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Perceptual Prediction: Rapidly Making Sense of a Noisy World

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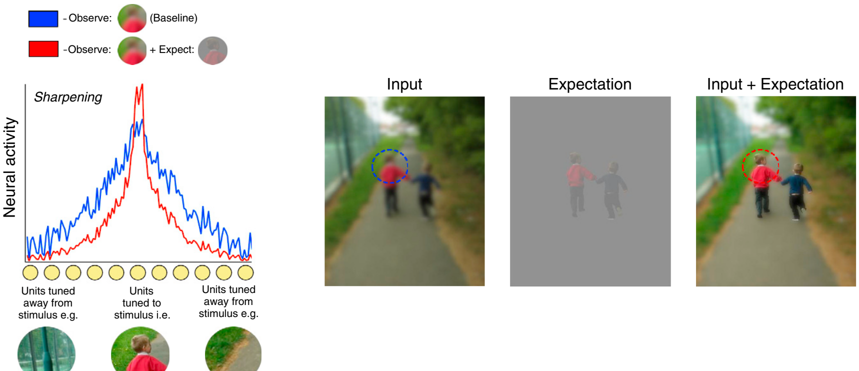
Prior knowledge shapes what we perceive. A new brain stimulation study suggests that this perceptual shaping is achieved by changes in sensory brain regions before the input arrives, with common mechanisms operating across different sensory areas.

Our brains have to make sense of the vast quantities of information constantly bombarding our senses. The information reaching our eyes, ears and other receptors changes rapidly across space and time, and the signals are imperfect [1]: for example, when we listen to a friend on the metro the sound of their voice is masked by the noise of the train. Our brains must rapidly generate a best guess about what we heard to guide our behaviour effectively — we will be a poor conversation partner if it takes us several seconds to work out what they said. A study by Gandolfo and Downing [2] reported in this issue of *Current Biology* shows how the brain can generate this best guess by sending predictive signals to brain regions involved in processing sensory input.

Work from the cognitive sciences across the last few decades has demonstrated that we likely use our expectations to help shape what we perceive. There are many statistical regularities within our environment and we can combine these with the sensory input to represent the likely state of the world. If our conversational partner is a fellow academic, it is more likely that they said ‘I love computers’ than ‘I love reviewers’, and biasing our perceptual experiences in line with these likelihoods will tend to increase their accuracy [1,3]. Biased perceptual decisions have been shown across a number of disciplines and with a number of methods. For example, we are faster to identify everyday household objects (for example loaves of bread), when they are preceded by observation of contexts in which they are typically seen (kitchen counters) [4], and we are more likely to report the presence of stimuli that are expected on the basis of arbitrary, probabilistically-paired cues [5]. Such biasing is also demonstrated through perceptual errors that occur when typical regularities are disrupted. For example, we report concave faces to have the more typical convex structure when shading cues are ambiguous [6], and that sensations last for a similar length of time to concurrently performed actions — likely because they typically last for comparable durations [7].

While cognitive scientists have reported for some time that perception is biased by our expectations, the precise mechanisms realising these influences have remained elusive. Indeed, some have even queried whether top-down knowledge really alters what we perceive at all or rather just the decisions we make about our experiences [8]. For example, producing slow actions may make us hallucinate that simultaneous events last for longer, because we typically experience slow actions to be accompanied by long sensations. Alternatively, this knowledge could just bias us to *report* that events have lasted for longer because we believe they should have done, while our perceptual experiences remain unchanged. We can



Current Biology

Figure 1. Combining noisy sensory input with our expectations is a powerful way to generate largely accurate representations of our environment efficiently.
Gandolfo and Downing [2] suggest that this is achieved by pre-activating sensory representations of expected stimuli, e.g., those of particular bodies within extrastriate body area, such that perception is biased towards what is expected and therefore more likely to be there.

disentangle these possibilities partly by using rigorous behavioural experiments that manipulate these processes [8] and constructing computational models of the decision process [5]. Neuroimaging methods have also been used to understand the underlying mechanisms, for example, examining pattern classification accuracy of sensory signals when sensations were expected or not [9–12]. These findings have prompted suggestions that expectations indeed influence perceptual experiences themselves via ‘pre-activation’ of sensory units tuned to expected events before the input is received [11]. This pre-activation is thought to lead to competitive interactions that inhibit units tuned to the unexpected, ‘turning up the volume’ (relative sensory gain) on expected inputs and thereby biasing perception towards what we expect (‘sharpening’ theories; Figure 1).

But it remains debated whether expectations really alter perception, partly because these changes in sensory brain areas may not in fact play a causal role in changing perception [13]. Gandolfo and Downing [2] addressed this question in a clever study using transcranial magnetic stimulation (TMS). In their task, participants made rapid judgements about observed bodies or visual scenes; for example, is this body slim? Stimuli were preceded by written cues to establish expectations about which particular stimulus would be shown; for example, ‘m’ predicted a male body. In line with previous work, the participants were faster and more accurate when their expectations were valid. More importantly, the authors applied TMS at the time of the cues — disrupting activity in either the extrastriate body area (EBA) or the occipital place area (OPA). They revealed a compelling double dissociation whereby disrupting activity in body-selective EBA abolished behavioural expectation effects for body stimuli but not scenes, and disrupting scene-selective OPA activity had the converse effect. Such a pattern provides convincing evidence that effects of expectations on perceptual decisions are indeed mediated by changes in specific sensory processing. It also provides evidence to support the idea that these modulations are realised through pre-activating units tuned to expected inputs before the sensory information even hits the receptors.

One particularly interesting feature of this new study [2] is the specific regions where effects are found. EBA and OPA are considered higher level sensory processing regions encoding the complex configurations of information that characterise bodies and scenes, respectively. Predictive sharpening effects have sometimes been observed predominantly in primary visual cortex [9,10], prompting suggestions that predictive influences are only realised through interactions at the earliest points in the cortical hierarchy. However, the predictive influence identified by Gandolfo and Downing [2] in these late visual brain areas suggests this is unlikely to be the case, raising the alternative possibility that previous effects have been confined to early processing regions because these areas are most sensitive to the stimuli used in these studies — gratings and edges [9] (see also [14]).

These findings suggest that, regardless of the particular sensory region, expectations may modulate processing in a similar way. Although EBA and OPA encode different kinds of visual information, influences of prediction appeared to be mediated through similar pre-activation processes. In other words, the same domain-general pre-activation mechanism may sharpen representations similarly in different domain-specific sensory regions. This finding concurs with recent results from our lab revealing that sensory predictions operate via common mechanisms across domains. In this instance, we demonstrated that the precise nature of the *predictive* (not *predicted*) information did not alter the nature of effects. Specifically, visual predictions made on the basis of action sharpened visual brain activity just like when the predictions are furnished by arbitrary sensory cues [12]. This finding in fact conflicted with previous reports [15] that action expectations have a distinct influence on perception, dampening, rather than sharpening, the processing of predicted inputs — it had been thought to be for this reason that we cannot tickle ourselves [16].

If predictive mechanisms work similarly across domains — regardless of the particular nature of the predictive or predicted information — then it seems logical that Gandolfo and Downing’s [2] findings would have implications for any domain where observers can rely on probabilistic knowledge. For example, as well as implications for action perception and normative sensory cognition, similar principles may explain findings from language [17] and social cognition [18] — with effects of expectations realised through pre-activation of relevant representations in different parts of the cortical hierarchy.

However, the idea that sensory-specific pre-activation drives our enhanced ability to identify expected events leaves open questions about the mechanisms that generate predictive dampening effects when these are found. Why do predictions sometimes attenuate rather than sharpen perception, for example, why can we not tickle ourselves? These findings of attenuated, rather than enhanced, processing of the expected are prominent in action control literatures but in fact are also found elsewhere [17,19]. Similar temporally-tuned methods to those employed by Gandolfo and Downing [2] may prove useful in disentangling the precise nature of mechanisms operating across the sensory hierarchy [20].

In conclusion, Gandolfo and Downing's [2] new work contributes to a lively debate about the role of prior knowledge in shaping what we perceive. Their findings provide compelling evidence that expectations alter perception through influences realised in specific sensory areas before the sensory events are presented, and contribute to an emerging view that a common set of domain-general principles may account for the effects of prediction across a host of disciplines.

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Evolution: The Flowering of Land Plant Evolution

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Two new studies that consider the timing of origin of angiosperms are poles apart in their estimates. However, their partisan molecular and palaeontological perspectives may hold the key to establishing a unified evolutionary timescale for flowering plants.

More than 90% of living land plants are angiosperms (flowering plants) and so it is difficult to conceive of a world without them. Angiosperms are not merely decorative, effecting incalculable ecosystem services, encompassing most commercial crop species while also serving as global climate engineers [1]. But there was a world before angiosperms, though no one can quite agree when it ended because of a long-standing controversy concerning the timing of origin of the living clade of (crown) angiosperms. For over a century, repeated sampling of the fossil record has failed to find evidence of crown-angiosperms before the Cretaceous, which began about 145 million years ago, yet almost from their introduction, molecular clock analyses have estimated a much more ancient origin, perhaps