Prediction and Learning: Understanding Uncertainty

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Abstract

We build models of the world around us to guide perception and learning in the face of uncertainty. New evidence reveals a neurocomputational mechanism that links predictive processes across cognitive domains.

Main text

Psychologists and neuroscientists have suggested that we can think of many aspects of cognition as inference under uncertainty. In perception, scientists have stressed that the signals provided by our senses are often too ambiguous or noisy to fully determine the state of the extracranial world. Similarly, researchers interested in learning and decision making have emphasised that we live in environments where it can be difficult to use the present state of the world to determine what will happen in the future. A new study from Lawson *et al*.[1] reported in this issue of *Current Biology* reveals a key role for the neuromodulator noradrenaline in shaping predictive processes in both learning and perception.

In both domains, researchers have stressed the importance of forming and using predictive models to guide perception and decision. On these accounts, we use past experiences to build models of what will happen in the future and use these to guide how we perceive and learn. For example, in perceptual theories there is a growing consensus that observers use their expectations to bias perception in line with what is likely to be true[2,3]

(Figure 1). By selectively 'sharpening' expected sensory representations[4,5] we can generate perceptions that are — on average — more veridical, because the events that we expect are (by definition) more likely to occur[6,7]. In contrast, learning researchers have focused on the idea that our confidence in our predictive models should guide how much we learn from new experiences. If we are uncertain about the reliability of our predictions, we should be more willing to revise them when presented with novel information[8].

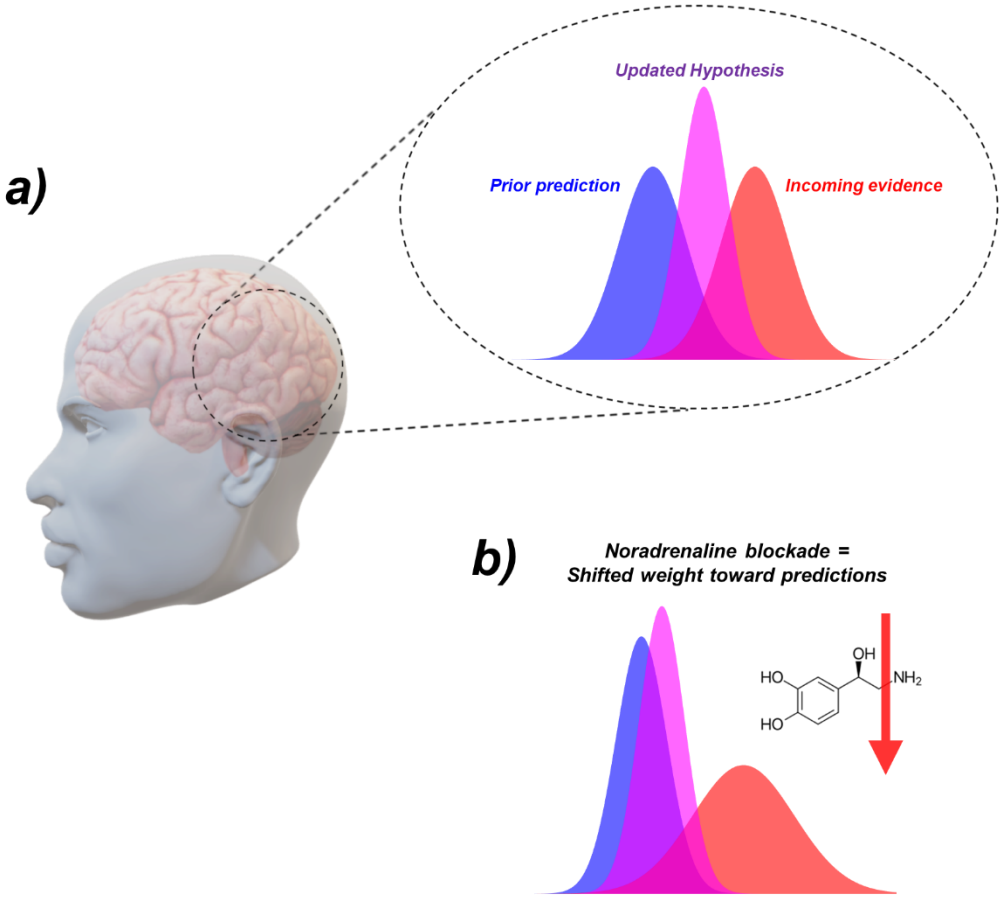

Figure 1. Manipulating the balance between top-down predictions and bottom-up evidence.

(A) Bayesian brain theories suggest that sensory systems generate hypotheses about the external world by combining prior predictions with incoming evidence[2,6,7]. (B) Recent results from Lawson *et al*.[1] suggest that antagonising noradrenaline (via propranolol) increases the relative weight given to predictions and reduces the relative weight given to incoming signals.

Research focusing on the role of uncertainty in prediction has suggested a key role for neuromodulators like noradrenaline. An influential idea suggests that noradrenergic circuits signal unexpected changes in the environment[9], reflecting (inversely) how confident we are that our current predictions will apply in the future. One hypothesis is that such signalling drives a form of 'network reset'[10], with noradrenaline enhancing the sensory gain afforded to incoming signals such that our old predictions are rapidly replaced with new ones better aligned to the current environment.

Several findings have supported the idea that noradrenergic circuits encode (un)certainty in our predictions. For example, unexpected changes in the environment lead to phasic changes in pupil size[11], which are in turn thought to reflect the activity of the locus coeruleus — the main noradrenergic nucleus of the brain[12]. However there has been little direct evidence that noradrenaline plays a causal role in controlling the weight we give to top-down predictions and bottom-up evidence. A new study from Lawson *et al*.[1] uses an elegant combination of drugs, experimental psychology and computational modelling to investigate this possibility.

In their task, participants made speeded perceptual decisions about whether a stimulus was a face or a house. Visual stimuli were preceded by auditory cues, which participants could use to furnish probabilistic expectations about the identity of an upcoming target. Typically, such tasks reveal that observers are faster to report stimuli that meet their expectations[2]. Lawson *et al*. investigated how expectations affect perceptual decisions in their task, and how any influences interact with propranolol — a common anxiolytic medication that blocks noradrenaline. This revealed that participants were indeed faster to make decisions when expected stimuli occurred, particularly when observed stimuli were noisy. Crucially, this effect was exaggerated under propranolol — suggesting the drug increased the weight participants afforded to top-down predictions.

If top-down predictions are indeed strengthened when noradrenaline is antagonised, it should also be the case that predictions are slower to update. The authors investigated this

possibility by reversing the predictive contingencies between auditory cues and visual outcomes at different points in the experiment, as well as manipulating whether these reversals occurred often (i.e. a volatile environment) or infrequently (i.e. a stable environment). Modelling decisions and reaction times with the hierarchical gaussian filter[13] revealed that propranolol impeded learning (i.e. lower ω_2), making observers slower to update their beliefs about which cues predicted which outcomes.

This combination of results is consistent with a view where noradrenergic signalling encodes our uncertainty about our predictions. Under this hypothesis, antagonising noradrenaline would artificially enhance an agent's confidence in their models of the world, increasing their reliance on their current expectations when making perceptual decisions and decreasing the rate at which these predictions are updated in the face of new evidence.

These results reveal an intriguing role for noradrenaline in gain modulation across perception and learning. This marries well with recent theoretical proposals suggesting that prediction, perception and learning are intimately related. For example, we have recently argued it is important to recognise these interdependencies given that what we predict shapes what we perceive, what we perceive shapes what we learn, and what we learn now determines what we will predict in the future[7,14]. While elegant experimental techniques have provided detailed insights into how catecholamines (including noradrenaline) modulate learning and beliefs about the stability of the environment[15], evidence that noradrenaline also alters perceptual prediction suggests it will be important for researchers to take account of how changes in learning are related to — and perhaps mediated by — modulations in what we perceive[7].

These results also bring into focus important questions about how neuromodulators like noradrenaline control the balance between predictions and evidence. There are at least two ways to explain Lawson *et al*.'s finding that observers rely more on top-down predictions when noradrenaline is suppressed. One possibility is that observers hold onto strong predictions because noradrenaline blockade has selectively disrupted signalling of surprise.

If noradrenaline plays a specific role in signalling unexpected changes[9,10], disrupting this mechanism could allow observers to hold onto existing predictions rather than revising them immediately when the environment changes — and such changes occur often in Lawson *et al*.'s task. However, a second possibility is that noradrenaline is not only involved in signalling unexpected environmental changes, but plays a more general role in setting the balance between top-down predictions and bottom-up evidence.

These possibilities could be disentangled by exploring whether similar interventions on the noradrenaline system enhance top-down perceptual predictions in more stable environments. If noradrenaline blockade leads to a specific disruption in surprise processing, such manipulations may have little effect in situations where participants rely on strong, over-learned predictions (e.g., the assumption that light comes from above[16]) where the stability of the environment means surprising errors are rare. In contrast, if noradrenaline blockade generally enhances top-down predictions and attenuates bottom-up evidence — irrespective of surprise — effects of expectation in these more stable environments should also be enhanced.

This puzzle also points to deep questions in existing models of perception and prediction. Bayesian models of perception typically suggest our uncertainty about the present state of our environment (*sensory uncertainty)* and uncertainty about what it will be like in the future (*model uncertainty*) are encoded in an opponent fashion (Figure 1): if we are very confident about incoming sensory signals we afford them relatively more weight than prior predictions, whereas if we are very confident in our predictions these are given more weight than evidence. Indeed, this effective 'zero-sum' weighting is central to the concept of 'precision-weighting' in predictive processing models of the brain[17,18], where assigning more weight to top-down predictions is functionally equivalent to reducing the weight on bottom-up evidence[19,20]. The approach introduced by Lawson *et al*. holds promise for interrogating this assumption and may help to reveal whether our brains do indeed rely on zero-sum estimates of uncertainty to weight bottom-up and top-down signals, or whether

uncertainty about our predictions and uncertainty about our sensations are represented independently.

In conclusion, Lawson *et al*. present compelling causal evidence that noradrenaline contributes to the strength and malleability of top-down predictions. These findings provide new insights into the neurocomputational mechanisms that underpin prediction in learning and perception and highlight exciting new puzzles for cognitive scientists to unpick in future work.

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