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Hallucinations as Top-Down Effects on Perception

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ABSTRACT

The problem of whether and how information is integrated across hierarchical brain networks embodies a fundamental tension in contemporary cognitive neuroscience, and by extension, cognitive neuropsychiatry. Indeed, the penetrability of perceptual processes in a "top-down" manner by higher-level cognition—a natural extension of hierarchical models of perception—may contradict a strictly modular view of mental organization. Furthermore, some in the cognitive science community have challenged cognitive penetration as an unlikely, if not impossible, process. We review the evidence for and against top-down influences in perception, informed by a predictive coding model of perception and drawing heavily on the literature of computational neuroimaging. We extend these findings to propose a way in which these processes may be altered in mental illness. We propose that hallucinations—perceptions without stimulus—can be understood as top-down effects on perception, mediated by inappropriate perceptual priors.

Keywords: Connectivity, Hallucinations, Neuroimaging, Neuropsychology, Predictive coding, Psychosis, Modularity

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Imagine you are walking home on a warm, early summer night. The sights and sounds that greet you are familiar—the bark of your neighbor's dog, the old oak tree on the corner, the echo of your footsteps as you get closer to your destination. Now imagine you are walking the same route after watching a scary movie. The same things might now seem strange and menacing to you. The dog's bark might seem like a growl; the oak tree's shadows may seem more prominent; those echoed footsteps might sound louder—or maybe they might not seem to be your own. Your aroused state makes you search for hidden threats, and your beliefs guide where you search (1). Could your fear even lead you to hallucinate footsteps when there are none? We consider these questions of how cognition alters perception, in light of recent advances in computational psychiatry.

Present-day cognitive scientists have argued that cognition does not influence perception (2). However, work in computational neuroscience calls this claim into question. We will argue that hallucinations, too, challenge strict, encapsulated modularity. Instead, they indicate penetrability of perception by cognition. We will illustrate these claims with phenomenology as well as neuro-computational work.

MODULES AND THE MIND

In *The Modularity of Mind* (1983), Jerry Fodor sketched a blueprint of mental architecture composed of modules—systems that process a single specific kind of information (3). For example, the early vision module takes in ambient light and outputs color representations. Fodor never gave a specific definition of a module (nor have other modularists), which makes the theory difficult to falsify. Twyman and Newcombe write: "Given this lack of agreed-upon definition, the modularity position becomes analogous to the Hydra, the many-headed monster that Heracles found difficult to combat because there were too many heads to take on simultaneously, and, worse, because other heads grew while he addressed a specific one" (4). Ultracognitive neuropsychologists even claim to shun brain localization, calling it mere hardware and irrelevant to the software in which they are interested (5). However, even the most ardent ultracognitivists use some lesion location information in rendering their arguments (6).

A strictly modular approach focuses on functional segregation, with brain regions responsible for discrete mental faculties that can be damaged in isolation (7). Such an approach eschews functional integration, which posits that complex mental functions are based on interactions among distributed regions (7). Human lesion cases also support integration (8–10). We appeal to functional and effective connectivity data for insights into integration. We view this work via a model of mind and brain that itself challenges encapsulated modularity—namely, predictive coding (11).

PREDICTIVE PERCEPTION IMPLIES COGNITIVE PENETRATION

An encapsulated perceptual system, kept separate from the influence of beliefs, could have the advantage of keeping our beliefs grounded in the truth offered by our senses (12). However, a cognitively penetrable perceptual apparatus may be equally adaptive, despite misperceiving and misbelieving,

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as long as the resulting behavior is adaptive (13,14). Hume (15) and Helmholtz (16) appreciated this: we perceive what would need to be present for our sensations to make sense. To solve this inverse problem, the brain uses an internal generative model of its environment to infer what it is sensing (16), combining feed-forward "bottom-up" information from sensory organs with feedback or "top-down" predictions from higher-level regions to compute precision-weighted prediction errors that guide formation of an optimal estimation of the surroundings (17–20). Combining top-down expectation and bottom-up input to explain perception has a rich history. McClelland and Rumelhart (21,22) proposed early models with this motif. Rao and Ballard (23) added neural data and Bayes theorem. Maia and Cleeremans (24) proposed that perception solves a "global constraint satisfaction" problem via the interplay between current top-down prefrontal cortical modulation and prior knowledge through learned synaptic connections across a hierarchy. Friston (25,26) first described how these mechanisms may be generalized to a broad model of brain function in terms of predictive coding.

Contrary to encapsulated modularity, some studies claim that early visual processing (i.e., not "post-perceptual processing") is influenced by nonperceptual information (27–30). For example, semantic priming increases the speed and accuracy of detection by minimizing prediction error (28). Behavioral and neurophysiological evidence shows prediction error signals generated in early visual regions in response to violations of semantic expectation (31,32). Word contexts result in ambiguous shapes being perceived as the missing letters that complete a word (33,34). Semantic categories including letters and animals improve accuracy and response times in orientation identification (28,35). Audiovisual integration induces response changes in primary sensory cortices, such that auditory stimuli engage V1 and visual stimuli activate A1 (36). These activations evolve via prediction error-driven learning (36). These phenomena challenge the informational encapsulation of perception (11).

THE BURDEN OF PROOF: ESTABLISHING TOP-DOWN INFLUENCES IN PERCEPTION

Studies that comprise the so-called New Look movement, purporting to demonstrate effects of language and culture on perception, have recently come under scrutiny. Firestone and Scholl (2) asserted such studies may be plagued by confounds that can be avoided by following these guidelines: 1) disentangle perceptual from decisional processes; 2) dissociate reaction time effects from primary perceptual changes; 3) avoid demand characteristics; 4) ensure adequate low-level stimulus control; and 5) guarantee equal attentional allocation across conditions.

These suggestions address issues inherent to tasks in which perception guides a behavioral decision. However, Bayesian formulations do not accept such separation (37). Signal detection theory appears to sharply distinguish sensation from decision. However, it, too, allows cognition to influence perception (38). Top-down processes can even alter the mechanical properties of sensory organs (39) by altering the signal-to-noise ratio (40). As we will argue in the following sections, top-down influences may be clearest when sensory input is completely absent: when experiences are hallucinated.

HALLUCINATIONS AS EXAMPLES OF TOP-DOWN PENETRATION

Hallucinations (41) can have contents consistent with one's affective state (42). When people are depressed, hallucinations can contain themes such as guilt and disease. Those experienced during mania may center around extraordinary powers (43). Changes in the content of hallucinations can be wrought by experimental mood manipulations (44). Thus, affect may penetrate perception. However, auditory-verbal hallucinations (AVHs) represent a derangement of normal function. Perhaps perception is normally impenetrable.

The existence of "nonclinical voice-hearers"—who have auditory hallucinations but do not reach clinical criteria for a psychotic disorder—argues against this hypothesis. Hallucinations of a loved one are common after bereavement (45–47). They are typically comforting and do not impair functioning (45–47); thus, hallucinations may not be abnormal per se. Nonclinical hallucinations also occur in the general population (48–52). Estimates of their prevalence are as high as 28% (53), and only 25% of those meet the diagnostic criteria for a psychotic disorder (54). Thus, hallucinations may best be described as an extreme of normal functioning (48) rather than a failure of modularity.

Are hallucinations top-down processes? In a recent investigation (55), prior knowledge of a visual scene conferred an advantage in recognizing a degraded version of that image. Patients at risk for psychosis were particularly susceptible to this advantage. A bias toward top-down information is the basis for "sensory conditioning" (56–60), wherein a visual stimulus is established as a predictor of a difficult-to-detect auditory stimulus and participants begin to report auditory stimuli that were not presented on the basis of the visual cue. This effect is amplified in individuals who hallucinate (57). Experiences of uncertainty can increase top-down effects. When a participant's sense of control over the environment is intentionally decreased (with spurious feedback), they tend toward illusory pattern perception, seeing nonexistent signal in noise and detecting illusory trends in the stock market (61).

The guidelines proffered by Firestone and Scholl (2) may serve as a useful roadmap for future studies of perceptual decision-making tasks. However, studying the penetrability of perception by way of hallucinatory experiences may circumvent these pitfalls. Participants report spontaneous, vivid experiences rich with sensory information that are unlikely to result from attentional biases. Neuroimaging data may likewise circumvent some critiques. We now try to integrate our understanding of hallucinations with notions of neural modularity and connectivity.

BRAIN LESIONS, MODULARITY, CONNECTIVITY, AND HALLUCINATIONS

We propose that interregional effects mediate the penetration of perception by cognition. Some have discussed these top-down effects in terms of attention (2). Predictive coding theory conceives of attention in terms of the precision of priors and of

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