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Convergent evidence for top-down effects from the “predictive brain”

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Abstract

Modern conceptions of brain function consider the brain as a “predictive organ,” where learned regularities about the world are utilised to facilitate perception of incoming sensory input. Critically, this process hinges on a role for cognitive penetrability. We review a mechanism to explain this process and expand our previous proposals of cognitive penetrability in visual recognition to social vision and visual hallucinations.

A neural mechanism for cognitive penetrability in visual perception.

In their target article, Firestone & Scholl (F&S) readily dismiss the extensive presence of descending neural pathways (Angelucci et al. 2002; Bullier 2001), claiming they have no necessary implications for cognitive penetrability. Yet it is precisely this architecture of feedforward and feedback projections, beginning in the primary visual cortex, ascending through dorsal or ventral visual pathways, dominated respectively by magnocellular and parvocellular cells (Goodale & Milner 1992; Ungerleider & Mishkin 1982), and matched with reciprocal feedback connections (Felleman & Van Essen 1991; Salin & Bullier 1995), that provides the starting point for evidence in favour of top-down effects on visual perception.

Numerous studies capitalised on inherent differences in the speed and content of magnocellular (M) versus parvocellular (P) processing to reveal their role in top-down effects (Panichello et al. 2012). Early work using functional magnetic resonance imaging (fMRI) suggested that formation of top-down expectations, signalled by a gradually

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increasing ventrotemporal lobe activity, facilitated the recognition of previously unseen objects (Bar et al. 2001). In subsequent studies using both intact line drawings and achromatic, low spatial frequency (LSF) stimuli (which preferentially recruit M pathways), early activity was evident in the orbitofrontal cortex (OFC) ~130 ms after stimulus presentation, well before object recognition-related activity peaks in the ventrotemporal cortex (Bar et al. 2006). An fMRI study using dynamic causal modelling later confirmed that M-biased stimuli specifically activated a pathway from the occipital cortex to OFC, which then initiated top-down feedback to the fusiform gyrus. This connectivity pattern was different from that evoked by stimuli activating the P pathway, where only feedforward flow increased between the occipital cortex and fusiform gyrus (Kveraga et al. 2007). OFC activity predicted recognition of M, but not P, stimuli, and resulted in faster recognition of M stimuli by ~100 ms. Another fMRI study showed that this OFC facilitation of object recognition was triggered for meaningful LSF images exclusively: Only meaningful images, but not meaningless images (from which predictions could not be generated), revealed increased functional connectivity between the lateral OFC and ventral visual pathway (Chaumon et al. 2013). We argue not only that these results demonstrate the importance of descending neural pathways, which F&S do not dispute (cf. sect. 2.2), but that these recurrent connections penetrate bottom-up perception and facilitate perception via feedback of activated information from the OFC.

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This top-down activity does not merely reflect recognition or “back-end” memory-based processes, as F&S suggest are commonly conflated with top-down effects. Instead, the rapid onset of OFC activation and subsequent coupling with visual cortical regions indicate that these top-down processes affect perception proper, which we suggest occurs in the form of predictions that constrain the ongoing perceptual process. These predictions categorise ambiguous visual input into a narrow set of most probable alternatives based on all available information. As a richly connected association region, receiving inputs from sensory, visceral and limbic modalities, the OFC is ideally situated to integrate crossmodal information and generate expectations based on previous experience that can be compared with incoming sensory input. Predictive information from the OFC is then back-propagated to inferior temporal regions and integrated with high spatial frequency information. Thus, by constraining the number of possible interpretations, the OFC provides a signal that guides continued, low-level visual processing, resulting in a refined visual percept that is identified faster (Trapp & Bar 2015).

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Another aspect of this top-down guidance process that can penetrate bottom-up visual perceptual processing involves constraints imposed by the stimulus context. In the model that emerged from these data, “gist” information is extracted from LSFs in the visual input, and predictions are generated about the most probable interpretation of the input, given the current context (Bar 2004). When bottom-up visual input is ambiguous, the same object can be perceived as a hair dryer or a drill, depending on whether it appears in a bathroom or a workshop context (e.g. Bar 2004, Box 1). A network sensitive to contextual information, which also includes the parahippocampal, retrosplenial, and medial orbitofrontal cortices (Aminoff et al. 2007; Bar & Aminoff 2003), has been implicated in computing this context signal. Crucially, this process is not simply influencing better guesswork. Using magnetoencephalography and phase synchrony analyses, these top-down contextual

influences are shown to occur during the formation stages of a visual percept, extending all the way back to early visual cortex (Kveraga et al. 2011).

The emerging picture from this work suggests that ongoing visual perception is directly and rapidly influenced by previously learnt information about the world. This is undoubtedly a highly adaptive mechanism, promoting more efficient processing amidst the barrage of complex visual input that our brains receive. In the next section, we extend this model by incorporating ecologically valid examples of how top-down effects on visual perception facilitate complex human interactions, and the ramifications when the delicate balance between prediction and sensory input is lost in clinical disorders.

Cognitive penetrability in broader contexts – visual hallucinations and social vision.

Top-down influences on visual perception are also observable in clinical disorders that manifest visual hallucinations, including schizophrenia, psychosis, and Parkinson's disease. Most strikingly, the perceptual content of visual hallucinations can be determined by autobiographical memories; familiar people or animals are a common theme (Barnes & David 2001). Frequency and severity of visual hallucinations is exacerbated by mood and physiological states (e.g. stress, depression, and fatigue), with mood also playing an important role in determining the content of hallucinations (e.g., when the image of a deceased spouse is perceived during a period of bereavement) (Waters et al. 2014). Such phenomenological enquiry into visual hallucinations suggests their content is influenced in a top-down manner, by stored memories and current emotional state. Anecdotal report is mirrored by experimental confirmation that the psychosis spectrum is associated with overreliance on prior knowledge, or predictive processing, when interpreting ambiguous visual stimuli (Teufel et al. 2015). Together, these mechanisms are consistent with a framework in which top-down influences tend to dominate visual processing in hallucinations. Important for theories of cognitive penetrability, visual hallucinations typically involve a hallucinated object being perceived as embedded within the actual scenery, such that the hallucination is thoroughly integrated with sensory input (Macpherson 2015). Existing neural frameworks for visual hallucinations account for an imbalance between bottom-up sensory information and top-down signals. These frameworks implicate overactivity in regions supplying top-down information during normal visual perception, including the medial temporal and prefrontal sites in the model outlined above. Abnormal activity in these regions, and in their connectivity with the visual cortex, plays a causative role in creating the hallucinatory percepts that effectively hijack visual perception (Shine et al. 2014). Electrical stimulation studies targeting these regions independently confirm that abnormal activity in temporal lobe and midline areas is capable of generating complex visual hallucinations (Selimbeyoglu & Parvizi 2010).

Visual information conveying social cues is some of the subtlest, yet richest, perceptual input we receive – consider the abundance of information delivered in a sidelong glance or a furrowed brow. Top-down influences allowing us to recognise patterns in our social environment and interpret them rapidly are a cornerstone of adaptive social behaviour (de

Gelder & Tamietto 2011). Available evidence suggests that social visual processing leverages precisely the same neural mechanism described above for object and scene recognition. However, because of typically greater ambiguity in social cues, social vision must rely on top-down expectations to an even greater extent than object recognition. Social cues, including eye gaze, gender, culture, and race are found to directly influence the perception and neural response to facial emotion (Adams & Kleck 2005; Adams et al. 2003; 2015) and exert increasing influence with increasing ambiguity in the given expression (Graham & LaBar 2012). Critically, these effects are also modulated by individual differences such as trait anxiety and progesterone levels in perceptual tasks (Conway et al. 2007; Fox et al. 2007) and in amygdala response to threat cues (Ewbank et al. 2010). Dovetailing with the model outlined above, fusiform cortex activation is found to track closely with objective gradations between morphed male and female faces, whereas OFC responses track with categorical perceptions of face gender (Freeman et al. 2010). As in object recognition, OFC may be categorising continuously varying social stimuli into a limited set of alternative interpretations. Social vision therefore provides an important example of cognitive penetrability in visual perception that utilises stored memories and innate templates to makes sense of perceptual input.

Conclusion.

The convergent experimental and ecological evidence we have outlined suggests a visual processing system profoundly influenced by top-down effects. The model we describe fits with a “predictive brain” harnessing previous experience to hone sensory perception. In the face of evidence reviewed here, it seems difficult to categorically argue that cognitive penetrability in visual perception is yet to be convincingly demonstrated.

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