-generated energy to probe the environment (*sensu* [43]). For instance, there is a wealth of studies on the highly refined active sensing of echolocating bats and dolphins and electrolocating fish [45,50,51]. Yet, work has also been devoted to other sensory modalities in which predators and prey use active sensing. Insects and terrestrial and marine mammals, for example, exhibit a diversity of active touch mechanisms to detect both prey and predators [52]. Regarding vision, peregrine falcons (*Falco peregrinus*) overcome constraints imposed by their visual system by following flight trajectories during attacks that allow them to maintain high resolution of their prey [53].

Such behavioral modifications that decrease stimulus ambiguity are also widespread in prey. For instance, antipredator vigilance, in which prey alter their posture and orientation, is one strategy prey employ to enhance predator detection. Foraging–vigilance tradeoffs are commonly parameterized in optimal foraging models, including those integrated with SDT [20,54]. Careful consideration, however, should be given to how an organism’s unique sensory system, foraging strategies, and vigilance behaviors interact to affect how the perceived stimulus ambiguity changes over time. Returning to visually-oriented vertebrate prey, the cell density profiles and visual fields of eyes are highly variable across taxa and can thus have a substantial impact on how a predator stimulus is perceived during bouts of foraging versus vigilance [36]. Signal detection models that address this variation will likely be useful in understanding how sensory system properties affect optimal foraging predictions.

Cross-context sensory tradeoffs likely commonly affect perceived ambiguity. Prey also balance predator detection with communication in a variety of contexts, potentially imposing sensory constraints that influence perceived ambiguity. For instance, active sensing for mating purposes (e.g., [37,46]) may indirectly modulate an organism’s sensory filters in a way that affects the perceived ambiguity of predatory stimuli. While research on such cross-contexts effects is limited, indirect sensory modulation may be particularly important to include in evolutionary models, given the intense selective pressure that can be imposed by eavesdropping enemies [55].

### Neural Noise

Internal stimulus ambiguity is in part attributed to **neural noise** (Figure 1D), which is generally assumed to be the sole modifier of PDFs in predator–prey signal detection models (e.g., [21]). Neural noise is known to affect the perception of stimulus ambiguity in humans [56]. Across taxa, neural noise occurring in visual systems is thought to limit detectability and discriminability thresholds [57,58]. While such limits potentially play a major role in predator detection and antipredator strategies, such as mimicry, the relative impact of neural noise on perceived stimulus ambiguity in predator–prey interactions, compared with other internal modifiers of ambiguity, remains unclear. The effects are likely nuanced across contexts and neural architectures, given that neural noise is produced and processed in complex ways. Potentially strong modifiers of variation in neural noise include highly modular state-dependent factors, such as **attention** and motivation [59]. In considering large networks of neurons dispersed through the brain, several studies reveal that

contribution from sensory stimuli and motor outputs characteristic of natural behaviors results in lower neural noise than previously expected [60–62]. Furthermore, the assumption that neural noise introduces error does not hold in all cases. Indeed, neural noise can also function to enhance detectability. ‘Stochastic resonance’ of electrical and chemical signaling at the neural level, for instance, can be beneficial by boosting a weak signal above a detection threshold [63]. Additionally, the central nervous system can reduce noise via neural averaging and integration with prior information [63]. Weakly electric fish, for instance, appear to use both stochastic resonance and neural averaging to improve coding of electrosensory information [64]. Averaging across redundant sensory stimuli has been invoked in sensory ecology as a mechanism receivers use to reduce the ambiguity between a stimulus and background noise [65]. Determining the effects of neural noise on perception remains a frontier in neuroscience [66]. Future work that assesses the magnitude of neural noise’s effect on perceived stimulus ambiguity will be particularly valuable when developing signal detection models.

### Iterative Sampling

Predator–prey signal detection models that incorporate internal variability occasionally model internal modifiers of perceived ambiguity that act alongside neural noise (e.g., [17,67]). Iterative stimulus **sampling** and its paralleled reduction in perceived ambiguity is one such modifier. Iterative sampling can shape ambiguity across time scales – from within interactions to over the life of an individual. Aerial hawking bats, for instance, rapidly increase their cry rate as they approach their prey, which provides more information of their moving target’s position in space [68]. A need for reducing ambiguity similarly affects the time spent visually assessing individual flowers for cryptic predators by bumblebees (*Bombus terrestris dalmatinus*), which vary the time they devote to sampling depending on perceived predation risk [69]. From short interactions to across an individual’s life, discriminability can also improve in response to postdecision payoffs (i.e., learning) via plasticity of higher level and peripheral processing [70]; for example, the honeybee’s antennal lobe, a chemosensory processing hub analogous to the human olfactory lobe, increases neural firing rates and stimulus discriminability when trained with a positive food reward [71,72]. Similar learning-induced enhancement of discriminability occurs in peripheral olfactory processing in mice [73]. While learning in predators and prey is well established [74,75], it remains unclear to what extent learning in these contexts can be attributed to shifting decision criteria, reductions in perceived ambiguity, or a combination of the two.

Signal detection models that incorporate iterative sampling assume that perceived ambiguity more accurately matches external stimulus ambiguity the more an organism samples the stimulus (Figure 1E). This assumption is supported by evidence that: (i) more sampling prior to making a decision can enhance discriminability via neural processes [76], and (ii) predators [68,77] and prey [69,78] repetitively sample stimuli. **Bayesian updating** has been useful in such contexts to model changes in a receiver’s perceived ambiguity over successive samples (Box 2). A consideration for signal detection models is that ambiguity decreases in a non-linear fashion over successive sampling (as parameterized in [17]). This nonlinearity, however, introduces a dilemma to the organism: given that sampling time is likely costly, how do diminishing improvements in the reduction of ambiguity affect how long an organism should sample?

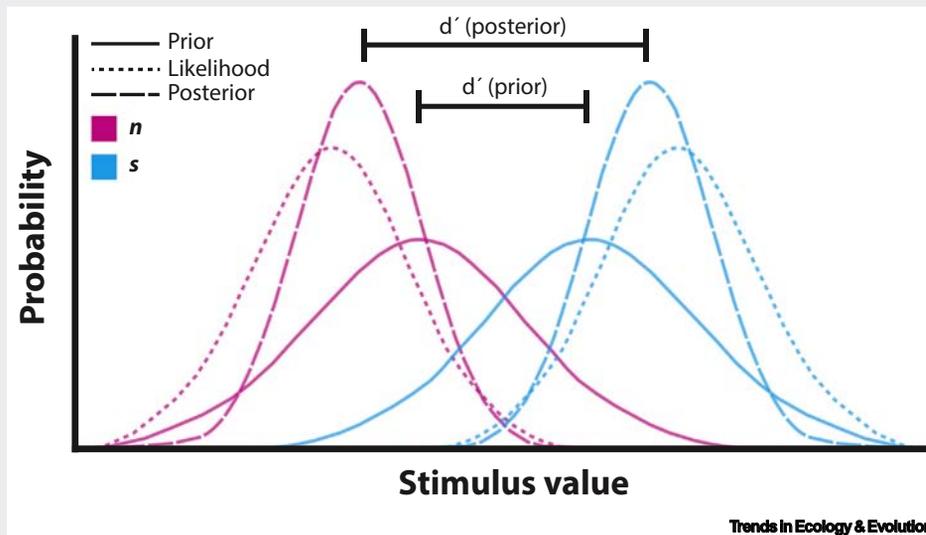
Indeed, many ecological factors, such as lost reproductive or foraging opportunities, impose speed–accuracy tradeoffs that constrain an organism’s sampling time [54,79,80]. In predator–prey contexts, integration of such speed–accuracy tradeoffs with signal detection models is uncommon. One signal detection model, however, linked stimulus ambiguity and sampling costs

## Box 2. Updating Probability Density Functions

Signal detection models that incorporate iterative sampling require that probability density functions are dynamically updated, which is a feature lacking from simple, static signal detection models. Adopting parameters from a Bayesian framework, however, offers a convenient solution (e.g., [1,23,81,82]). Predator–prey signal detection models have incorporated Bayesian updating (Figure 1) with decision-making in response to a discrete sample [3,83] and successive sampling [77], or integrated both processes in a broader framework [17,84] or model [54]. Predictions from Bayesian models of decision-making are often supported empirically [85,86], including predator–prey SDT studies (e.g., [77]). Yet, while many results agree with Bayesian models, the role of Bayesian updating as a cognitive mechanism in stimulus detection and discrimination is difficult to measure and therefore largely unsubstantiated [84]. A notable exception comes from work in human neuroscience, which has shown that humans exhibit separate neural processes for prior and likelihood estimates [87].

For many organisms, calculating the information required for Bayesian analyses may go beyond their cognitive abilities [88]. These organisms may instead use simplified ‘rules of thumb’ (*sensu* [89]) to update their perception of a variable stimulus. A model developed by Lange and Dukas [90] predicts that simplified approximations of Bayesian calculations can, in many contexts, lead to similar behavioral outcomes when compared to a model that fully incorporates Bayesian calculations. Approximations of this kind occur in many neural processes. Instead of computing variance, as required for Bayesian calculations, certain sensory neurons compute moving averages of sensory parameters over time [91].

A traditional approach to model accumulated evidence is with a variant of signal detection models known as sequential sampling models: specifically, a random walk process when modeling discrete samples or a drift diffusion model for continuous sampling [92,93]. Sequential sampling models can be especially advantageous in that they account for the impact of noise on both the speed and accuracy of decisions [93,94]. Other neural processes are best supported by a model in which sampling results in a steady rate of increase in the log likelihood of a given stimulus [81]. However, signal detection models can also be extended to accommodate iterative sampling [1,23,95]. Understanding the specific neural mechanisms driving receiver processing, while ambitious, can provide valuable information to tailor decision-making models.



**Figure 1. The Process of Bayesian Updating.** Under a Bayesian framework, the cognitive processes that follow reception of ambiguous stimuli – represented here as background noise,  $n$  (magenta) and signal,  $s$  (cyan) – generate ‘likelihoods’ of variability. Organisms are assumed to have expectations of variability prior to receiving the stimuli, the distributions of which are modeled as ‘prior probabilities.’ The integration of prior probabilities with the likelihood functions then results in the receiver’s perceived ‘posterior probabilities’ of variability. In this example, the integration of prior and likelihood probabilities results in posterior probabilities with greater  $d'$  (discriminability) values than the prior probabilities. Thus, the organism’s perceived ambiguity has been reduced via Bayesian updating. A decision criterion is assumed to be associated with the posterior probabilities.

associated with iterative sampling of prey to reveal that a predator’s decision to reject or accept a mimic depends on the degree of perceived ambiguity and density of alternative prey [17]. While densities of focal and alternative prey have long been recognized as highly influential

factors driving predator foraging decisions [96], explicit consideration of a predator's cognitive ecology has received less attention and could benefit from modeling that provides a quantitative framework. Modeling speed–accuracy tradeoffs in the mammalian brain, which is thought to have evolved distinct short- and long-term stimulus processing centers, is an example of how such approaches can lead to cognitively-framed, testable predictions concerning decision-making [54].

### Attention

Animal cognition is limited by the amount of sensory information that can be processed at a given time [97]. Such attentional constraints may come with a fitness cost. Salmon (*Salmo salar*), for example, are more likely to make prey discrimination errors in the presence of a predator [98]. Similarly, blue jays (*Cyanocitta cristata*) are less likely to detect objects in their periphery, such as potential predators, when presented with a more difficult foraging task [99]. Blue jays also detect prey at higher rates when searching for a single cryptic prey type than when searching for multiple types of cryptic prey [100]. These behavioral responses, combined with theoretical predictions based on neurophysiological studies [13], suggest that the tradeoff of attending to one stimulus of interest over another is an additional factor that shapes perceived ambiguity.

Yet, within this tradeoff, selective attention can dynamically improve a receiver's discrimination performance by increasing neural response and selectivity [101–104]. As with bats that rapidly increase their sampling rate [68] and peregrine falcons that optimize their flight path to maintain high resolution of their prey [53], selective attention is another way organisms can increase their effort per-unit-time to more quickly reduce perceived ambiguity [105]. In a visual discrimination task, humans reduced perceived ambiguity when attention was focused on one component of a complex signal, versus when attention was divided among all components [106]. Mechanistically, as attention shifted to single components, neural activity increased for the visual cortex region responsible for processing that component [106]. This neural response supports the notion that sensitivity to complex stimuli is constrained by neural processing limitations but can be modulated by attending to specific signal components at a given time. Selective attention may then be particularly important to model for organisms that must make decisions in response to multiple stimuli of interest, as occurs when evaluating complex warning signals of defended prey [107] or navigating simultaneous risks of predation and parasitism [108].

Attentional constraints have not been incorporated into most predator–prey signal detection models. An exception [17], however, proposes that ‘attentional allocation’ can impact an organism's uncertainty when dealing with simultaneous discrimination tasks, such as discriminating a mimic from model while also scanning for predators. Specifically, this study suggests that attentional allocation reduces the perceived ambiguity of the attended stimulus's PDF. To provide ecological context, they present a hypothetical scenario where a predator faces task one of discriminating between a model and mimic while simultaneously facing task two of detecting alternative, cryptic prey. One prediction is that attention should in general be biased towards the task with the greatest perceived ambiguity. However, if the perceived ambiguity within task one is sufficiently high and alternative prey is of great enough abundance, predators will shift to foraging on alternative prey. That is, allocating attention to task one is not worth the cost of wasted sampling time. Such a substantial cost to the predator is predicted to protect imperfect mimics from attack. While imperfect mimicry is widespread in nature and several hypotheses have been proposed to explain this phenomenon [109], to our knowledge the attentional allocation hypothesis has not been directly tested. Further empirical examination of this hypothesis is needed, as attention likely plays a critical role in the ecology and evolution of predator–prey relationships.

### Multidimensional Integration

Predator–prey studies that incorporate SDT almost exclusively model two stimuli (one stimulus of interest and noise) with overlapping physical properties that are distributed across a single sensory dimension. However, prey can use multiple senses to detect predators [110,111] and frequently emit complex and multimodal signals to ward off predators [107]. Multidimensional signals – that is, signals comprised of multiple components and/or sensory modalities – can interact to affect how a receiver responds to a signal [112,113]. For instance, bees (*Bombus impatiens*) integrate visual and olfactory stimuli to reduce perceived ambiguity of rewarding versus nonrewarding flowers [114]. Conveniently, SDT can accommodate multiple dimensions (see [115–117] for detailed descriptions of multidimensional signal detection models). Predator–prey signal detection studies rarely incorporate **multidimensional integration** despite empirical evidence that suggests multimodal warnings from prey can in some cases improve a predator's ability to discriminate amongst prey [118]. In an exception, discrimination of Batesian mimics from models using either one or two stimulus dimensions was investigated under a signal detection framework using humans as predators of digital prey [119]. Humans generally weighed one signal dimension more than the other, indicating that their decision criteria deviated from the optimal thresholds predicted from the multidimensional model. It was unclear however, how perceived ambiguity was affected by multidimensional stimuli. Future multidimensional signal detection models that account for perceived ambiguity will be critical to understand how discriminability interacts with weightings among multiple sensory dimensions.

### External Modifiers of Stimulus Ambiguity

Prior to an organism's reception of a stimulus, the combined effects of variation in stimulus production and fluctuating transmission properties generate external stimulus ambiguity (Figure 1A,B). Studies of predator–prey interactions investigating stimulus ambiguity have focused on questions concerning variation that is external to the receiver's perceptual space, referred to as 'true' or 'real-world' variation [17]. Most of these studies address variation resulting from differences in stimulus production among individuals, such as models and mimics that collectively exhibit phenotypes with overlapping PDFs (e.g., [26]). Variation in stimulus production within individuals (phenotypic plasticity), to our knowledge, has not been incorporated in predator–prey signal detection models despite being a widespread strategy across organisms [120]. While plasticity in a receiver's decision criterion has been modeled [121], it remains to be seen how incorporating predator or prey stimulus (i.e., phenotype) plasticity (and the corresponding changes in a receiver's perceived ambiguity) might affect predictions across predator–prey signal detection models. Using a SDT framework in this context may be especially informative given that predator-induced plasticity in prey phenotypes can have direct effects on prey population stability and indirect effects on community structure and dynamics [122].

In addition to variation in stimulus production among individuals, many signal detection predator–prey models make predictions concerning how spatiotemporal fluctuations in the abundances of stimuli interact with stimulus ambiguity to affect predator–prey interactions (Figure 1A). Signal detection models of predators that discriminate among prey predict that the relative abundance and/or density of nutritionally superior and inferior prey [123,124], aposematic and cryptic prey [24,77,125–127], unprofitable models and their mimics [3,17,26,126,128–133], and even alternative prey [17,25], interact with stimulus ambiguity to shape foraging decisions. In general, the combination of stimulus ambiguity and spatiotemporal fluctuations is predicted to result in the receiver shifting its decision criterion. Spatiotemporal fluctuations, however, are in certain cases predicted to directly impact stimulus ambiguity via interactions with heterogeneous environments, which can lead to cascading ecological and evolutionary effects. For instance, pollinators that must avoid ambush predators positioned on flowers may be exposed to dynamic variation in

predator conspicuousness due to naturally occurring shifts in frequencies of predators on concealing versus revealing backgrounds. In this scenario, integrating SDT with game theory generates a model that predicts that predator spatiotemporal distributions interact with the ability of pollinators/prey to discriminate predators against background floral colors [24]. Such fluctuations of predators in time and space in turn affect the evolution of floral colors, highlighting potential cascading effects at the community level. The consequences of variation in spatiotemporal dynamics on stimulus ambiguity and the countering strategies predicted for both predators and prey deserve further attention.

Furthermore, incorporating spatiotemporal fluctuations in transmission will likely result in significant changes to the predictions of predator–prey signal detection models. Once a stimulus is generated, it propagates through the environment and is subjected to biotic and abiotic factors that modify its physical properties (Figure 1B; [134]). As proposed by the sensory drive hypothesis [65], spatiotemporal heterogeneity in the sensory environment dynamically influences ambiguity, ‘driving’ the evolution of sensory systems and the stimuli to which they are tuned. Consideration of the environment in which stimuli are transmitted seems essential given the evidence supporting habitat-mediated signal modification as a strong selective factor acting on sensory systems and signal properties, particularly in organisms living in aquatic habitats and reliant on visual communication [135–137]. Yet, no signal detection predator–prey study explicitly accounts for the effect that transmission has on stimulus properties.

### Concluding Remarks

More than ever, ecologists and evolutionary biologists are now primed to integrate their research with advances in neuroscience (Box 3). Ongoing examinations of animal cognition are revealing in great detail how an animal’s perception of stimulus ambiguity is shaped by dynamic, interactive processes, such as attentional allocation, sampling effort, and state-dependent effects. Neuroscientists, in turn, are poised to benefit from the functional and evolutionary implications of these mechanisms when observed under natural conditions [138]. At all levels of analysis, predator–prey systems offer excellent natural laboratories to probe how organisms make decisions in response to ambiguous stimuli. Predation imposes intense selective pressure on prey defenses

#### Box 3. New Ventures in Cognitive Ecology: Linking Contemporary Neuroscience with Sensory Ecology, Behavior, and Evolution

Research in cognitive ecology is entering an exciting time in which neuroscientists are using sophisticated tools to examine decision-making of freely behaving organisms in great detail. Optogenetics, a technique which uses light-triggered opsin genes to rapidly target the activation and inactivation of specific cellular processes, has been used in mice to determine the neural computations underlying detection and discrimination [139] and stimulus salience in response to threats [140]. In the relatively simple neural circuit of *Caenorhabditis elegans*, researchers have also begun to unravel how multisensory integration and active sensing interact with differing levels of hunger in balancing foraging opportunities with risk of death [141]. Regarding neural noise, results from studies that capitalized on a suite of advanced techniques to obtain large-scale neural recordings in freely behaving animals recently challenged current understanding of noise in the nervous system [60–62]. These examples collectively illustrate how modern approaches are broadening our understanding of the neural building blocks of decision-making. Moreover, they highlight the nuances inherent in the processing of stimulus ambiguity, which are found across taxa and complexities of neural architectures.

A caveat to the study of model organisms is that, while practical in neuroscience experiments, they provide limited inference to many questions concerning natural ecological and evolutionary processes. Even so, neuroethologists can capitalize on the growing interest in model organisms’ natural histories (e.g., [142–144]) to test ecologically meaningful hypotheses relating to the mechanistic underpinnings of decision-making. Determining how model systems then relate to the diversity of neural architectures and natural histories among taxa, while a first step, will offer insights into how organisms, in general, respond to stimulus ambiguity. As genomic and neurophysiological tools become more accessible for use in nonmodel systems, particularly with regard to measuring neuronal activities in freely behaving animals, the field of cognitive ecology is poised to make tremendous strides in how organisms make decisions in times of uncertainty.

### Outstanding Questions

As we have discussed, external and internal modifiers shape stimulus ambiguity. How does the relative influence of each modifier on perceived ambiguity (i.e., its effect size) vary across taxa (e.g., phylogenetic inertia), habitats (e.g., marine and terrestrial), sensory environments (e.g., diurnal and nocturnal), life history strategies, etc.?

How do adaptations to reduce stimulus ambiguity in nonforaging contexts impose constraints on perceived ambiguity in predator–prey interactions?

How do changes in stimulus ambiguity interact with selection on the decision criterion in real time? Is there error in the placement of a decision criterion when stimulus ambiguity is modified dynamically over the course of an interaction?

How do the cognitive strategies outlined here relate to decision-making mechanisms used by non-animal organisms? Can these mechanisms be expanded to understand, for instance, antiherbivore defense in plants [83]? And ultimately, can SDT provide a framework to understand decision-making across kingdoms?

Given that humans have driven rapid and widespread changes to the sensory environment (e.g., increased sound and light levels), to what extent do these evolutionarily novel forms of sensory pollution alter external and internal stimulus variation, thereby affecting decision-making?

and sensory systems, which has led to an incredible diversity of antipredator defenses and corresponding predatory behavioral and sensory adaptations [75].

The mechanisms driving predator and prey decisions are complex [145]. When modeling or empirically testing hypotheses concerning these decisions, assumptions of how organisms perceive stimuli produced by predators or prey – within encounters and across lifetimes, within populations and across species – must be carefully considered with respect to the organism's biology, ecology, and evolution. Few predator–prey signal detection models incorporate both internal and external modifiers of ambiguity (for exceptions, see [17,24,26]), which is perhaps unsurprising given the field's emphasis on external modifiers of ambiguity. We propose that robust examinations of decision-making by predators and prey are those that link predictions generated by cognitively-framed models with experimental studies that expose organisms to ecologically-relevant modifiers of external ambiguity. Overall, investigations that take a holistic approach to the study of decision-making in predator–prey interactions, integrating the cognitive underpinnings of predator and prey decisions with ecological and evolutionary processes, promise to advance our understanding of predator–prey dynamics and decision-making as a whole (see Outstanding Questions).

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