

Expectation in perceptual decision making: neural and computational mechanisms

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Abstract | Sensory signals are highly structured in both space and time. These structural regularities in visual information allow expectations to form about future stimulation, thereby facilitating decisions about visual features and objects. Here, we discuss how expectation modulates neural signals and behaviour in humans and other primates. We consider how expectations bias visual activity before a stimulus occurs, and how neural signals elicited by expected and unexpected stimuli differ. We discuss how expectations may influence decision signals at the computational level. Finally, we consider the relationship between visual expectation and related concepts, such as attention and adaptation.

Humans and other primates mainly rely on vision to detect, recognize and classify information in the world around them. In the laboratory, perceptual decisions are typically studied by asking human volunteers or experimental animals to classify an isolated visual stimulus, such as a cloud of randomly moving dots, using one of two responses. Combining visual psychophysics with quantitative modelling and neural recordings has provided a unique window into the mechanisms underlying perceptual choice at each stage of the primate visual processing hierarchy^{1–3}.

However, in natural environments, visual stimuli rarely occur in isolation. Rather, they typically occur in the context of other scene elements that predict their identity or location^{4,5} (FIG. 1). In a natural image, the presence of grass, trees and a greenhouse might suggest a garden scene. These elements might lead observers to expect the occurrence of another garden-related object, such as a lawnmower, but not an object normally found indoors, such as an armchair. Empirical work dating back to the 1970s demonstrates that object recognition is influenced by the context in which information occurs. For example, jumbling the background information in a visual scene slows down and impairs object recognition⁶. Similarly, objects that are unexpected in a visual scene by virtue of their size, position or relation to other scene elements are detected more slowly and provoke more recognition errors⁷. Thus, spatial context allows expectations to form about the location or identity of a visual object, promoting its eventual recognition.

In psychophysical experiments, trial sequences are often carefully crafted such that the probability of occurrence and transition probability are equal for all stimuli. This ensures that stimuli cannot be predicted on the basis of the past occurrence of other stimuli. In the real world, however, some objects occur more frequently than others. If a friend has a new house pet, you might expect it to be a cat or a dog, but perhaps not an alligator or a koala. Moreover, one stimulus often predicts another. If you hear a barking sound, you expect the approach of a dog and not a cat. Infants learn early to track transitional probabilities between sensory events, both in the visual⁸ and the auditory domain, where statistical learning facilitates language acquisition⁹. By adulthood, responses to visual stimuli are robustly facilitated by their conditional probability of occurrence^{10,11} — for example, when searching for a visual target, the viewer might predict its position provided by the context of surrounding distracters¹². Moreover, the probability of occurrence of a stimulus is strongly conditioned on whether it has been viewed recently or not, because in most environments, visual information remains relatively stable over time. Imagine you are standing on the banks of the River Thames in London looking east towards St Paul's Cathedral. If you glance down to look at a map, on returning your gaze the skyline should look largely unchanged, aiding recognition — a phenomenon known as repetition priming¹³. The visual system can thus capitalize on information about stimulus frequency, conditional probability and temporal autocorrelation in the visual signal to build expectations about forthcoming sensory information.

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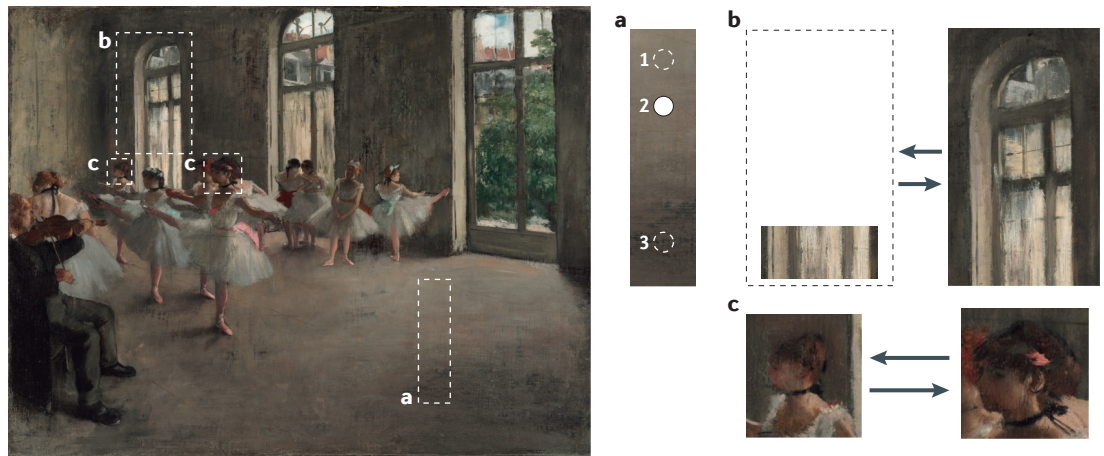


Figure 1 | Expectations in visual perception. We illustrate some of the ways in which expectations shape perception using an example from Edgar Degas' celebrated 1878 painting *The Rehearsal* (left panel). **a** | Autocorrelation in visual signals. In this excerpt taken from the floor, it is easy to predict the colour of the missing circular patch (2) from the background. Notably, because of the smoothly varying saturation of the background colour, it should be more similar to patch 1 than to patch 3. **b** | Hierarchical organization of visual information. Viewed through an aperture (left panel), this portion of the image is hard to identify. This is the problem faced by neurons in the early visual system with small receptive fields. Contextual information from a wider aperture (right panel) aids the interpretation of the visual signals. In the visual system, top-down signals from subsequent processing stages, in which receptive fields are larger, may provide contextual information. **c** | Prior information and priming. Stimuli that are ubiquitous in the visual environment, such as faces, come to be expected and garner dedicated processing mechanisms. Stimuli that have occurred recently are also more likely to reoccur, and repeated stimuli can thus facilitate perception, a phenomenon known as priming. For example, a saccade to the unambiguous face (right panel) will aid subsequent interpretation of the ambiguous face (left panel). Image courtesy of Harvard Art Museums/Fogg Museum, Bequest from the Collection of Maurice Wertheim, Class of 1906, 1951.47, Imaging Department © President and Fellows of Harvard College.

In this Review, we consider how detection and recognition judgements about the visual world are modulated by expectations. In particular, we discuss studies that have investigated how expectations might be incorporated into quantitative models of decision making, including signal detection theory, the sequential sampling framework and predictive coding. In parallel, we consider data from both brain imaging and single-cell recording studies that have highlighted how expectations influence neural responses in the visual cortex and beyond. Finally, we discuss the relationship between visual expectation and other related concepts, such as attention and adaptation. Throughout the Review, we use the term 'perceptual decision making' to refer to the process by which a visual stimulus is detected, recognized and classified, with or without a specific commitment to action¹⁴.

Decision-theoretic approaches

Good decisions are made after accounting for all of the available information. We begin by reviewing two decision-theoretic models of perceptual choice, which offer a formal account of how information about what is probable (expectations) and what is present (sensory input) should be combined to make optimal choices.

Signal detection theory. Consider a participant in a psychophysics study who is classifying a grating as being tilted left or right of the vertical axis, or a pedestrian who is looking up to assess the chance of rain. Formal theories

state that decisions respect the relative likelihood of evidence x provided by the stimulus (for example, white or grey clouds) given one option R (for example, rain) over the other $\neg R$ (for example, no rain). For convenience, this is expressed as the log of the likelihood ratio (LLR):

$$LLR = \log \frac{p(x|R)}{p(x|\neg R)} \quad (1)$$

Thus, R will be chosen if $LLR > 0$ and $\neg R$ will be chosen if $LLR < 0$. Under a formal framework, expectations can be formalized as the prior probability of occurrence of a stimulus. According to Bayes' rule, the likelihood ratio becomes the log posterior when supplemented with prior beliefs about the underlying options or hypotheses (R versus $\neg R$):

$$LLR = \log \frac{p(R)}{p(\neg R)} + \log \frac{p(x|R)}{p(x|\neg R)} \quad (2)$$

In other words, when one option occurs more frequently than another, this should engender a shift in the criterion that separates the two categories. For example, if you are in Scotland, where $p(\text{rain}) > p(\text{no rain})$, then this will shift the LLR towards R , perhaps prompting the decision to take an umbrella, whereas in Southern California, the converse will be true (FIG. 2a). This account of how choices are biased by prior probabilities of stimulus occurrence makes a clear prediction that where $p(R) > p(\neg R)$, observers will be biased to choose R , irrespective of whether the true stimulus is R or $\neg R$. Many decades of psychophysical research have confirmed this

Bayes' rule

Bayes' rule describes how the relative probability (or odds) of two possible hypotheses changes (from prior odds ratio to posterior odds ratio) as new evidence is acquired. Formally, the posterior odds ratio is calculated by multiplying the prior odds ratio by the likelihood ratio (also known as the Bayes factor), which is the probability of observing the new evidence, given the two hypotheses.

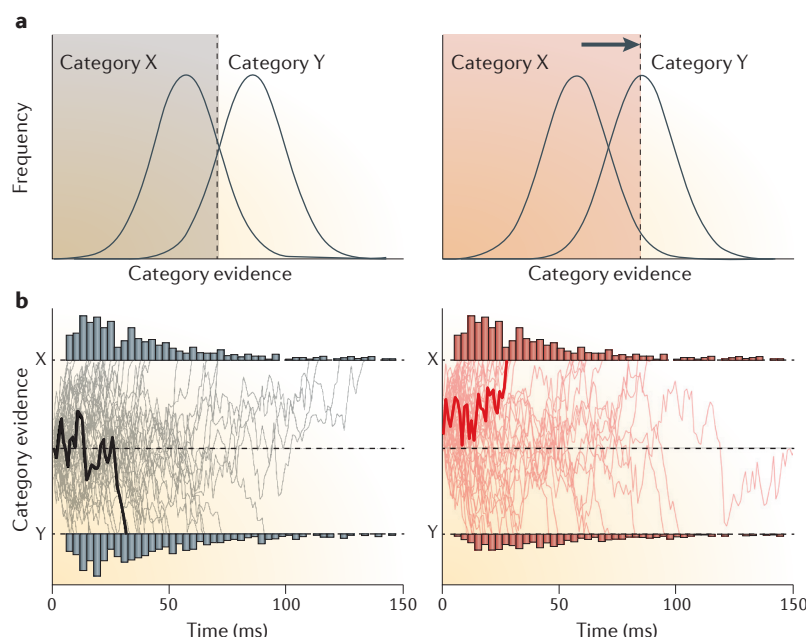


Figure 2 | Decision-theoretic approaches to understanding expectation.

a | In signal-detection theory, the observer learns the distributions of evidence associated with each category (category evidence)¹⁵. Left panel: decisions reflect a criterion (indicated by the dashed line). When both categories are equally probable, the optimal position for the criterion is between the two distributions, where the log-likelihood ratio is equal to zero. Right panel: expectations change the position of the criterion. Here, the criterion shifts to the right, meaning that decisions favouring X are more likely to occur. **b** | In the drift-diffusion model, noisy category evidence (shown by the thin grey traces in the left panel and the thin red traces in the right panel; each trace is one simulated trial) diffuses to one of two bounds¹⁸ (indicated by the dashed lines). Diffusion latency allows us to model reaction-time distributions (shown in the histograms). When both categories are equally probable, the optimal origin (that is, starting point) for the diffusion process lies equidistant between the two category bounds. The right panel shows that when category X is more probable than category Y, the origin shifts towards the bound for X. This means that decisions in favour of category X are made faster and more often (histograms) than decisions in favour of category Y. In both panels, the thick line shows diffusion on the trial with median reaction time, defined as its latency of diffusion-to-bound.

prediction¹⁵. For example, when detecting a low-energy stimulus, observers will respond “yes” more often when the stimulus is probable. Yet their ability to distinguish between signal and noise, indexed by decision-theoretic measures such as d-prime, is not typically found to change (however, see below).

Sequential sampling models. Sequential sampling models propose that perceptual decisions follow the integration of information over time, until a threshold level is reached. For example, when viewing a noisy psychophysical stimulus such as a random dot kinematogram (RDK), participants can optimize perceptual decisions by integrating motion information over successive frames. Similarly, a clinician will make a more judicious diagnosis after considering all of a patient’s symptoms. One such model, known as the sequential probability ratio test (SPRT), is based on the Bayesian principle that decisions should be based on the sum of the log likelihoods accruing from each of n samples of evidence¹⁶. Formally, expectations about stimulus occurrence can

be incorporated in the fashion described above¹⁷, as an early offset in the evidence favouring the expected stimulus:

$$LLR = \log \frac{p(R)}{p(\neg R)} + \log \frac{p(x_1 | R)}{p(x_1 | \neg R)} + \dots + \log \frac{p(x_n | R)}{p(x_n | \neg R)} \quad (3)$$

The SPRT can be approximated by the drift-diffusion model¹⁸. In this model, decisions are based on the accumulation over successive samples k of sensory evidence I , which is a scalar quantity that expresses the relative evidence for the two contentions, plus zero-mean Gaussian noise, towards symmetric decision thresholds. Evidence I may be scaled by a multiplicative drift parameter δ , which expresses the gain of the evidence (equivalent, in Bayesian terms, to the inverse variance or precision of the likelihoods; DV denotes decision variable):

$$DV_k = DV_{k-1} + \delta \cdot I_k + N(0, \sigma^2) \quad (4)$$

The accumulation begins at an origin (denoted α) that reflects baseline evidence for each alternative, equivalent to the prior probability (FIG. 2b):

$$DV_0 = \alpha \quad (5)$$

In line with the formal accounts described above, decisions about stimuli with asymmetric prior probabilities can be accounted for by adjusting the starting point (α) of the diffusion process (this is known as the origin model). This account correctly predicts a large number of fast responses in which an unexpected stimulus is mistaken for an expected one^{17,19,20}, because in the early stages of the trial, decisions are strongly governed by the placement of the origin (α). An alternative account suggests that the drift rate (δ) might be selectively increased when evidence favours an expected stimulus (this is known as the gain model) — that is, it proposes differential drift rates for expected (validly cued) and unexpected (invalidly cued) inputs²¹. However, this model does not account so well for the relative proportions of fast and slow errors made during biased decisions¹⁹. Taken together, this suggests that some additive offset in pre-stimulus evidence levels is required to account for the effect of expectations in perceptual decisions.

Expectation biases pre-stimulus signals

A natural way to implement an early, additive bias to evidence integration is to increase baseline neural activity in decision circuits that integrate information towards a response (FIG. 3). During RDK discrimination, neurons in macaque parietal and prefrontal cortices exhibit firing rates that reflect the integrated tally of evidence in favour of one saccadic response over another^{1,22}, and have thus been considered to be decision related. Baseline responses in these neurons are biased by the probability of stimulus occurrence²³. Neurons in the superior colliculus, a downstream structure involved in saccadic control, also show probability-modulated responses²⁴. Comparably, in humans performing RDK discrimination, decision-related build-up activity has been observed in the form of steady increases in lateralized oscillatory activity recorded

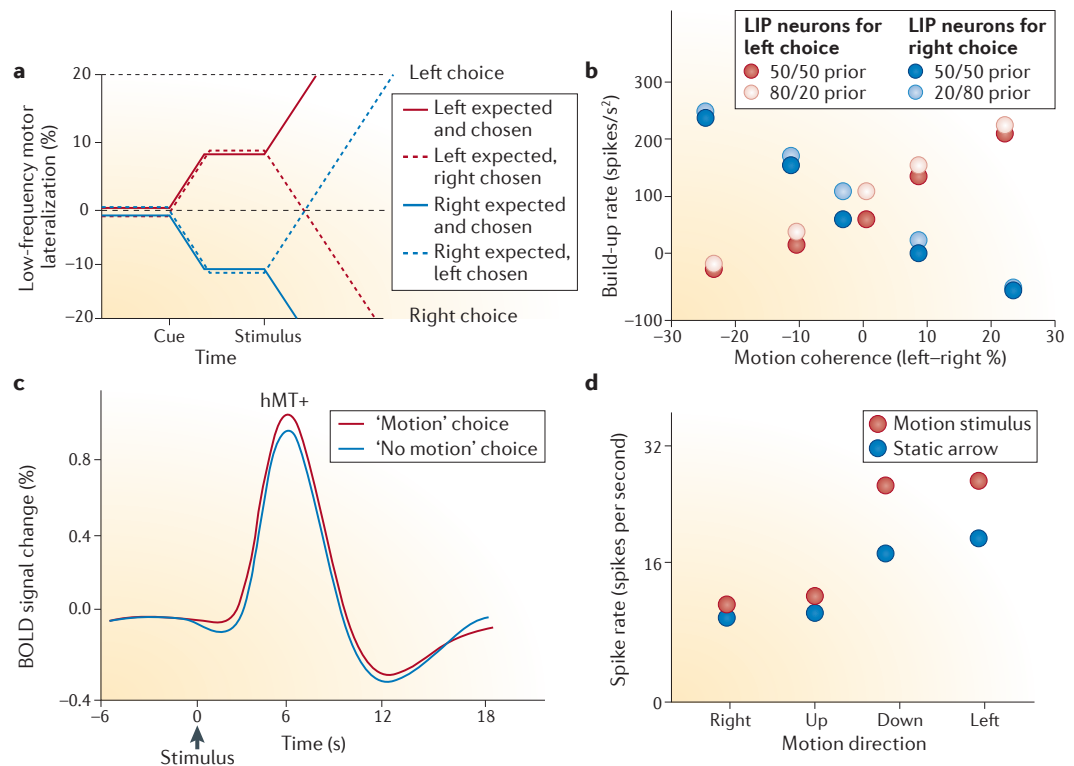


Figure 3 | Biasing of neural signals by expectation at different processing stages. Biasing of neural signals can be observed when participants make perceptual judgements about the net direction of motion (left versus right) in a random dot kinematogram. **a** | Increasingly lateralized low-frequency oscillatory magnetoencephalography activity over the motor cortex is a neural signature of sensory evidence accumulation when different perceptual choices are coupled to specific effectors. When one stimulus is cued as more probable than another (that is, when it is expected), the choice build up begins in the pre-stimulus period. **b** | Build-up rates of neurons in the lateral intraparietal cortex (LIP) for leftwards choices (shown in red) and rightwards choices (shown in blue) as a function of motion coherence. Dark red and dark blue dots show data from blocks in which left and right motion occur with an equal probability; light red and light blue dots show data from blocks in which left and right dot motion, respectively, was expected. Data from REF. 23. **c** | When participants decide that dots are moving coherently as opposed to randomly, blood-oxygen-level-dependent (BOLD) signals from human motion-sensitive visual area MT (hMT+) are biased by endogenous signals in the pre-stimulus period (that is, at $t = 0$), as shown by the red trace (versus the blue trace). **d** | When one visual stimulus predicts the next visual stimulus, the neuron that encodes the expected stimulus — for example, a neuron in area MT — shows activation not only when the stimulus is shown, but also when the predictor stimulus is shown. The figure shows the mean firing rate of a representative MT neuron to four different motion directions (red dots) and to four static arbitrary shapes that predicted the corresponding motion direction (blue dots). In this example, the MT neuron responds to downwards-moving stimuli and to leftwards-moving stimuli, but also increases its firing rate in response to a downwards-pointing arrow and to a leftwards-pointing arrow.

using magnetoencephalography (MEG) over motor areas²⁵. Moreover, following a cue that predicts whether the motion direction of the RDK stimulus is likely to be leftwards or rightwards, neural signals that correspond to the associated stimulus–response mapping begin to build up prominently in the pre-stimulus period, leading to a baseline offset by the time the stimulus occurs²⁶ (FIG. 3a). Finally, in a study combining modelling and functional imaging, individual differences in the best-fitting origin of diffusion predict blood-oxygen-level-dependent (BOLD) signals in the frontal and parietal cortices during RDK discrimination¹⁹.

Probability-modulated responses are not just observed in decision-related and motor regions; the responses of sensory neurons are also biased by expectations in the pre-stimulus period. During visual associative learning,

in which one visual stimulus predicts the next, neurons encoding the expected stimulus in both the inferotemporal cortex^{27,28} (for object stimuli) and visual area MT (also known as V5)^{29,30} (for motion stimuli; FIG. 3d) become active in the delay period that precedes its occurrence³¹. At the macroscopic level, several studies have reported that cues predicting the occurrence of a visual stimulus lead to increases in BOLD signal in category-specific extrastriate regions. For example, when the word ‘FACE’ predicts the subsequent occurrence of a face, it provokes higher BOLD signals in the fusiform gyrus³². Similarly, when participants discriminate faces that emerge gradually from noise, an advance cue that predicts stimulus category leads to larger fusiform BOLD signals^{33,34}. Even in the absence of an overt cue, expectations about what is likely to occur can wax and wane with spontaneous

activity in visual cortical regions. For example, pre-stimulus BOLD signals in extrastriate visual cortex predict whether observers will judge Rubin's vase illusion to be a face or a vase³⁵, or whether they will decide that dots are moving randomly or coherently³⁶ (FIG. 3c). Moreover, expectations affect the sensory response in the absence of visual input; when an expected visual grating is omitted, the omission evokes a neural activity pattern in early visual cortex which is similar to that evoked by the corresponding actual stimulus, suggesting that prior expectation triggers the formation of specific stimulus templates³⁷. Similarly, the existence of an expectation *per se*, relative to a neutral condition in which no stimulus is expected, seems to bias both posterior α -band (8–13 Hz) MEG signals²⁵ and BOLD activity in the visual cortex³⁸. In other words, expectations may bias neural activity in the sensory cortices, thereby pushing the interpretation of sensory information towards one perceptual hypothesis over another.

Neural signatures of expectation

Canonical models of perceptual decision making propose that momentary sensory evidence is read out and accumulated in decision circuits^{1,3}. For example, in a primate performing the RDK task, pooled activity from the motion-sensitive area MT may be integrated towards a decision threshold in the lateral intraparietal cortex (LIP)¹. Boosting activity in sensory regions before stimulus presentation, as described above, might thus have an additional multiplicative influence on choices because enhancing the input increases the rate at which evidence drifts towards the bound³⁹. Therefore, when trial difficulties (for example, levels of motion coherence) are intermingled within an experimental block, some additional adjustment to the drift rate is optimal. Biasing the drift rate ensures that expectations have the most impact during prolonged deliberation, which occurs, on average, in trials in which evidence is noisy or weak (for example, when motion coherence is low). Biasing in this fashion thus implements the Bayesian principle that priors should influence decisions the most when the signal-to-noise ratio is low — that is, when the evidence is ambiguous or imprecise⁴⁰. Correspondingly, in addition to shifts in the origin of integration, adjustments to drift rate have been reported to account for reaction-time data when stimulus probabilities are asymmetric^{21,23}.

One might thus hypothesize that decision-related signals recorded from integration neurons such as those in area LIP would be boosted when stimuli are expected. This was reported in a recent study²³ showing that expected RDK stimuli elicit a faster-growing LIP signal than those that were unexpected and that this effect was most pronounced when motion coherence was low (FIG. 3b). The authors argued that expectation is implemented as a time-varying bias that ensures that the prior has the greatest influence on the trials with the longest response times — that is, trials in which the stimulus is (on average) weaker. This is consistent with the normative Bayesian perspective that prior information should hold most sway over decisions when sensory evidence is imprecise or ambiguous.

However, the picture is complicated by reports from a number of electrophysiological and neuroimaging studies investigating the effects of expectation on the sensory response (FIG. 3). At the macroscopic level, expected stimuli tend to dampen BOLD signals and reduce the amplitude of cortical potentials, an effect known as 'expectation suppression' (REF. 41) (FIG. 4). Evidence for this phenomenon first emerged in the auditory domain, where classically described scalp-evoked potentials — such as the N1 and P3b — were heightened when an auditory tone was unexpected⁴². Moreover, oddball responses to visual stimuli have also been reported in neuroimaging studies⁴³, and larger responses to stimuli rendered unexpected by a conditional cue^{44,45} or context^{46,47} rule out explanations based on habituation alone (see below).

Modulations by expectation seem to occur maximally at the sensory neurons that encode the expected stimulus. For example, in one study⁴⁵ BOLD signals were recorded from the fusiform face area (FFA) when participants viewed pictures of faces and buildings that were rendered expected or unexpected by probabilistically pairing each stimulus with an arbitrary colour cue that briefly preceded the stimulus (FIG. 4b). When a face was not presented, FFA BOLD signals were strongest when a face was expected — a finding that is consistent with a pre-stimulus biasing signal. However, in the context of a face stimulus, stronger BOLD signals were observed for unexpected faces than for expected faces, which is consistent with an effect of expectation suppression. In other words, expectation engenders changes in neural activity that occur before and during the presentation of a visual stimulus. Interestingly, a recent report has also documented expectation suppression in single-neuron responses in the macaque temporal lobe after visual statistical learning⁴⁸.

Predictive coding

The sequential sampling framework offers an elegant account of the mechanisms that underlie perceptual inference, and provides simple tools for understanding how perception is biased by expectation. In doing so, however, it overlooks some important features of the neuroanatomy and neurophysiology of mammalian sensory systems. For example, our visual system is hierarchically organized, and the size and complexity of receptive fields increases with each subsequent processing stage⁴⁹. Second, message passing is reciprocal between adjacent stages; in most cases, backwards projections outnumber forwards projections by a large margin⁵⁰. This complexity of organization might be important in real-world environments, where there are not just two but multiple possible interpretations of the information detected at the sensory receptors. A more neurobiologically plausible theory — known as predictive coding — seeks to account for these neurophysiological features while preserving the iterative Bayesian framework in which sequential sampling models have their basis. The theoretical roots of predictive coding can be traced back, via a number of other distinguished theorists, to Helmholtz^{14,51–55}.

N1

A negative evoked potential (measured by electroencephalography or magnetoencephalography) that peaks between 80 ms and 120 ms after the onset of a sensory stimulus (which can be visual, auditory or somatosensory). This potential is sensitive to manipulations of stimulus predictability.

P3b

A large positive evoked potential that peaks between 250 ms and 500 ms after the presentation of a stimulus. The P3b is associated with decision processes and strongly reacts to rare, surprising events.

Oddball

In the oddball paradigm, participants are subjected to frequent 'standard' stimuli interspersed with rare 'oddball' stimuli that require a response. Oddball stimuli elicit enhanced sensory and decision-related neural responses.

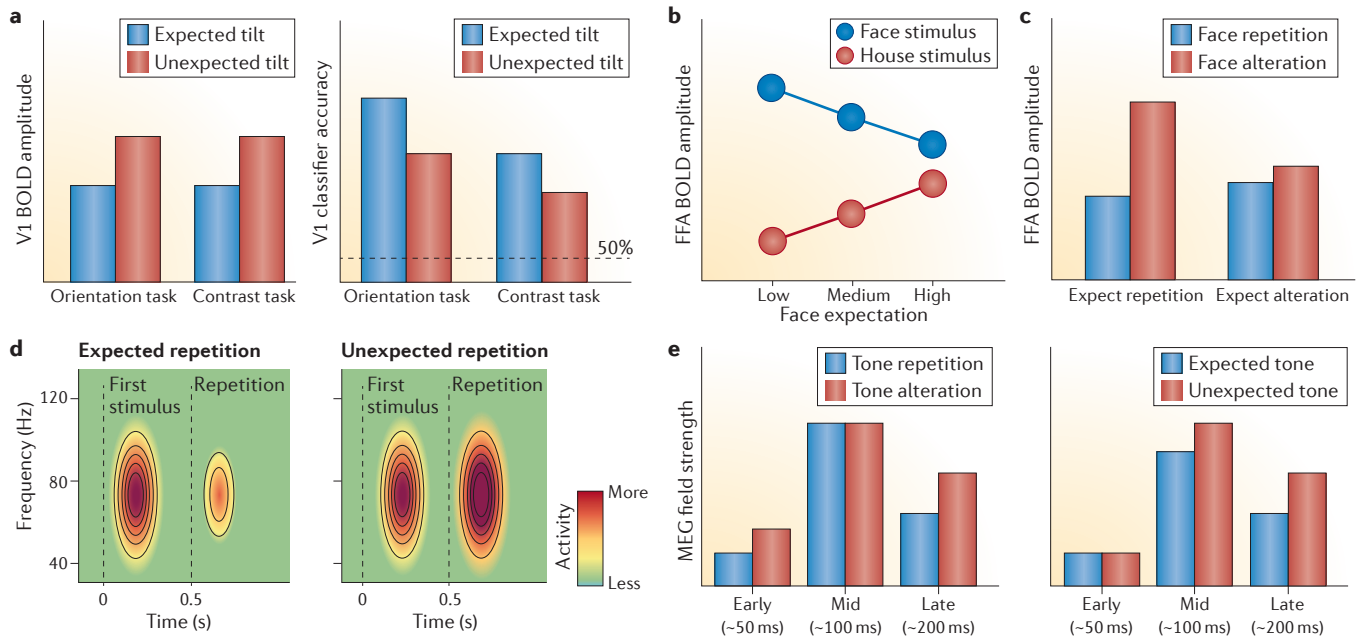


Figure 4 | Repetition suppression and expectation suppression. **a** | In a task in which participants view gratings and are asked to make a judgment about either the orientation of the gratings (orientation task) or the contrast of the gratings (contrast task) relative to a previously shown grating, gratings with expected orientations elicit attenuated blood-oxygen-level-dependent (BOLD) signals in the primary visual cortex (V1; left panel, blue bars) compared with gratings with unexpected orientation (left panel, red bars). However, expected stimuli can be decoded from multi-voxel patterns with greater accuracy (right panel, blue bars) than can unexpected stimuli (right panel, red bars), suggesting that expectation sharpens neural representations¹³¹. **b** | BOLD signals in the fusiform face area (FFA) are reduced upon presentation of an expected face stimulus relative to BOLD signals upon presentation of an unexpected face stimulus (blue line). By contrast, the expectation of a face stimulus boosts BOLD signals in the FFA when a non-face stimulus (such as a house) is presented (red line)⁴⁵. This is consistent with the predictive coding account of perception. **c** | Repetition suppression (the attenuation of BOLD signals elicited by the repeated presentation of a stimulus) in the FFA is stronger when repetitions are expected (left bars) than when they are unexpected (right bars)⁴⁷. **d** | Repetition suppression can also be observed in high-frequency (γ -band) oscillatory activity measured over the auditory cortex with magnetoencephalography (MEG) in response to expected repetition of a particular auditory stimulus^{41,95}. **e** | Repetition suppression (left panel) and expectation suppression (right panel) in the auditory cortex have different time courses, with the former beginning at 50 ms and the latter at 100 ms. Data from REF. 41.

Under predictive coding, evidence accumulation is best conceived of not as a particle diffusing between symmetric bounds, but as an evolving probability distribution over multiple possible causes (that is, a generative model) of sensation. Causes are represented over several hierarchically organized levels, with greater complexity at higher stages (for example, whole objects) than at lower stages (for example, oriented line segments). Inference at each stage occurs when two sources of information are combined: predictions (that is, priors) from the immediately higher stage, where units enjoy a greater purview in space and time; and sensory evidence (that is, likelihoods) from the stage below. As in the sequential sampling framework, this updating occurs repeatedly, and beliefs are gradually refined until the sensory system settles on the most likely interpretation of the inputs.

Under this framework, updating takes the form of a comparison between predicted and observed inputs, generating a prediction error term (which is equivalent to the likelihood term under the sequential sampling framework). Prediction errors flow forward to gradually adjust

belief at the subsequent processing stage, via a Kalman filtering process⁵⁶. Neural activity elicited by expected events is thus silenced or ‘explained away’ by backwards-flowing, predictive information from the subsequent processing stage, providing a mechanistic interpretation of expectation suppression in the sensory cortex. Moreover, in emphasizing the reciprocal nature of message passing in sensory systems, predictive coding helps to explain the baseline or pre-stimulus biasing observed for conditionally probable stimuli⁴⁵.

In the visual domain, predictive coding provides a plausible description of how visual responses are modulated by context, accounting for several modulatory effects of stimulation beyond the classical receptive field^{50,55}. For example, some neurons of the primary visual cortex (V1) display ‘end stopping’ — the paradoxical effect that a neuron ceases to respond to an optimally oriented stimulus if the size of the stimulus extends beyond the neuron’s classical receptive field⁵⁷. Predictive-coding theorists have argued that in this case, the neuron’s response is ‘explained away’ by feedback signals from neurons at a subsequent stage, which are able to

pool inputs over a larger retinal area. Rao and Ballard⁵⁵ constructed a hierarchical model of visual perception and trained it — using the principles of predictive coding — on a bank of natural images. The filters that developed matched the receptive field properties of neurons in the visual system closely and displayed ‘extra-classical’ effects, such as end stopping⁵⁵.

Predictive coding also accounts for neural responses to visual features that are not physically present but that are suggested by elements located outside the classical receptive field. For example, early visual neurons respond to the illusory contours of the Kanizsa triangle^{58,59}. These extra-classical effects can also be observed using neuroimaging⁶⁰. In an inventive functional MRI (fMRI) study⁶¹, participants viewed natural images in which one quadrant was obscured; the authors then examined the cortical representation of the obscured quadrant using multi-voxel pattern analysis (MVPA) and were able to decode the identity of the image. Illusory motion can also generate a differential BOLD signal in V1 voxels that respond to the retinotopic location in the absence of any motion input — an effect that can be explained by feedback from motion-sensitive area MT^{62,63}. Evidence from simultaneous electrophysiology and anatomical tracing suggests that the extent of these extra-classical influences cannot be accounted for by horizontal connections alone, but must involve feedback from cells with more spatially extensive receptive fields⁵⁰.

Predictive coding implies that neural signals for visual expectation filter down from higher to lower stages of sensory processing. It follows that early activation should increase when it cannot be predicted from the processing occurring at a subsequent stage. Accordingly, Murray and colleagues⁶⁴ observed that V1 BOLD signals were increased in response to lines that failed to form a coherent shape, relative to those that formed two-dimensional or three-dimensional objects, whereas the reverse was true in the object-sensitive lateral occipital complex. Similarly, an enhanced response to incoherent relative to coherent motion was observed in V1, even when elements were spaced so as to ensure that any interactions could not be accounted for by lateral connections within that region⁶⁵. Moreover, inactivation of higher levels of the hierarchy will disrupt predictions and their neural concomitants at the lower level. Accordingly, end stopping is eliminated following cooling of visual area 2 (V2) in the squirrel monkey⁶⁶. Inactivation of area MT leads to suppression of the extra-classical response in early visual regions, particularly when it is useful for segmenting objects from their background⁶⁷. In humans, inactivation of area MT with transcranial magnetic stimulation eliminates the detection advantage enjoyed by targets that are predicted by an illusory motion signal, relative to those that are unpredicted⁶⁸.

Dissociating attention and expectation

Visual expectation is closely related to visual attention⁶⁹. Selective attention is often guided by expectation⁷⁰. For example, when searching for your lost keys, you will probably allocate attention to those locations where they are most likely to be found⁷¹. Superficially, the computational

goals of expectation and attention seem to be similar. Expectation facilitates the detection and recognition of features, locations or objects that are likely to be present in the visual environment. Likewise, selective attention facilitates perception by prioritizing sensory inputs according to their salience or relevance to current goals⁷². Accordingly, many experimenters have used probabilistic cues to direct attention to a spatial location where a stimulus is expected⁷³, and conversely expectations are often manipulated by varying the conditional occurrence of visual objects or features, relying on paradigms that resemble those used to investigate feature-based attention⁴⁵. Consensus has yet to be reached on how the terms ‘expectation’ and ‘attention’ should be used, and it remains unclear whether these concepts map neatly onto brain mechanisms that are computationally or neurophysiologically dissociable.

Nevertheless, it may be useful to distinguish manipulations of the probability of sensory events from manipulations of their relevance to a current task or goal. Labelling these manipulations as expectation and attention, respectively, allows us to distinguish the two concepts, because a stimulus can be conditionally probable or improbable, irrespective of whether it is relevant or irrelevant for behaviour⁶⁹. Indeed, several studies have observed neural modulations by expectation in humans and non-human primates during states of inattention⁷⁴, during sleep⁷⁵, anaesthesia⁷⁶ and even in patients experiencing disorders of consciousness⁴⁶. Thus, although priors frequently guide attention, attention is not a prerequisite for the biasing effects of expectation on neural processing.

How, then, might we best distinguish the computational mechanisms underlying expectation and attention? Under the predictive coding framework, one suggestion is that expectations encode predictions about a feature or its location (determining the precision of the prior distribution), whereas attention allows us to weight sensory information according to its relevance to the current decision (determining the precision of the error signals that control belief updating)^{77,78}. This distinction is supported by a simulation of predictive coding in which attention is modelled as enhancing the precision of prediction errors, which accounts for cue validity effects in the Posner task, and their neural concomitants in scalp EEG data⁷⁷. This distinction echoes the dichotomy introduced above concerning the sequential sampling framework, whereby expectations determine the origin of evidence accumulation (or prior belief) and attention controls the drift rate (or sensory gain). Indeed, longstanding psychophysical evidence indicates that probability cues bias participants to make one response over another, whereas relevance cues render them more sensitive to the attended feature or location⁷⁹. However, a more recent study has suggested that cues manipulating the probability and relevance of sensory signals may both increase the sensitivity of perceptual decisions, albeit in distinct ways. The effects of probability cues were strongest for weaker signals, and were best explained by an early boosting of the gain of the input signal. By contrast, relevance cues decreased noise at the decision stage, and this increased sensitivity most sharply for stronger signals⁸⁰.

Selective attention

The cognitive function by which information is selected for further processing on the basis of its salience or relevance to a current task or goal.

Related conceptualizations of attention and expectation have been put forward. One model proposes that attention diverts processing away from unexpected or unexplained portions of the visual signal, helping observers to ignore unwanted or irrelevant aspects of a visual scene, such as a contour that occludes a target object⁸¹. A closely related view suggests that attention boosts predictions (rather than their violation), making anticipated information more salient^{82,83}. In the predictive-coding framework, this would be equivalent to enhancing the top-down expectation signals that flow backwards through the processing hierarchy⁸⁴. A different model has been proposed that aims to reconcile predictive coding with ‘biased competition’ models of attention, but without optimization of precision⁷².

It remains unclear how attention and expectation interact. Thus far, only a handful of psychophysical and neuroscientific studies have attempted to address this question. For example, one study⁸⁵ manipulated spatial attention and expectation orthogonally. The authors found that expectation reduced the sensory responses in the absence of attention but that this pattern reversed in the presence of attention⁸⁵. One interpretation of this interaction is that attention reverses expectation suppression, for example, by increasing the gain of the error units⁷⁷. Jiang and colleagues⁸⁶ reasoned that if attention boosts the gain (or ‘precision’) of error signals, then neural pattern classifiers should be better able to distinguish expected from unexpected signals when stimuli are attended; but alternatively, if attention silences prediction errors, then activity patterns for expected and unexpected stimuli should become more similar. The authors found strong evidence for the idea that attention increases the gain of prediction errors in category-specific extrastriate regions. These studies notwithstanding, the issue is far from resolved, but it is fortunately receiving more attention from researchers.

Stimulus repetition and expectation

Visual signals are not only spatially but also temporally autocorrelated⁸⁷. This means that, on average, we can expect information in the visual world to remain stable (that is, to repeat) rather than to change (that is, to alternate). Expectation suppression might thus partly explain repetition suppression, the well-described attenuation of the neural response elicited by the second and subsequent presentation of a stimulus⁸⁸. Alternatively, repetition suppression might be fully explained by a low-level adaptation to stimulation mediated, for example, by ‘neuronal fatigue’ alone⁸⁹. To arbitrate between these views, one study⁴⁷ measured the attenuation of BOLD responses in the FFA to repeated faces in contexts where repetitions were either expected or unexpected. Expected repetitions elicited stronger repetition suppression, suggesting that the suppression can partly be explained by a reduction in visual prediction error⁹⁰ (FIG. 4c). This finding has since been replicated with faces^{91–93}, as well as simple shapes⁹⁴, auditory tones^{41,95} (FIG. 4d), voices⁹⁶ and somatosensory stimulation⁹⁷, although mixed findings for objects^{98–100} have raised questions about the generality of the effect.

MEG recordings suggest that repetition suppression and expectation suppression may have a distinct temporal profiles⁴¹ (FIG. 4e).

Predictive coding holds that segregated signals for expectations and their violation are computed at each processing stage. When stimuli are repeated several times in succession, one might thus expect the existence of unique neuronal subpopulations that show diminished responses (repetition suppression, as error signals are eliminated) and enhanced responses (repetition enhancement, as expectations build up). Averaging across fusiform voxels usually reveals face repetition suppression rather than face repetition enhancement, but it is possible that repetition enhancement was obscured by spatial smoothing and averaging of BOLD signals. Indeed, two recent studies reported segregated activity patterns exhibiting repetition suppression and repetition enhancement of BOLD signals in the FFA during viewing of repeated faces^{101,102}. Consistent with this finding, at the single-cell level, distinct neurons show preferences for matching versus mismatching visual information, with the latter cells outnumbering the former by a 2/1 ratio¹⁰³. This ratio has also been independently inferred from fMRI data modelling of expectation-related and prediction error-related population responses in the visual cortex⁴⁵.

A biological implementation of expectation

At first glance, predictive coding and sequential sampling models take quite different approaches to understanding perceptual choices. Rather than a feedforward readout and linear integration of noisy sensory information, predictive coding proposes a reciprocal exchange of top-down and bottom-up information — ‘explaining away’ sensory inputs — as well as nonlinear dynamics of integration^{104,105}. However, it is important to emphasize that under some assumptions, predictive coding and evidence accumulation can be shown to be formally equivalent¹⁰⁶. Moreover, more elaborate (and perhaps more biologically plausible) sequential sampling models have been proposed to allow information loss and inhibitory interactions between competing percepts that can collectively lead to complex, nonlinear attractor dynamics^{107,108}. For example, in the leaky competing accumulator (LCA) model, the drift rate is dynamically modulated by competition between alternatives racing towards a decision threshold. A currently favoured perceptual alternative receives less inhibition from its weaker competitors, boosting evidence for that choice yet further (this potentially runaway process is tempered by a gradual leak of evidence back to baseline). The LCA thus emulates two of the key features of predictive coding — competition between multiple alternatives and nonlinear dynamics — but retains the parsimony of the sequential sampling approach. Just as for the drift-diffusion model, prior beliefs can be incorporated as an offset at the starting point of integration for a more-favoured alternative, but the attractor dynamics ensure that this initial bias will translate into a more rapidly growing choice signal. In nonlinear models, thus, there is no clear distinction between a bias to the origin or drift of accumulation because one naturally provokes the other.

Nonlinear integration might be required to account for the distribution of reaction times observed in multi-alternative decision making¹⁰⁹, and perhaps also for the behaviour of neurons that integrate sensory signals, such as those in area LIP¹¹⁰. Moreover, nonlinear models might help us to understand how the three-way relationship between stimulus, neuronal activity and choices evolves across the decision epoch. Neuronal activity recorded from visual regions predicts an observer's perceptual choices, even when the sensory input is held constant^{111–116}. These positive-choice probabilities are naturally explained by 'causal' or feedforward models, such as the drift-diffusion model, in which both noise and signal are pooled and integrated to a threshold in decision circuits¹¹⁷. Empirically, however, the predictive relationship between sensory neurons and decisions grows across the course of a decision, even when choices and their neural underpinnings cease to depend on stimulus input after the early stages of the decision^{114,118}. This finding can only be explained if choice probabilities in the latter portion of the neural activity train are driven by endogenous factors unrelated to stimulus input, such as a heightened expectation for a particular percept^{3,114}. Indeed, even at rest, background patterns of neuronal activity might represent the average information over an animal's lifetime experience¹¹⁹, forming a natural prior that could be iteratively combined with samples of sensory information¹²⁰.

Expectation as a gain control mechanism

It is often proposed that mammalian sensory systems implement a form of Bayesian inference, optimally combining priors (expectations) and likelihoods (sensory input) to identify the most probable interpretation of the external world. However, Bayesian inference is computationally costly because it requires an almost unlimited number of possible hypotheses about the world to be considered at once. For example, if there is a knock on your front door, the prior probability that your visitor will be the President of Venezuela is very small, especially if you live in Oxford. Nevertheless, it remains possible, and so in a strictly Bayesian model, that probability would be computed alongside that of more plausible options, such as that the postman needs to deliver a parcel.

As described above, neural adaptation is one mechanism by which the brain deals with the scale and complexity of visual input¹²¹. All sensory systems adapt to background levels of stimulation because the gain of neural processing varies according to the context in which input occurs (a process known as adaptive gain control). For example, photoreceptors in the retina adapt to diurnal changes in illumination through simple biophysical mechanisms¹²². As we have seen in the early visual cortex, neurons are only weakly driven by uniform stimulation but respond vigorously to discrepancies between their classical receptive field and the surround, making them most sensitive to fluctuations in information relative to the average provided by the local context¹²³. In more complex systems, adaptive gain control has been observed in cells coding for economic value¹²⁴, in which rescaling of responses

in the orbitofrontal or parietal cortices may lead to preference reversals and other violations of axiomatic rationality^{125,126}.

Adaptation thus allows resources to be focused on only those alternatives that are expected, given the background information or context. Cheadle and colleagues¹²⁷ asked participants to integrate discrete cues that signalled the probability of reward given a rightwards or leftwards response. They found that cues that were expected (that is, cues that fell close to the mean information provided by previous cues) had more effect on subsequent choices than cues that were unexpected. Moreover, expected cues were associated with neurophysiological signatures of heightened gain in pupillometric and functional neuroimaging data. Their findings were captured by a computational model in which the gain of sensory processing adapted towards those features that were the most likely to occur. A related account has been proposed to account for pupillometric responses during a psychophysical detection task¹²⁸.

One mechanism for controlling the gain of sensory processing is to modulate the shape of neural tuning curves, either at the single-cell level or the population level. For example, neurons coding for expected information might become more sensitive, whereas those coding for unexpected information might show dampened responses — a pattern of influence similar to feature-similarity gain¹²⁹. This 'expectation as sharpening' theory predicts that expected stimuli should elicit reduced aggregate neural activity because fewer neurons are activated by a stimulus¹³⁰, but it also predicts that neuronal representations should be crisper and thus easier to decode at the population level using multivariate techniques. Consistent with this view, a recent study¹³¹ showed that when an auditory tone predicts the occurrence of an oriented grating, the expectation suppression in V1 is accompanied by heightened ability of multivariate classifiers to classify grating orientation (FIG. 4a). One interpretation of this pattern of activity is that when neurons that code for expected stimuli are pre-activated, they both inhibit units coding for the alternative hypothesis (via lateral inhibition) and suppress their own inputs (via local inhibition), leading overall to a sharper representation of expected information¹⁰⁴.

Conclusions and future directions

The visual system has evolved to rapidly identify features and objects in a complex and cluttered environment. Although the context in which visual input occurs can be distracting, it also allows us to form expectations about what is likely to occur. These expectations are combined with visual signals over time, via reciprocally interlinked top-down and bottom-up processes, to facilitate detection and recognition judgements. Neural systems also adapt to the background and context, processing expected information with heightened gain. As such, visual expectation interacts intimately with visual selective attention and adaptation.

Many questions remain unanswered. In particular, the mechanisms of visual expectation remain poorly characterized at the cellular level. A great deal has been

learned about how the responses of visual neurons are modulated by attention, but some of these studies have also varied the probability of occurrence of a target stimulus. We argue that disentangling the relationship between attention and expectation at the single-cell level might help to resolve current controversies over the computational mechanisms of attention. Another key challenge is to understand how the microcircuitry of the visual system allows top-down and bottom-up inputs to be segregated to generate both predictions and prediction errors¹³². One possibility is that laminar differences in cell types, connectivity, oscillations and neurochemistry might be key¹³². Invasive recordings using multiple concurrent laminar probes, as well as high-field imaging, which potentially allows for dissociable responses to be

identified at the laminar level, could be important tools for clarifying these mechanisms at the systems level^{133,134}. Another key outstanding question concerns the brain regions from which neural signals coding for expectations ultimately arise. Visual statistical learning depends on the integrity of medial temporal lobe structures^{135,136}, where activity patterns become more consistent as visual associations are formed¹³⁷. However, the striatum might also be important^{44,138}. Other studies have shown that contextual information about visual objects might activate retrosplenial and parahippocampal sites¹³⁹, and that orbitofrontal regions might participate in visual prediction^{140,141}. However, the ultimate origins of predictive neural signals in natural vision still remain unknown and form an important topic for future research.

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Competing interests statement

The authors declare no competing interests.