Target article: **Firestone and Scholl**

Word count abstract:
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Title: Hallucinations and mental imagery demonstrate 'top-down' effects on visual perception

Authors: Piers D. L. Howe, Olivia L. Carter

Institution: University of Melbourne

Address: School of Psychological Sciences, The University of Melbourne, Victoria 3010, Australia

Tel: +61 3 8344 6287 (PH)

Email addresses:
PH: pdhowe@unimelb.edu.au
OC: ocarter@unimelb.edu.au

Home pages:
PH: http://psych.unimelb.edu.au/people/piers-howe
OC: http://psych.unimelb.edu.au/people/olivia-carter

Abstract (60 words max)
In this commentary we present two examples where perception is not only influenced by, but in fact driven by, top-down effects: hallucinations and mental imagery. Crucially, both examples avoid all six of the potential confounds Firestone and Scholl (2014) raised as arguments against previous studies claiming to demonstrate the influence of top-down effects on perception.

Main text
In the target article Firestone and Scholl make the bold claim that higher-level cognition does not affect perception. They acknowledge that there have been a very large number of experiments that would seem to contradict them but argue that all this previous work fell foul of at least one of six potential confounds. They challenged the academic community to find evidence for the effects of top-down cognition on perception that does not suffer from any of these potential confounds.

Hallucinations are one example that clearly meets this challenge. In psychotic disorders such as schizophrenia, hallucinations are most commonly reported in the auditory domain (e.g. hearing voices). However, pure visual hallucinations are also possible and are associated with hyperconnectivity between the

amygdala and the visual cortex (Ford et al, 2015), underscoring the role of top-down feedback in their formation. There is also a range of natural and artificial compounds known to cause visual hallucinations when consumed. These drugs frequently induce vivid geometric kaleidoscope-type patterns when the eyes are closed. Depending on the specific drug and dose they can also lead to pure hallucinations involving creatures and scenes (Vollenweider, 2001). Such drug-induced hallucinations are further demonstrations of top-down effects on perception. They are impossible to explain or conceptualise in terms of changes occurring within the bottom-up flow of external sensory information through the visual hierarchy.

Although it could be argued that such hallucinations should be considered an anomaly independent of normal cognitive processes, other forms of hallucination are harder to dismiss. About 10-30% of individuals who suffer from a severe visual impairment, such as glaucoma, experience Charles Bonnet (CB) Syndrome (Vukicevic & Fitzmauric, 2008; Schultz et al., 1996). These individuals typically have no other neurological or psychiatric conditions yet they frequently experience hallucinations. It is not that CB sufferers merely think or sense the hallucinations, rather the hallucinations appear so realistic that they are sometimes mistaken for reality (Schultz et al., 1996). In addition, these hallucinations will often interact with the participant's visual perception of the external world. For example, a hallucinated figure may obscure part of the visual scene that would otherwise be visible to the observer, thereby preventing the observer from seeing it – a clear example of top-down cognition influencing stimulus-based visual perception.

Mental imagery (i.e. visualisation) is a further example of where perception is obviously affected by top-down cognition. For some people, their mental images are exceptionally vivid, almost as vivid as visual perception (Pearson et al., 2011). As with hallucinations, these mental representations are pictorial. People actually see the mental images, as opposed to merely being aware of them (Kosslyn, Behrmann & Jeannerod, 1995).

Both hallucinations and mental imagery activate the visual cortex in a very similar way to that of normal visual perception, which helps explain why people describe hallucinations and mental imagery as true perceptual experiences. While hallucinations typically activate higher cortical areas (ffyche et al, 1998; Vollenweider, 2001), mental imagery is able to additionally activate the primary visual cortex (Albers et al., 2013; Slotnick, Thompson & Kosslyn, 2005; Stokes et al. 2009). The BOLD fMRI activation caused by mental imagery is so similar to that generated by observed visual stimuli, that a model based on tuning to low-level visual features (e.g., spatial frequency and orientation) that was trained on the BOLD fMRI activity generated when participants observed real images was able to determine which of those images the participants were subsequently visualising solely from the BOLD fMRI activity generated during these visualisations (Naselaris et al., 2015). Further, this low-level coupling between mental imagery and visual perception is unlikely to be epiphenomenal as magnetic pulses delivered to the primary visual cortex disrupted both mental imagery and visual perception to a similar extent (Blasel & Salama, 1986).

Hallucinations and mental imagery demonstrate that top-down cognitive and emotional processes can affect perception in a manner that avoids all six of the potential confounds raised by Firestone and School (2015). There is no doubt that perception can be altered depending on which locations, features or objects in the external world the observer attends to (Collins & Olson, 2014; Vetter & Newen, 2014). The fact that hallucinations and visual imagery are not driven by bottom-up stimuli and are often unconstrained to specific locations in visual space, makes it difficult to conceptualize how such phenomena could be explained by such peripheral attention effects (confound 5) or indeed by low-level differences in the visual input (confound 4). Furthermore as hallucinations and mental imagery are clearly perceptual they also avoid confound 2 (perception versus judgment) and confound 6 (memory and recognition). Additionally, they avoid the El Greco fallacy (confound 1) and cannot be attributed to demand and response bias (confound 3). As such hallucinations and visual imagery avoid all the potential confounds raised by Firestone and Scholl.

In conclusion, it is clear that top-down processes can affect perception in a variety of ways. In clinical or drug-induced psychosis a person's visual experience can be generated independent of bottom-up stimulation. In the case of mental imagery, percepts can be generated by directing top-down attention to internal mental states and representations. Finally, while CB hallucinations appear to be beyond voluntary cognitive control (Schultz & Melzack, 1991), they are clearly also caused by top-down processes. Moreover, these hallucinations can interact with visual perception, thereby providing a clear demonstration of a top-down effect influencing stimulus-based visual perception. These examples show that top-down cognitive processes are not only able to penetrate visual perceptions, but they can also cause them.

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