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Predictions penetrate perception: Converging insights from brain, behaviour and disorder

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ABSTRACT

It is argued that during ongoing visual perception, the brain is generating top-down predictions to facilitate, guide and constrain the processing of incoming sensory input. Here we demonstrate that these predictions are drawn from a diverse range of cognitive processes, in order to generate the richest and most informative prediction signals. This is consistent with a central role for cognitive penetrability in visual perception. We review behavioural and mechanistic evidence that indicate a wide spectrum of domains—including object recognition, contextual associations, cognitive biases and affective state—that can directly influence visual perception. We combine these insights from the healthy brain with novel observations from neuropsychiatric disorders involving visual hallucinations, which highlight the consequences of imbalance between top-down signals and incoming sensory information. Together, these lines of evidence converge to indicate that predictive penetration, be it cognitive, social or emotional, should be considered a fundamental framework that supports visual perception.

1. Introduction

Visual perception is not a passive or exclusively stimulus-driven process. Instead, there is a proactive interplay between incoming stimuli and predictions based on internally generated models, which shapes our conscious perception of the world around us (Bar, 2004; Bullier, 2001; Engel, Fries, & Singer, 2001). This enables our perceptual system to harness a lifetime of experience with the world, leveraging our past to aid our interpretation of the present. Along these lines, a predictive coding framework for visual perception is well established, fitting with a broader general principle of the brain as a predictive machine (Clark, 2013; Dayan, Hinton, Neal, & Zemel, 1995; Friston, 2010). Echoed across perceptual modalities, motor outputs and learning systems, hierarchically organised top-down pathways convey information about what to expect based on

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our prior experience. These predictions are combined with incoming sensory information to sculpt the most likely interpretation of the world around us. Sparingly, only mismatches between the descending predictions and lower-level sensory information are carried forward in the form of prediction error signals, to be reconciled at higher levels of the processing hierarchy, where new hypotheses are generated to accommodate the incoming input (Friston, Stephan, Montague, & Dolan, 2014).

Predictive coding is both a biologically and computationally plausible description of information flow in the brain, yet the intimately related process of cognitive penetration in perception is hotly debated (Firestone & Scholl, 2015, in press; Macpherson, 2012; O'Callaghan, Kveraga, Shine, Adams, & Bar, in press; Raftopoulos, 2014; Stokes, 2013; Vetter & Newen, 2014; Zadra & Clore, 2011). Cognitive penetration entails that a myriad of information from other modalities can influence the earlier stages of the perceptual process. Access to a wide variety of information processing systems when generating predictions will ensure that the predictions will be rich and most effective for minimising global prediction error (Lupyan, 2015), emphasising a central role for cognitive penetration in visual perception.

The predictive nature of the visual processing system itself is apparent from the basic tenets of object perception, (Bar et al., 2006; Enns & Lleras, 2008), but there is less clarity regarding the extent to which other cognitive systems shape perception. Here we start by using object recognition to demonstrate the mechanisms of top-down influence on perception. We then extend this framework to show that beyond features intrinsic to an object itself, contextual factors, as well as other cognitive and affective processes, all converge to provide a source of top-down prediction that influences visual perception. We explore these patterns both in social and affective neuroscience, and then describe novel insights on how a failure of this system can manifest neuropsychiatric disorders such as visual hallucinations.

2. Object recognition

The premise for a predictive coding account of visual perception relies on descending neural pathways throughout the visual processing system (Angelucci et al., 2002; Bullier, 2001). This structure allows for feed-forward projections, originating in the primary visual cortex and ascending via dorsal and ventral streams, to be matched with reciprocal feedback connections (Felleman & Van Essen, 1991; Gilbert & Li, 2013; Salin & Bullier, 1995). Under this scheme, top-down predictions are generated at higher levels and compared with lower-level representations of sensory input, with any resultant mismatch coded as a prediction error (Clark, 2013; Friston, 2005b; Friston et al., 2014; Rao & Ballard, 1999). In the case of object recognition, the orbitofrontal cortex has emerged as a source of such top-down expectations (Bar et al., 2006).

Earlier work characterised the ascending dorsal and ventral visual pathways as dominated respectively by magnocellular and parvocellular cells (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982). The magnocellular (M) pathway carries achromatic, low spatial frequency information rapidly and is sensitive to high temporal frequencies, whereas the parvocellular (P) pathway transmits fine detail in the luminance channel, low spatial frequency information in the colour channel, has slower conduction velocities and can only process lower temporal frequencies (Maunsell, Nealey, & DePriest, 1990; Nowak & Bullier, 1997; Tootell, Switkes, Silverman, & Hamilton, 1988). Studies have since capitalised on the different properties of M and P pathways to reveal the time course and sources of top-down modulation of vision. Using low spatial frequency (LSF) stimuli to preferentially recruit M pathways, a combined approach of magnetoencephalography (MEG) functional magnetic resonance imaging (fMRI) revealed early activity was evident in the orbitofrontal cortex ~130 ms post stimulus presentation, well before object recognition-related activity peaks in the ventrotemporal cortex (Bar et al., 2006). A similar time window for top-down responses to categorising LSF scenes versus HSF scenes, where fMRI showed increased activity in the left prefrontal cortex and left middle temporal cortex, was associated with ERP activation in the 140–160 ms period (Peyrin et al., 2010). Although these time scales do not represent the earliest temporal component in visual processing (i.e., 0–100 ms), they are occurring at the short latency between 100 and 200 ms, suggesting that these top-down influences on object recognition modulate processing from reasonably early stages.

In order to provide a clearer picture of the spatiotemporal trajectory of top-down feedback, an fMRI study using dynamic causal modelling confirmed that early activation in the orbitofrontal cortex in response to M-biased stimuli then initiated top-down feedback to the fusiform gyrus (Kveraga, Boshyan, & Bar, 2007). P-biased stimuli in the same study were associated with a different connectivity pattern where only feedforward information flow increased between occipital cortex and fusiform gyrus. By comparison, orbitofrontal cortex activity only predicted M- and not P-biased stimuli, which resulted in faster recognition of M stimuli by ~100 ms. Similar evidence of early orbitofrontal activation preceding temporal lobe activity has been found when individuals make initial judgements about the coherence of degraded visual stimuli (Horr, Braun, & Volz, 2014) as well as during categorisation of face versus non-face images (Summerfield et al., 2006). These studies highlight the orbitofrontal cortex as an origin for top-down effects that can modulate processing in earlier visual processing areas.

The above findings support a predictive coding account of object recognition, whereby cursory visual information is sufficient to engage a memory store of information about the basic category of the object, used to generate the most likely prediction about the object's identity (Bar, 2003; Oliva & Torralba, 2007). Rapidly extracted predictions about the general category of an object is fed back to lower levels of the visual processing hierarchy to enable faster recognition by constraining the number of possible interpretations. Fitting with the predictive coding framework that we generate top-down hypotheses based on our knowledge of stored regularities in the world, another fMRI study revealed this orbitofrontal cortex facilitation