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Visual Decision-Making in an Uncertain and Dynamic World

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Abstract

The right decision today may be the wrong decision tomorrow. We live in a world in which expectations, contingencies, and goals continually evolve and change. Thus, decisions do not occur in isolation but rather are tightly embedded in these streams of temporal dependencies. Accordingly, even relatively straightforward visual decisions must take into account not just the immediate sensory input but also past experiences and future goals and expectations. Here, we evaluate recent progress in understanding how the brain implements these dependencies. We show that visual decision-making relies on mechanisms of evidence accumulation and commitment that have been studied extensively under relatively static, isolated conditions but in general can operate much more flexibly. A deeper understanding of these mechanisms will require identifying the principles that govern this flexibility, which must operate across different timescales to produce effective decisions in uncertain and dynamic environments.



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INTRODUCTION

A visual decision is a deliberative process that converts retinal activation patterns into a commitment to a categorical proposition about the presence, location, or identity of the source(s) of those patterns. Individual decisions have been studied extensively and use processes that are analogous to a judge or jury that must take time to weigh evidence for alternative interpretations, consider the consequences, and render a verdict (Gold & Shadlen 2007). However, decisions do not occur in isolation. In the judicial system, judges and jury members often have predispositions that can substantially influence their judgments. News of external events might arrive mid-trial even to a sequestered jury, causing a mistrial. Evidence and potential consequences are interpreted in the context of current laws and standards, which themselves are typically built on precedent established by previous decisions. Our goal is to evaluate and synthesize findings that bear on how these kinds of time-dependent factors affect visual decisions.

Immediate sensory evidence is not the sole source of relevant information for visual decisions because the world is both uncertain and dynamic. Visual uncertainty can come from many sources. For example, identifying a particular visual object (say, the face of a friend in a crowd) can be difficult when the relevant features are partially occluded (someone just walked in front), ambiguous (everyone is wearing the same kind of sunglasses), or unclear (it is a foggy day). These features must then be processed by noisy neurons in the brain, providing additional uncertainty that can vary with attention (that phone call is distracting), processing time (hurry up!), and other factors. Moreover, both the external and internal sources of uncertainty, along with the visual world itself, can change at any moment. Accordingly, visual decisions represent a form of inference, essentially a best guess of what the correct decision ought to be, given the currently available, uncertain evidence (Helmholtz 1924). This kind of guesswork is naturally sensitive to predispositions, new evidence, context, and other factors that, if interpreted correctly, can be used to reduce uncertainty at the time of the decision and help to ensure the best possible outcome.

A powerful framework for understanding decision-making in uncertain and dynamic environments is Bayesian decision theory (BDT). BDT provides a minimal yet complete and general description of the entire decision process. This description includes the available visual evidence, the inference process that combines the evidence with prior knowledge, and finally the commitment to a decision that provides the most favorable expected outcome according to some reward structure. A particularly compelling feature of BDT is that it establishes a normative role for factors other than the immediate sensory evidence in making decisions. Thus, for example, prior knowledge is not simply a nuisance or a source of bias or inefficiency but rather an inherent component of the decision-making process that helps to maximize the probability of making the correct decision. There is extensive evidence, primarily from quantitative studies of perception-driven behavior (visual psychophysics), that visual decision-making is often very well described by BDT (Knill & Richards 1996). Consequently, in this review, we consider BDT as a useful starting point: a quantitative benchmark describing how different sources of information should, and in many cases do, affect visual decisions.

However, a weakness of BDT, in its most general form, is that it provides little guidance for how the underlying processes, including the use of prior knowledge, are implemented in the brain. We therefore begin by describing several computational frameworks for understanding visual decision-making at a more mechanistic level. These frameworks have been particularly useful in bridging the divide between the probabilistic language of BDT and specific computational mechanisms that can be used to implement, or approximate, it in the brain. Our overall theme, which we then use to organize subsequent sections, is that these computations are best understood when considering a particular decision process as it is embedded in time. What historical factors are relevant to how the visual input is represented and interpreted? How do these representation

and interpretation processes unfold in time? How does the outcome of this decision affect future decisions? Answering these questions requires understanding visual decisions not as independent, static computations but rather as dynamic processes that depend on past and present information to help make effective judgments about current and future sensory input.

COMPUTATIONAL FRAMEWORKS

Signal detection theory (SDT) has profoundly affected how psychophysical measurements are interpreted by formalizing the distinction between the sensory evidence and the decision rule (Green & Swets 1966, Macmillan & Creelman 2004). In this formulation, the aggregated sensory evidence, also referred to as the decision variable, is described in terms of the combination of signal and noise that comprises the internal, graded representation of the relevant sensory stimulus. In contrast, the rule determines how the graded representation of evidence is converted into a categorical judgment. In its most basic, and prevalent, form, the evidence corresponding to each alternative (e.g., signal plus noise versus noise alone) is distributed as a random variable along a single dimension, and the rule is a criterion value placed somewhere along that dimension (**Figure 1a**). This conceptual distinction has been useful for identifying correlates of sensory evidence in the brain, independent of the decision rule (Parker & Newsome 1998).

The distinction between the decision variable and the decision rule also can begin to illustrate the importance of considering the decision process as it occurs at a particular moment in time. For example, in a simple detection task, a decision threshold that distinguishes signal plus noise from noise alone can be conservative, resulting in fewer false positives (signal reported when none is present) but also fewer hits (signal correctly reported). Alternatively, it can be more liberal, resulting in more of both. These different rules can reflect different task instructions or goals of the decision maker. They also can reflect intrinsic variability that, in some cases, can include sequential structure from one decision to the next (Maddox 2002). Thus, the probability of making a particular decision depends on the rule, which, in turn, likely depends on multiple factors that can vary over time.

The idea that time plays a role in the decision process is the key conceptual advance from SDT to sequential analysis (**Figure 1b**). It has long been recognized that even simple perceptual decisions take a measurable, and variable, amount of time for the brain to generate (Luce 1986). This time, which typically lasts tens to hundreds of milliseconds for different kinds of visual decisions, occurs in addition to the time needed to extract the sensory input and generate the motor output (Sternberg 2001). Sequential analysis accounts for this time in terms of a dynamic process that arrives at a decision only after sampling the ongoing, noisy neural representation of the sensory input. In certain popular models, such as the drift-diffusion model, this sampling process acts as a temporal integrator, accumulating noisy evidence in a manner that steadily increases the signal-to-noise ratio (SNR) of the resulting decision variable (Stone 1960, Laming 1968, Link & Heath 1975, Ratcliff & Smith 2004). This relationship between SNR and viewing time can account for the inherent trade-off between speed and accuracy that governs many visual (and other) decisions (Schouten & Bekker 1967, Wickelgren 1977).

These models have made a lasting impact on our understanding of decision-making. In a single framework, they can account for measured relationships between stimulus strength, choice accuracy, response times (average values and full distributions), and, at least under certain conditions, reported confidence in those choices (Ratcliff & Smith 2004, Voss et al. 2004, Ratcliff & McKoon 2008, Pleskac & Busemeyer 2010). Under certain assumptions, these models also relate closely to normative theory, which dovetails with the idea that evolutionary pressures have optimized the brain's ability to make decisions on the basis of noisy visual signals (Gold & Shadlen 2002, Bogacz et al. 2006, Bitzer et al. 2014). Finally, these models have also been used to identify neural

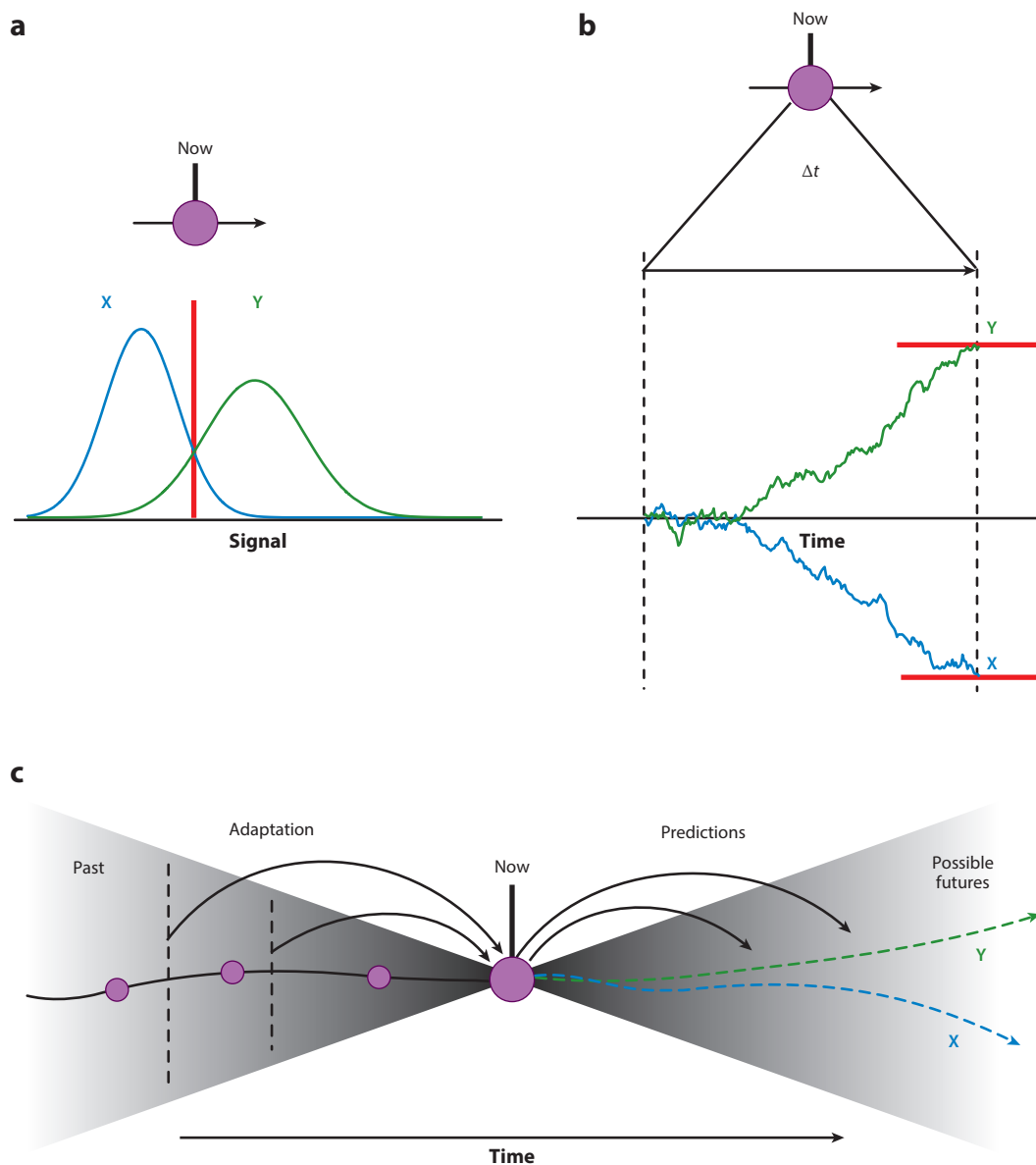


Figure 1

Temporal dependencies in decision-making. (a) Signal detection theory (SDT) represents the most parsimonious description of decision-making: a measurement that is sampled from one of two distributions representing the two alternatives X and Y is either above or below a critical value (criterion), corresponding to a decision in favor of either alternative X or Y. However, SDT treats decision-making as a point process with no explicit notion of time. (b) Sequential analysis is an extension of SDT that accounts for the fact that a decision is not an instantaneous event but occurs over a time interval Δt of deliberation and commitment. The framework does not explicitly account for dynamics beyond the decision process itself, although these dynamics are likely to determine some of the model parameters such as the bound heights. (c) Information flow for decision processes in an uncertain and dynamic world. The entire history and experience of a decision maker are collapsed and projected onto the context of the present decision (“now”). This state history is not completely random but instead is predictive of the future and thus of the current decision, although, naturally, the predictive power decreases the further back in time we go. In this review, we discuss this predictive information flow across different timescales and review our current understanding of how it affects visual decision-making.

signatures of the decision process, even as ongoing debates highlight gaps in our knowledge of how and where in the brain, down to the level of individual neurons, the key computations are implemented (Gold & Shadlen 2007, Heitz & Schall 2012, Kelly & O'Connell 2015, Latimer et al. 2015, Shadlen et al. 2016).

However, both SDT and sequential analysis-based models are typically used under a set of assumptions that seem to be of limited relevance to real-world conditions. These assumptions include fixed (often unbiased) expectations, a steady stream of noisy but statistically stable visual evidence, and a goal defined by a balance of speed and accuracy. However, expectations, evidence, and goals change constantly. These dynamics operate over multiple timescales and can have a major impact on how incoming visual information is interpreted to form a given decision. For the next several sections, we consider in detail the kinds of factors that operate over these different timescales, from long before, to during, to after a given decision, and how these factors impact the decision-making process (**Figure 1c**).

LONG BEFORE THE DECISION: STATISTICAL REGULARITIES

The future is difficult to predict. Thus, long before a decision, very little information is available that is predictive of that decision. However, the amount of predictive information is not necessarily zero, largely because of the statistical structure of visual input. The space of all possible retinal images is huge. In principle, every one of the ~ 100 million photoreceptors of the human retina could receive independent photon flux. Assuming for simplicity just two different levels of photon flux (bright/dark), this simplification still gives rise to $10^{30,000,000}$ possible retinal images (by comparison, the total number of atoms in the visible universe is approximately 10^{80}). However, the physical structure of our natural environment imposes spatiotemporal dependencies that result in retinal images that occupy only a small subspace of those that are theoretically possible (Simoncelli & Olshausen 2001). This subspace can be described by the characteristic distributions over low-level visual features. For example, the distributions of local contrast values, spatial frequency, or local orientation have been shown to be robust across many different visual environments (e.g., natural versus human-made) and settings (Ruderman 1994, Coppola et al. 1998, Mante et al. 2005). Similarly, certain structural aspects of the observer itself, such as the position of the eye relative to the environment or the optical transfer function of the eye, are static or change slowly with development and age but substantially impact the nature of visual information that enters the brain.

The efficient coding hypothesis postulates that evolutionary pressure has forced biological systems to use their necessarily limited neural resources to most efficiently represent, or encode, visual evidence by exploiting and adapting to these characteristic statistical structures of the visual environment (Attneave 1954, Barlow 1961). The goal of this encoding scheme is to obtain a best possible representation of the visual evidence given the available neural resources, which then informs potential decisions. Efficient coding implies that the sensory representation avoids redundancies and that the precision with which visual features are represented depends on their frequencies of occurrence. This idea has made several successful predictions, particularly for early visual stages of the visual pathway. For example, in nonhuman primate retina, the receptive fields of cone photoreceptors, and their specific connectivity to retinal ganglion cells, are predicted by efficient coding considerations (Doi et al. 2012). Likewise, tuning characteristics of both simple and complex cells in primary visual cortex are predicted by a coding algorithm that is optimized to most efficiently represent images of natural scenes with a limited number of neurons (Olshausen & Field 1996, Karklin & Lewicki 2009). In some cases, efficient neural codes may be optimized for specific tasks (Salinas 2006, Sims 2016). However, efficient coding is typically thought to optimize encoding according to general principles, such as maximizing the mutual information

a neural population is able to convey about the stimulus values, subject to certain overall constraints on the available sensory capacity (Laughlin 1981, Atick & Redlich 1990, Z. Wang 2016). This kind of generality can make the encoded signals more useful to a broader range of future decisions.

Although efficient coding has been successful in explaining certain neural tuning characteristics in early stages of the visual pathway, the degree to which these efficient sensory representations affect the interpretation, or decoding, of visual information to form decisions that guide behavior is less understood. Efficient coding generally implies that not all visual evidence is encoded by the visual system with the same precision, which also implies that the visual system's ability to discriminate visual information is not uniform. Back in the nineteenth century, Gustav Fechner argued that the accuracy with which sensory information is represented directly determines an observer's ability to discriminate small changes in the stimulus value (the just noticeable difference, or JND). This idea led him to formulate the famous Weber-Fechner law, which states that sensory magnitude variables are encoded in a logarithmic fashion, corresponding to a discrimination threshold that is proportional to the magnitude [Fechner 1966 (1860)]. Combined with the efficient coding hypothesis, Fechner's idea suggests a direct relationship between the psychophysical measure of discrimination threshold and the stimulus statistics. More specifically, discriminability should follow the stimulus distribution, such that discrimination threshold is lowest for stimulus values that are most frequent, and vice versa (Seung & Sompolinsky 1993, Wei & Stocker 2016b). Recent studies have confirmed this idea for certain low-level visual variables such as spatial frequency and visual orientation (Ganguli & Simoncelli 2014).

Understanding the more general impact of efficient coding on decision-making requires a deeper understanding of how efficiently encoded information is decoded to form the decision. Like encoding, decoding can be made more effective by taking into account the long-term statistics of the visual environment. In the context of optimal, probabilistic decision processes, these statistics are expected to take the form of appropriate prior beliefs. Consistent with this idea, a light-from-above prior influences the perception of shapes from shading, and a prior on visual orientation affects orientation discrimination (Adams et al. 2004, Girshick et al. 2011). Priors on low-level visual features also can affect judgments on higher-level categorization tasks, like in tasks that superimpose two gratings that can be perceived as either a coherently moving plaid stimulus or two transparent grating stimuli, depending on their speed (Hedges et al. 2011). Generally, most studies assume that prior beliefs about low-level visual features reflect the long-term statistics of those features in the visual environment (Knill & Richards 1996). However, validating this assumption is difficult, because these statistics are rarely easy to measure (Stocker & Simoncelli 2006).

Thus, long before a decision, there is little information available that is specific to that decision. Nevertheless, a decision maker can (and should) be adapted to the statistical regularities of the visual environment that are likely to remain unchanged through the decision. This adaptation, when considered in the joint context of efficient coding and BDT, leads naturally to an understanding of how statistical regularities impact both the nature of prior beliefs and the accuracy of sensory representation based on those beliefs (**Figure 2**) (Wei & Stocker 2015, 2016a). This approach also makes some surprising predictions that can account for several unresolved bias effects observed in the perception of low-level visual stimuli. Future work will be needed to fully understand the degree to which these long-term stimulus statistics influence visual decision-making by shaping both the encoding and decoding process. Because these are long-term changes, they likely will ultimately affect how neural populations are organized (e.g., wiring and tuning characteristics) instead of being reflected in changes of active signals like baseline or evoked firing rates that cannot efficiently be maintained over such long durations (Ma et al. 2006, Fiser et al. 2010).

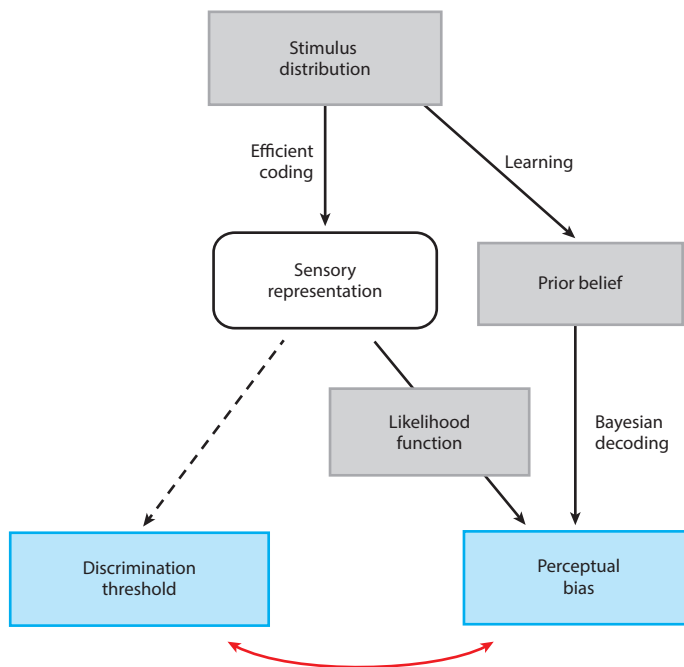


Figure 2

A Bayesian observer model based on efficient sensory representations (Wei & Stocker 2015). Statistical regularities (the stimulus distribution) constrain both the observer's prior beliefs (via learning/updating) and the accuracy of the sensory representation and thus the likelihood function (via efficient coding). That is, encoding and decoding are matched. The model makes some surprising predictions regarding the perceptual behavior characteristics of the observer, including a lawful relationship between perceptual discrimination threshold and bias. Adapted from Wei & Stocker (2016a).

NEARING THE DECISION: PERCEPTUAL LEARNING

Over shorter timescales, spanning minutes to years, a number of other learning processes can also affect a range of neural mechanisms that impact future visual decisions. Here, we focus on perceptual learning, which involves training- or exposure-induced changes in perceptual sensitivity. Early psychophysical experiments in visual perceptual learning typically focused on how explicit training resulted in improvements in sensitivity to low-level visual features such as the orientation of short line segments (Sagi 2011, Watanabe & Sasaki 2015). A commonly reported feature of these improvements was that they tended to be specific to the stimulus configuration during training, including stimulus orientation, size, and retinotopic location. Such specificity implies a relatively limited impact on future visual decisions, restricted to those decisions that repeat the exact conditions used during training.

However, recent studies have begun to identify certain conditions that can lead to more generalized learning and thus a broader impact on future decisions. For example, mere exposure to weak sensory stimuli that are below the threshold for attentional control and are appropriately timed relative to reinforcement signals can lead to task-irrelevant perceptual learning (Seitz & Watanabe 2009). Likewise, training-plus-exposure paradigms can promote generalization, even when the untrained stimulus is merely expected and not actually presented (Zhang et al. 2010). The ability to generalize perceptual learning is also at the heart of numerous studies that have shown generalized improvements on certain visual perceptual tasks following video gaming

experience, although at least some of these conclusions have been called into question (Green et al. 2010, Boot et al. 2011). Together, these results imply that some forms of visual experience can shape the mechanisms that will be used for a broad range of future decisions.

The exact nature of these experience-dependent changes in visual processing is not fully known, but numerous candidate mechanisms have been identified. These mechanisms are not necessarily mutually exclusive, may be used differentially depending on the exact task conditions, and could subserve either a stimulus-specific or more general learning process (Ahissar & Hochstein 2004, Watanabe & Sasaki 2015). One set of mechanisms likely involves changes in early visual cortex, where individual neurons represent visual information with spatial and feature specificity that can match the specificity of some forms of visual perceptual learning. Accordingly, both human functional magnetic resonance imaging (fMRI) and animal single-unit studies have found changes in stimulus-driven activity in early visual areas, including V1, V2, and V4 (Sagi 2011, Watanabe & Sasaki 2015). In some cases, these changes involve context-mediated changes in neuronal response properties that are likely driven from elsewhere in the brain (Li et al. 2004, Piëch et al. 2013). For other task conditions, perceptual learning may involve only limited or no changes in the response properties of task-relevant sensory neurons in visual cortex (Ghose et al. 2002, Law & Gold 2008).

Other studies have identified changes at later stages of processing, including at the level of weighing the outputs of the visual representation to the decision process (Doshier & Lu 1998, Petrov et al. 2005, Law & Gold 2008, Jacobs 2009, Bejjanki et al. 2011). This kind of reweighting scheme can help to calibrate a decision process to maximize accuracy, given the noisy sensory representation of the trained stimulus (Law & Gold 2009). By including input from different visual representations, reweighting schemes can also account for various forms of specificity and transfer of perceptual learning (Doshier et al. 2013). In principle, the underlying learning process can involve the same kinds of reinforcement-based mechanisms that are also used to learn other task features that are relevant to future decisions, including statistical regularities in the stimulus to establish appropriate priors, behavioral policies that maximize positive feedback, and the decision rule that governs the speed-accuracy trade-off (Sutton & Barto 1998, Simen et al. 2006). Some forms of perceptual learning might in fact be a by-product of these other processes that, for example, learn to associate a particular behavioral response with an increasingly restricted subset of the most-sensitive sensory neurons (Law & Gold 2009).

Some forms of visual perceptual learning might also involve even higher-order processes. For example, learning can transfer completely from a trained to an untrained stimulus if both stimuli represent the same task-relevant visual feature (R. Wang et al. 2016). This transfer can occur even if the two stimuli are sufficiently different that they likely are represented in different parts of the brain, such as orientation defined by luminance gratings encoded in V1 versus bilaterally symmetric dot patterns encoded in higher visual areas, or motion direction defined by luminance-modulated (first-order) versus contrast-modulated (second-order) motion stimuli. This result implies that at least some forms of visual perceptual learning can occur on the conceptual, not just stimulus-based, representation of a visual feature. Such a process might be just one facet of a more complex, hierarchical learning system in which learned concepts and statistical structures are used to guide the interpretation of subsequent visual inputs for learning and decision-making (see also **Figure 4**) (Rao & Ballard 1999, Lee & Mumford 2003, Friston 2010, Bastos et al. 2012).

JUST BEFORE THE DECISION: TOP-DOWN AND BOTTOM-UP FACTORS

When the task is known, numerous factors are often modulated just in advance of a decision that can affect its outcome. One such set of factors involves task-specific, top-down expectations

about the prior probabilities of particular alternatives under consideration (Knill & Richards 1996, Serès & Seitz 2013). Under some conditions, these effects can be modeled as a biased offset in an accumulate-to-bound model (Bogacz et al. 2006). Neural correlates of this offset have been identified in baseline neural activity in several oculomotor brain areas in monkeys performing tasks that manipulated the prior probability that a particular visual stimulus, associated with a particular saccadic response, would occur (Basso & Wurtz 1997, Dorris & Munoz 1998, Platt & Glimcher 1999, Rao et al. 2012). A similar finding has been reported using magnetoencephalography in humans performing a visual discrimination task linked to finger movements (de Lange et al. 2013). However, under these conditions, it remains unclear whether and how these neural changes can distinguish expectations about the visual decision (what do I expect to see?) versus expectations about the associated action (what do I expect to do?), which are often conflated in these task designs and in these neural representations.

Neural representations of learned or instructed prior expectations that are more closely associated with a particular stimulus or stimulus feature have been more difficult to identify. For example, in one of the visuomotor tasks that showed changes in oculomotor baseline activity of neurons in the lateral intraparietal area (LIP), there were no apparent changes in the activity of neurons in the middle temporal area (MT) of extrastriate visual cortex that encode the visual motion information used to instruct the saccadic response (Rao et al. 2012). However, imaging studies have begun to identify correlates of prior expectations, or at least inferred consequences of those expectations, in sensory cortical areas of humans performing visual tasks (Summerfield & de Lange 2014). These results, which in some cases primarily involve decrements in activity to expected stimuli, have been interpreted as support for hierarchical BDT models of perceptual inference (Rao & Ballard 1999, Lee & Mumford 2003, Friston 2010, Bastos et al. 2012). These models are based on direct interactions between top-down predictions and bottom-up stimuli at even early levels of stimulus processing, typically involving prediction errors that correspond to lower activation when expectations are met. In contrast, feed-forward decision models, like the accumulate-to-bound framework, can be implemented by integrating sensory information and expectations later, at the level of the decision variable, and typically do not involve explicit computations of prediction errors.

Reward expectation can also affect visual decisions. For example, given asymmetric rewards, subjects tend to choose the preferred alternative more often and more quickly than the other, even when both alternatives are equally probable. Like changes in prior probabilities, these effects can be modeled as a change in the starting point of accumulate-to-bound decision models (Feng et al. 2009, Rorie et al. 2010, Mulder et al. 2012). Both prior- and reward-induced effects can modulate activity in parts of a frontoparietal network that appears to play a general role in biasing choices (Boettiger et al. 2007, Basten et al. 2010, Fleming et al. 2010, Rorie et al. 2010, Scheibe et al. 2010, Summerfield & Koechlin 2010, Mulder et al. 2012, Chen et al. 2015). Other brain regions that are also likely directly involved in reward-driven choice biases include the orbitofrontal cortex and other regions that encode reward preference and basal ganglia circuits that contribute to reward-induced biases in response times on simple visually guided saccade tasks and to value-based decisions (Hikosaka 2007, Rushworth et al. 2011).

Reward expectation might not simply add biases at the level of decision variables represented downstream from the sensory representation but also affect the sensory representation itself. For example, in a recent study, monkeys were trained to discriminate the direction of rotation of a structure-from-motion cylinder, which likely depends on depth and motion signals encoded in area MT (Cicmil et al. 2015). Using symmetric but changing reward magnitudes, electrical microstimulation in MT, and analyses in an accumulate-to-bound decision framework, the results implied that both sensory and reward information were already combined in MT. These

results complement findings from imaging studies, which together imply that visual decisions may rely on neural representations of visual input that are constantly modulated by preferences and expectations (Serences & Saproo 2010, Weil et al. 2010).

Expectation-related signals can also be compared and contrasted to effects of attention. In many experiments, attention has been manipulated in the same way as prior expectations, via indications such as explicit visual cues that a particular stimulus or feature is more or less likely to appear (Posner et al. 1980). Accordingly, attentional effects that are related directly to differences in expectations have been interpreted as criterion shifts in SDT, initial offsets of the decision variable in accumulate-to-bound decision models, and the precision of prior distributions in BDT (Swets et al. 1961, Terman & Terman 1972, Dayan & Zemel 1999). In contrast, many other attention effects do not reflect differences in expectations but instead can be thought of as affecting the relevance of a visual feature to a given decision (Summerfield & de Lange 2014, Summerfield & Egnér 2016). The consequences of attending to relevant features on neural responses are highly diverse, including changes in contrast gain, response gain, synchrony, and noise correlations that can occur across many levels of visual processing and can depend on context (Carrasco 2011). In terms of decision-making, these effects govern how sensory evidence is processed and thus are reflected in changes in sensitivity in SDT, in the drift rate in accumulate-to-bound models, and in the likelihood function in BDT. However, the distinction between expectation and relevance might not be so clean in terms of their effects on visual perception, as several studies that have attempted to manipulate them separately nevertheless found mixed results, including effects of both on perceptual sensitivity (Kok et al. 2012, Wyart et al. 2012).

In the real world, these attentional effects often operate in the context of search problems, in which relevant visual information must be identified and selected from complex and dynamic scenes (Peelen & Kastner 2014). Under these conditions, bottom-up, stimulus-driven factors are also likely to interact with top-down goals and expectations. For example, the sudden appearance of surprising stimuli can draw attention toward or away from other visual features that are relevant to the decision (Carrasco 2011, Peelen & Kastner 2014, Horstmann 2015). Surprising events might also have a more general impact on how other stimuli that appear at around the same time are processed, possibly mediated via neuromodulators like norepinephrine (NE) that are released phasically in response to surprising events and can affect sensory processing (Aston-Jones & Cohen 2005, Sara & Bouret 2012). Consistent with this idea, pupil diameter, which can reflect the activation of NE-releasing neurons in the locus coeruleus, can reflect various forms of uncertainty, including surprise, along with perceptual biases and reports (Preusschoff et al. 2011, Nassar et al. 2012, de Gee et al. 2014, Kloosterman et al. 2015, Joshi et al. 2016).

Relationships between surprise and visual decision-making also likely involve mechanisms of sensory adaptation. At the single-neuron level, sensory adaptation typically decreases responses to persistent stimuli, resulting in relatively strong responses to novel stimuli that thus may be easier to detect or discriminate (Kohn 2007). An alternative, but not necessarily incompatible, view is that adaptation serves primarily to improve encoding efficiency by adjusting neuronal responses to match their dynamic range to the inputs that have been experienced (Stocker & Simoncelli 2005, Wark et al. 2007). Both of these effects appear to involve complex, history-dependent dynamics of adaptation that operate over multiple timescales for both onset and recovery (Webster 2011, Solomon & Kohn 2014). For example, motion-sensitive neurons in area MT exhibit adaptation on at least two timescales, one a rapid form that operates over tens of milliseconds and may contribute to sensitivity to the acceleration of moving objects, the other a more prolonged form that can contribute to other perceptual effects, including the motion aftereffect (Roach & McGraw 2009). Recent studies have begun to paint an even more complex picture, including dynamic changes in the time course of adaptation that might facilitate inferences about the dynamic inputs (Grzywacz

& de Juan 2003, Kording et al. 2007, Wark et al. 2009). However, it is not yet clear how mechanisms of sensory adaptation, which tend to boost single-neuron responses to improbable stimuli, interact with inference processes that tend to result in decisions that are biased away from those stimuli.

DURING THE DECISION: EVIDENCE ACCUMULATION AND DELIBERATION

During the decision, multiple mechanisms operate over multiple timescales to accumulate and interpret the visual input. For relatively short viewing durations (up to several hundred milliseconds), the temporal filtering properties of neurons relatively early in the visual pathway give rise to perceptual sensitivity that depends on the product of stimulus intensity and duration (i.e., Bloch's law) (Duysens et al. 1991). For longer durations, the relationship between duration and perceptual sensitivity more strongly reflects readout mechanisms that are consistent with an accumulation of sensory information over time (Smith & Ratcliff 2004, Gold & Shadlen 2007).

Human studies have identified neural substrates of this accumulation process in several ways. The low temporal resolution of fMRI makes it ill suited to identify such temporal dynamics, and it has instead been used primarily to identify other features of decision-related activity, like selectivity for difficulty and choice (Heekeren et al. 2008). However, other studies have used the very gradual presentation of visual evidence to identify fMRI correlates of gradually growing decision variables (Carlson et al. 2006, James & Gauthier 2006, Ploran et al. 2007), although a recent study using more symbolic evidence did not find such signals (Wheeler et al. 2015). Other studies have used high-temporal-resolution measures like electroencephalograms, in some cases combined with fMRI, to identify correlates of visual evidence accumulation in the human brain (Kelly & O'Connell 2015).

Monkey studies that combine behavior and single-unit recordings have provided higher-resolution measures of these evidence-accumulation processes. In monkeys trained to indicate perceptual decisions with saccadic eye movements, the decision variable is represented in the average activity patterns of neurons in several highly interconnected brain regions that encode the saccadic response. These brain regions include area LIP in parietal cortex, the frontal eye field and other parts of the prefrontal cortex, the caudate nucleus of the basal ganglia, and the superior colliculus (Horwitz & Newsome 1999; Kim & Shadlen 1999; Roitman & Shadlen 2002; Ratcliff et al. 2007; Ding & Gold 2010, 2012). These areas might also contribute to visual decisions that are not linked directly to specific eye movements, although different brain areas are likely engaged and disengaged depending on the behavioral context of the decision (Gold & Shadlen 2003, Bennur & Gold 2011, de Lafuente et al. 2015). Ongoing studies and debates will continue to help clarify our understanding of exactly how the process of evidence accumulation is implemented across such broad networks of brain regions and the causal role of each region in the decision process (Latimer et al. 2015, Katz et al. 2016, Shadlen et al. 2016).

A complementary and relatively new line of research is beginning to identify more complex, history-dependent properties of the evidence-accumulation process. Most studies to date have used tasks in which the visual evidence presented on any given trial is noisy but statistically stable. Under these conditions, normative decision processes use perfect accumulation (integration) of that information over time to reduce uncertainty (Smith & Ratcliff 2004, Bogacz et al. 2006, Gold & Shadlen 2007). However, perfect accumulation is not the normative solution when the source of the evidence undergoes unpredictable changes at any time, as is the case in the kinds of dynamic environments that we encounter every day. Instead, normative evidence accumulation in dynamic environments is a flexible process that adapts to the dynamics of the environment (Adams & MacKay 2007, Fearnhead & Liu 2007, Wilson et al. 2010, Veliz-Cuba et al. 2016). Thus, for

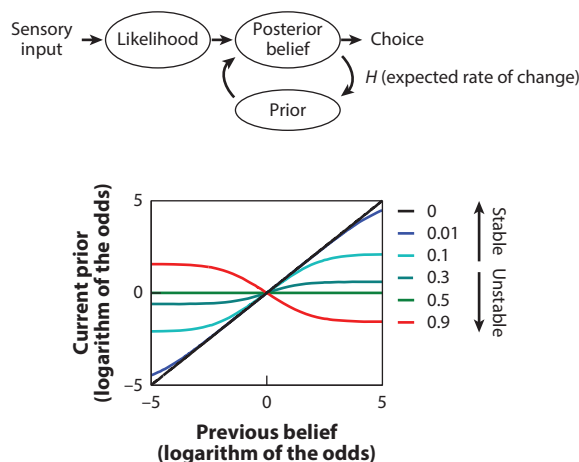


Figure 3

Adaptive evidence accumulation. Evidence accumulation can be thought of as an ongoing belief-updating process, in which sensory input is converted into evidence (e.g., a conditional probability, such as a likelihood) and then combined with the prior to update the current belief. That belief is then used as the prior on the next time step, and the process continues. In a completely stable environment, the prior is equal to the previous belief (*black line*) and the process reduces to perfect accumulation of likelihoods. However, in unstable environments, the possibility of change can be modeled as adaptive effects on the conversion from belief to prior, resulting in leaky and other nonlinear forms of evidence accumulation (*colored lines*). Adapted from Glaze et al. (2015).

example, more unstable environments should promote increasingly leaky accumulation, which naturally discards historical information that is likely to become obsolete (**Figure 3**). This kind of adaptive decision-making appears to govern behavior on a range of cognitive and perceptual tasks that require inferences about changing and uncertain stimuli (Behrens et al. 2007, Krugel et al. 2009, Nassar et al. 2010, Ossmy et al. 2013, McGuire et al. 2014, Glaze et al. 2015).

A key feature of the normative models that describe these adaptive decisions is that the adaptation depends on learned expectations about the dynamics of the evidence. This idea implies that how incoming evidence is accumulated for a given decision can depend critically on past experience, particularly as it relates to the source of evidence. Thus, for example, the decision processes that reflect perfect accumulation found in many studies may reflect learned expectations of perfect statistical stability under the conditions tested. Consistent with this idea, perceptual training under stable conditions can lead to less leaky accumulation (Brown & Heathcote 2005). Likewise, the persistence of leaky accumulation under some conditions, which have typically been interpreted as resulting from inefficiencies in the neural implementation of the decision process, might instead reflect a normative process based on persistent expectations of some lingering instability in our dynamic world (Usher & McClelland 2001, Tsetsos et al. 2012). Conversely, under other conditions, subjects might have a greater expectation of stability than is warranted, leading to serial dependencies across decisions that might also be reflected in within-decision accumulation processes (Fischer & Whitney 2014). More generally, other modulations of the accumulation process, such as those related to urgency that can, in principle, involve increasing gain on the inputs to promote faster decisions, might include components that depend on learned expectations about the structure of the evidence or of the task (Reddi & Carpenter 2000, Ditterich 2006, Cisek et al. 2009, Drugowitsch et al. 2012).

Little is yet known about where and how in the brain these adaptive evidence-accumulation processes are implemented for visual decisions. However, several studies have begun to identify neural mechanisms that likely contribute to this process. Many of these studies have focused on the role of the cingulate cortex and noradrenergic, cholinergic, and other neuromodulatory systems in encoding key contextual variables, such as uncertainty and surprise, that relate to the environmental dynamics that must be learned to adjust the decision process (O'Reilly 2013). However, to date, there has been little, if any, progress in understanding exactly how these variables are learned or used to modify how evidence is accumulated to form the decision.

One obvious possibility is that the circuits that can encode perfect or nearly perfect accumulation under statistically static conditions also have the capacity for adaptive adjustments under more dynamic conditions (Horwitz & Newsome 1999; Kim & Shadlen 1999; Roitman & Shadlen 2002; Ratcliff et al. 2003; Ding & Gold 2010, 2012). There is some evidence that the dynamics of evidence accumulation in these brain regions can reflect learned expectations. For example, when unequal prior probabilities are combined with stimulus uncertainty, their effects include dynamic adjustments to the evidence-accumulation process represented in area LIP (Hanks et al. 2011). Such changing dynamics might reflect more general mechanisms for history-dependent, adaptive control of these decision processes.

END OF THE DECISION: COMMITMENT

The process that terminates evidence accumulation and commits to an alternative can depend on both past experiences and future goals, thus further embedding the decision process in time. A prominent example is the use of a flexible decision bound in accumulate-to-bound decision models (Smith & Ratcliff 2004, Bogacz et al. 2006, Gold & Shadlen 2007). Within a trial, this bound is often assumed to remain fixed, representing the total amount of accumulated evidence needed to commit to a particular alternative as prescribed by normative theory. Alternative rules have also been proposed, including a collapsing bound that reduces the total amount of evidence needed to form the decision as time elapses. The rationale for using this rule has included emphasizing other goals that can depend strongly on context, including reducing computational costs, promoting urgency, or recalibrating the decision process to account for uncertain evidence and unequal prior probabilities (Ditterich 2006, Brown & Heathcote 2008, Cisek et al. 2009, Hanks et al. 2011, Drugowitsch et al. 2012, Murphy et al. 2016). However, whether and when such a mechanism explains behavioral data more effectively than a fixed bound remains an open debate (Boehm et al. 2016).

A well-established benefit of a bounded accumulation process, which has roots in statistical decision theory, is that the bound can be adjusted to mediate the trade-off between speed and accuracy that is inherent to many decisions (Barnard 1946, Wald 1947, Schouten & Bekker 1967, Wickelgren 1977, Gold & Shadlen 2002). A low bound emphasizes speed over accuracy, whereas a high bound emphasizes accuracy over speed. Accordingly, instructions to emphasize speed or accuracy affect choice and response time (RT) behavior in a manner consistent with changes in the bound height of these models (Palmer et al. 2005, Ratcliff & McKoon 2008). Likewise, internal goals, such as maximizing quantities like reward rate that require a balance of speed and accuracy over the course of many sequential decisions, can be used for ongoing calibration of the decision process that corresponds to changes in the bound height (Gold & Shadlen 2002, Simen et al. 2009).

Thus, identifying neural mechanisms responsible for the speed-accuracy trade-off represents an important step toward understanding how immediate sensory input is combined with longer-term goals in the brain to form decisions. Imaging studies in humans have begun to make progress on this problem. For example, changes in this trade-off have been shown to modulate activity

in a network of brain regions, including parts of prefrontal cortex and the striatum (Forstmann et al. 2008, van Veen et al. 2008). These findings are roughly consistent with modeling studies that posit a primary role for the basal ganglia in adjusting the decision bound, which may be just one part of a more general role in adjusting behavior to maximize reward (Lo & Wang 2006, Cohen & Frank 2009, Bogacz & Larsen 2011).

However, numerous questions still remain about the nature of the termination rule and its neural implementation and control in the context of the speed–accuracy trade-off. For example, a single-unit study of the caudate nucleus, which is a primary input structure of the basal ganglia, in monkeys performing a visual decision task found activity that encodes the rising dynamics but not convergence to a bound prescribed by accumulate-to-bound models (Ding & Gold 2010). This result implies that decision commitment may be computed elsewhere, including possibly at later stages in the basal ganglia that have yet to be tested. A separate study showed that neural activity in the frontal eye field, where correlates of the decision bound have been identified, is sensitive to instructed changes in the speed–accuracy trade-off (Hanes & Schall 1996, Heitz & Schall 2012). However, these effects included modulations of the timing and strength of neuronal responses that were not easily interpreted as changes in the height of the decision bound. This result emphasizes that accumulate-to-bound models are algorithmic and thus do not necessarily provide accurate descriptions of how those algorithms are implemented in the brain.

AFTER THE DECISION: EVALUATION AND CONSISTENCY

Decisions rarely occur in isolation. Therefore, feedback and reward signals associated with the outcome of a given decision can provide useful information for future ones. For example, feedback can drive reinforcement-learning processes that can be used to establish the appropriate sensory-motor association and then improve perceptual sensitivity (Law & Gold 2009). In principle, feedback-driven learning can also help to establish and update appropriate prior probabilities (Serriès & Seitz 2013). This kind of learning process is thought to contribute to prior-driven performance biases in reaching and targeting tasks (Trommershauser et al. 2003, Berniker et al. 2010). Recent studies that use changing environments have begun to gain insights into the computational principles that are used to update priors from one decision to the next under these conditions but typically in the context of explicit prediction tasks (O'Reilly 2013). It remains to be seen whether and how these principles apply to how priors are updated and used for perceptual decisions.

Sometimes, explicit feedback is not available. In these cases, the decision maker may generate a self-assessment of the quality of the decision, a process known as metacognition (Kepecs et al. 2008, Grimaldi et al. 2015). Under some conditions, this assessment is consistent with a direct readout of the decision variable representing the total accumulated evidence used to form the decision (Kepecs et al. 2008, Kiani & Shadlen 2009, van den Berg et al. 2016). Alternatively, under other conditions, confidence itself can be influenced by prior expectations, suggesting additional processing beyond the decision variable (Sherman et al. 2015, Fleming & Daw 2017). In either case, these confidence judgments can have direct effects on subsequent decisions. For example, when human subjects are tasked to perform two visually guided categorical decisions correctly in a row to be rewarded, they tend to optimally adjust the amount of time to integrate evidence for the second decision on the basis of their confidence in being correct in the first decision (van den Berg et al. 2016). This strategy can be modeled using an accumulate-to-bound framework in which the bound height of the second decision is adjusted according to the confidence in the first decision being correct.

Making a decision can also change the decision maker's sensitivity to subsequent visual information in a sequential-sampling task. For example, subjects who were asked to make a categorical

decision after exposure to just half of the stimulus samples showed substantially reduced sensitivity to the information contained in the second half when making the final decision (Bronfman et al. 2015). This result implies that prior beliefs are updated by the decision, even though doing so can be detrimental to overall performance. For cases in which no further sensory evidence is provided, human subjects seem to rely fully on the committed decision to interpret the evidence upon which it was based (Jazayeri & Movshon 2007). This behavior can be explained as a form of self-consistency in an otherwise optimal Bayesian decision process (Stocker & Simoncelli 2008, Luu & Stocker 2016): Without further evidence, the decision maker assumes the decision was correct in the context of any subsequent inference step. Because this procedure limits the inference process to only solutions that are consistent with the initial decision, such a decision strategy is overall suboptimal. However, a precise quantitative framework that captures the trade-off between performance and self-consistency has yet to be developed. Several studies have shown that decision signals are fed back along the visual pathway all the way to primary visual cortex, thus providing a potential mechanism for how decision signals may affect the processing and impact of subsequent visual information (Nienborg & Cumming 2009, Siegel et al. 2015). Precise formulations for such a mechanism that could link this kind of neural information flow with decision-making have yet to be proposed and tested.

SYNTHESIS AND FUTURE DIRECTIONS

Sequential-sampling models can provide a parsimonious account of decision processes that result in relationships between stimulus strength, choice accuracy, and RT that are found across a wide variety of tasks and conditions (Gold & Shadlen 2007). However, these models are incomplete. They account for temporal dynamics within a given decision but not for the many temporal

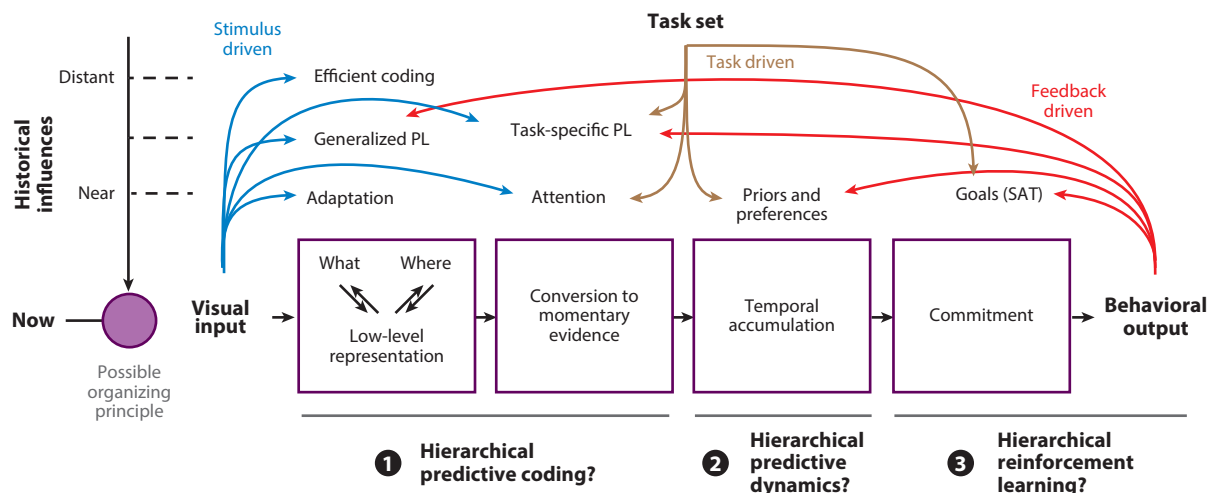


Figure 4

Historical dependencies of the decision process and possible organizing principles. Incoming visual information is encoded in multiple hierarchical pathways in the brain. Decision processes interpret particular activation patterns from various stages of these pathways as evidence to support or oppose the alternatives under consideration. This evidence is accumulated over time until reaching a commitment that guides behavior. Each of these processing stages is influenced by historical factors, including those related to visual input (*blue*), externally or internally generated feedback of the decision process (*red*), and the specific task (*brown*). Our understanding of these dependencies will likely benefit from several recently developed frameworks based on hierarchical and predictive processing, as discussed in the text. Abbreviations: PL, perceptual learning; SAT, speed-accuracy trade-off.

dependencies that exist across decisions and over time (**Figure 4**). As we have discussed, visual experience, learning, expectations, attention, and other factors can influence how visual information is represented and interpreted in the brain. Moreover, the commitment to a decision can itself establish expectations, promote consistency, and result in feedback, each of which can affect future decisions (Stocker & Simoncelli 2008). Thus, a deeper understanding of neural mechanisms of visual decisions will require new ways to conceptualize the key components of the decision process as a function of history.

Understanding these historical dependencies may benefit from three recently proposed sets of ideas. They address how each of the three key components of the decision process—interpreting incoming sensory information as evidence that supports or opposes the alternatives under consideration, accumulation of the available evidence, and commitment to an alternative—might be implemented in the brain in a manner that naturally takes into account complex dependencies that operate over multiple timescales (**Figure 4**).

The first concerns the evidence for a visual decision, which is provided by the task-specific readout, or decoding, of relevant encoded sensory information. It can be convenient to consider encoding and decoding as separate processing stages—for example, for learning processes that can be used to establish an appropriate task-specific decoder for a relatively fixed encoding scheme (Petrov et al. 2005, Law & Gold 2009). However, such separation would likely exacerbate the challenges of dealing with historical dependencies (Sompolinsky et al. 2001, Wu et al. 2001, Latham & Nirenberg 2005, Averbeck et al. 2006, Jazayeri & Movshon 2006). How would a decoder remain “faithful” to a changing encoding scheme? How would a changing decoder remain well matched to the encoding scheme? One possible answer to these questions, at least in principle, is that encoding and decoding are not separate processing stages in the brain but rather are intertwined parts of the visual hierarchy (Wei & Stocker 2015). This idea is central to recent proposals that consider the visual hierarchy as an inherently predictive system, with bottom-up signals propagated as errors between actual inputs and those predicted by the next-higher level of abstraction (Rao & Ballard 1999, Lee & Mumford 2003, Friston 2010, Bastos et al. 2012). It is not yet clear how this error-driven processing scheme can be reconciled with the primarily stimulus-driven response properties of most individual neurons in the visual system (Summerfield & de Lange 2014). Nevertheless, it may provide new ways of thinking about visual decisions, which instead of reading out feed-forward responses in the visual pathway may tap into ongoing inference processes implemented there. In this scheme, efficient coding, perceptual learning, sensory adaptation, and even some forms of attention might serve to facilitate predictions that are represented at different levels of the hierarchy with different spatial and temporal scales. These predictions may come from higher-level representations that include objects, visual features, or learned associations that are appropriate for a given task.

The second concerns the accumulation of evidence over time, which serves to improve signal fidelity and is a central feature of many decisions, accounting for inherent trade-offs between speed and accuracy. It is not known how this accumulation process might contribute to the kind of hierarchical inference process described above, in which each level of the visual hierarchy establishes predictions that are supported or opposed by incoming visual evidence that might require at least some temporal accumulation. However, the accumulation process that accounts for most of the decision time in many visual tasks is consistently represented in downstream sensory-motor and motor brain areas but not the visual pathway, implying a separate set of mechanisms (Gold & Shadlen 2007, Kelly & O’Connell 2015). As discussed above, this accumulation process appears to be adaptive, with temporal dynamics that adjust to expected environmental dynamics (Glaze et al. 2015, Veliz-Cuba et al. 2016). This idea implies that yet another complex inference process may be required to form visual decisions—in this case, to infer from experience the expected stability

of the incoming evidence. This expectation, in turn, would control the evidence-accumulation process that governs the decision about the content of the evidence. In principle, expectations about environmental stability can also be learned via hierarchical, probabilistic inference (Wilson et al. 2010). However, how such a complex process is implemented in the brain remains unknown.

The third concerns the commitment to a decision, which is most readily apparent when it triggers an immediate associated motor response. In that regard, decision commitment can be thought of as a part of a set of behavioral policies that generally serve to minimize costs and maximize benefits. Behavior is inherently hierarchical and can be broken down into discrete tasks that can be further divided into subtasks, action sequences, and specific movements. Accordingly, models of learning and behavior have begun to emphasize this hierarchical structure to develop appropriate behavioral policies in complex environments (Botvinick et al. 2008, Ribas-Fernandes et al. 2011, Frank & Badre 2012). An important challenge is to understand how that system also can form hierarchical decisions that may require commitments to intermediate propositions, operating over many timescales, to guide the context-dependent interpretation of other visual features and subsequent behavior (Lorteije et al. 2015, Purcell & Kiani 2016). Finally, some hierarchical decision tasks can be simply too complex and nested to be solved within a given time limit. Understanding the behavioral strategies and discerning the underlying mechanisms in such regimes of so-called bounded rationality are interesting open challenges (Simon 1972, Ortega & Stocker 2016).

Thus, visual decision-making may rely on multiple hierarchical inference and learning processes to extract the relevant visual evidence, accumulate that evidence over time in an effective and adaptive manner, and then commit to an alternative that is consistent with an overall behavioral policy. These ideas are just beginning to be formalized into computational theories, which can guide studies of whether and how they are implemented in the brain. A longer-term challenge is to understand how these kinds of complex mechanisms operate in concert, particularly with respect to the multiple timescales over which each must operate, to form visual decisions.

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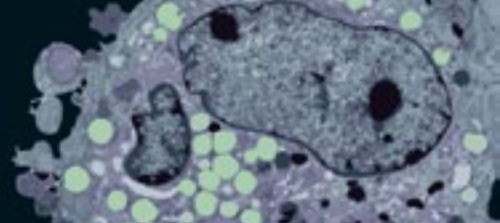
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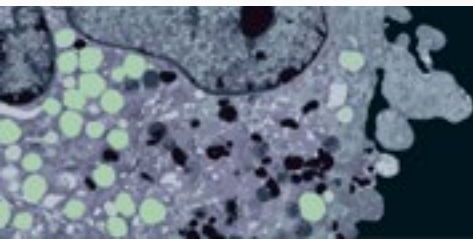
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