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When attended and conscious perception deactivates fronto-parietal regions

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ABSTRACT

The finding of increased fronto-parietal activity during conscious and attended perception forms a key basis for theories of consciousness and attention. However, this finding comes largely from studies that required explicit detection of events in a way that made detection the goal of the ongoing task. This is an important confound because goal completion itself elicits fronto-parietal activity. In everyday life attended and conscious perception is instrumental in achieving our goals but rarely a goal in itself. Here we examined whether conscious perception that was instrumental to participants' current goals, but not a goal in itself, elicited increased fronto-parietal activity. In Experiments 1 and 2 participants attended to a stream of letters (1 per second) to detect occasional targets in their midst. We found that consciousness of, and attention to, these highly visible non-targets events deactivated fronto-parietal regions. In Experiment 3 participants heard a loud auditory cue that had to be retained in memory for up to 9 sec before being used to select the correct rule for completing the goal. No increased fronto-parietal activity was observed even for such salient, attended and remembered event. In contrast, robust fronto-parietal activation was observed across all the experiments for goal completion events. The results indicate that increased fronto-parietal activity is not a necessary correlate of conscious and attended perception. We speculate that fronto-parietal deactivation during non-target events may be related to the suppression of potential interference from salient, conscious, but non-goal stimuli.

1. Introduction

Certain perceptions have a special status. Not only do stimuli induce activity in our neural systems, we are also aware that we have perceived them. One tractable first stage within a scientific approach to subjective awareness is to identify neural correlates of consciousness (NCC), neural concomitants that correlate only with conscious awareness (Baars, 1993; Crick, 1995; Lau and Rosenthal, 2011; Tononi and Koch, 2008). NCC studies typically take advantage of situations in which the sensory aspects of the environment remain constant but participants are sometimes consciously aware of a stimulus and sometimes not. Examples include

Abbreviation: FP, Frontal and/or Parietal; BR, Binocular Rivalry; NCC, Neural Correlate of Consciousness; IFS, Inferior Frontal Sulcus; IPS, Intra Parietal Sulcus; AI, Anterior Insula and Frontal operculum; APFC, Anterior Prefrontal Cortex; ACC, Anterior Cingulate Cortex; pre-SMA, Presupplementary Motor Area.

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brief masked visual presentations close to the threshold for detection (e.g., Dehaene & Changeux, 2011; Lau & Passingham, 2007) and binocular rivalry (BR) paradigms in which, when separate images are presented to each eye, one dominates awareness at any given moment (Knapen et al., 2011; Lumer, Friston & Rees, 1998; Wheatstone, 1838). In the former, increased frontal and/or parietal (fronto-parietal, FP) activity has been reported for conscious detection versus unconscious trials and, in the latter, for switches in awareness (for reviews see Bisenius et al., 2015; Dehaene and Changeux, 2011; Rees, 2007). Such findings are attractive because they suggest possible mechanisms for consciousness, e.g., consciousness of the percept arises from higher level re-representations in FP regions of first order perceptual states in sensory cortices (Lau and Rosenthal, 2011); or that it arises from the global neuro-cognitive broadcast of local perceptual information (Baars et al., 2013); or that it arises from a maximally differentiated and widespread activity in an integrated network of brain regions (Koch et al., 2016). For other views dependent on such findings see Engel and Singer (2001), Seth and Baars (2005), Dehaene and Changeux (2011) and Bor and Seth (2012).

However, it has increasingly become apparent that past studies investigating NCC suffer from many confounds (see also Aru et al., 2012; de Graaf et al., 2012). The requirement to detect difficult-to-perceive and ambiguous stimuli, and report awareness has a high task demand and requires meta-cognitive judgment (see Tsuchiya et al., 2015 for a review). Both of these have been linked to increased FP activity (Crittenden and Duncan, 2014; Fleming and Dolan, 2012). Knapen et al. (2011) suggested that increased FP activity during BR switches relative to activity during the passive viewing of similar transitions, was related to the longer duration and hence greater cognitive demands of BR switches. Frassle et al. (2014) suggested that part of increased FP activity during BR switches may stem from the requirement to report these changes. Specifically, such activity decreased (but was not eliminated) when switches were inferred from optokinetic nystagmus rather than self-report. Nevertheless, these studies could not adjudicate if any frontal and/or parietal activity is necessary for conscious perception (see also Blake et al., 2014).

A fundamental confound that we consider here is that participants in past studies were to explicitly detect difficult-to-perceive sensory events (e.g., masked stimuli, changes in percept during metastable perception etc.): Detection and report was their goal. Goal completion brings with it enormous changes in cognitive control and organization as well as motivational and emotional responses, and is linked with widespread FP activity (e.g., Farooqui et al., 2012; Kruglanski & Kopetz, 2009). Indeed, unattended and task-irrelevant stimuli presented whilst participants focused elsewhere on a concurrent task elicit activity limited to occipital (Pitts et al., 2014; Tse et al., 2005) or occipital and parietal regions (Scholte et al., 2006). However, the nature of awareness of such unattended and task irrelevant stimuli would be unclear (e.g., Overgaard & Fazekas, 2016). Moreover, any fronto-parietal activity elicited by them is likely to be very small, and hence difficult to discern in the context an ongoing task that itself elicits such activity. This makes the null result of these studies difficult to interpret.

Unlike these studies here we looked for activity elicited by easy to perceive, unambiguously conscious, attended, and task-relevant stimuli where, critically, their detection did not complete the participant's current goal. Most conscious perception in everyday life involves easily perceived sensory events that are attended and task relevant, and which are instrumental to achieving a goal, but such perception is not a goal in itself. In addition we are rarely asked to make explicit metacognitive judgments about our awareness. If you are searching through a pile of journal articles to find a particular paper, for example, you attend to other papers (unlike other parts of your desk) and scan their titles but this awareness does not constitute attainment of your current goal. Would awareness of these task relevant, attended, conscious but non-goal stimuli be associated with increased FP activity?

Relatedly, some of the above issues also confound the purported relation between increased FP activity and attention. In the paper search example, each article must be sequentially attended to achieve the goal. It has been proposed that while all sensations impinging our senses reach early sensory cortices, attention acts to amplify and broadcast representation beyond these regions into FP areas (e.g., Dehaene et al., 2006; Duncan, 2006; Miller and Cohen, 2001). However, evidence supportive of this comes, again, largely from paradigms in which attention and goal are closely aligned (e.g., targets during visual search; Corbetta & Shulman, 2002; Dehaene et al., 2006; Duncan, 2006). In contrast, many goals require attention to objects and spaces that are instrumental to their completion but which do not constitute completion. Neural responses – and specifically FP responses – to such attended events that do not constitute goal attainment are unclear.

There are, however, some hints. Shulman et al. (2003, 2007) asked participants to view rapid sequences of digits (50 msec/presentation with an average gap of 72 msec in between presentations) for the occurrence of letter targets. As expected, target detection was accompanied by very widespread FP activity. Non-targets produced mixed findings with, deactivation in some FP regions (e.g., middle frontal gyrus, inferior parietal regions) accompanied by increased activation in other dorsal frontal, parietal regions, and the anterior insula. While this study suggested a categorical difference between attended events based on whether they completed a goal, including FP deactivation for attended but non-goal events, it remained unclear if the increased FP activity also seen for this condition reflected a) the source of top-down attentional focus, b) a consequence of conscious perception or c) resulted from effort/task difficulty involved in discriminating fleeting percepts.

Here, in the first two experiments of the current study we used a similar task to Shulman et al. (2003). Unlike that task however, perceptual events were presented for longer intervals such that they were unambiguously conscious and had to be attended with no requirement for highly-paced, effortful search. In each trial of both experiments participants were asked to monitor a stream of highly visible 1-per-s letters for the occurrence of three pre-designated target stimuli also presented for 1 sec and in the same font/color as the non-targets, within the stream (specific digits in Experiment 1, specific letters in Experiment 2). The key question was

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