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Functional connectivity indicates differential roles for the intraparietal sulcus and the superior parietal lobule in multiple object tracking

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ABSTRACT

Attentive tracking requires sustained object-based attention, rather than passive vigilance or rapid attentional shifts to brief events. Several theories of tracking suggest a mechanism of indexing objects that allows for attentional resources to be directed toward the moving targets. Imaging studies have shown that cortical areas belonging to the dorsal frontoparietal attention network increase BOLD-signal during multiple object tracking (MOT). Among these areas, some studies have assigned IPS a particular role in object indexing, but the neuroimaging evidence has been sparse. In the present study, we tested participants on a continuous version of the MOT task in order to investigate how cortical areas engage in functional networks during attentional tracking. Specifically, we analyzed the data using eigenvector centrality mapping (ECM) analysis, which provides estimates of individual voxels' connectedness with hub-like parts of the functional network. The results obtained using permutation based voxel-wise statistics support the proposed role for the IPS in object indexing as this region displayed increased centrality during tracking as well as increased functional connectivity with both prefrontal and visual perceptual cortices. In contrast, the opposite pattern was observed for the SPL, with decreasing centrality, as well as reduced functional connectivity with the visual and frontal cortices, in agreement with a hypothesized role for SPL in attentional shifts. These findings provide novel evidence that IPS and SPL serve different functional roles during MOT, while at the same time being highly engaged during tracking as measured by BOLD-signal changes.

Introduction

Whether on a crowded beach watching your children play by the water, or in a dimly lit laboratory tracking objects on a computer screen, attention enables us to selectively monitor those aspect of the environment that are relevant to us, while ignoring those that are deemed less important. As the incoming flow of visual information gets analyzed and represented by the cortex, visual objects are thought to compete for access in the limited representational space of the perceptual system (Franconeri et al., 2013). The mechanism through which selective attention operates involves biasing this competition through top-down enhancement of visual perceptual representations (Desimone and Duncan, 1995), thus allocating processing resources toward task relevant information, while also exerting top-down inhibition of those representations which are irrelevant for the momentary task demands (Bundesen et al., 2005; Frith, 2001). Using a paradigm known as multiple object tracking (MOT; Cavanagh and Alvarez, 2005; Scholl, 2009), several studies have now investigated the load-capacity of visual top-down attention (Holcombe et al., 2014; Scimeca and Franconeri, 2014), as well as the cortical and subcortical areas involved (Alnæs et al., 2014; Culham et al., 1998, 2001; Jovicich et al., 2001; Tomasi et al., 2004, 2007). Several studies have revealed explicit brain networks that are involved when attentively tracking dynamically moving objects (e.g., Alnæs et al., 2015; Howe et al., 2009; Tomasi et al., 2013). The MOT task requires the participant to divide and then sustain split attention in order to track a set of targets moving among identical distractor objects, and at the end report which objects in the display where the original designated targets. By requiring sustained object-based attention, rather than passive vigilance or fast attentional shifts between the objects, the task is well suited to study how attention connects to objects and sustains this connection as the object positions change over time, with no need to move the eyes, i.e. through covert attentional pursuit (Cavanagh and Alvarez, 2005; Horowitz et al., 2004).

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During attentive tracking, the “object” is the primary unit of selection, as well as the limiting factor for performance (Scholl et al., 2001). Several models of attentive tracking propose an indexing mechanism underlying tracking capability, linking visual information to discrete object pointers, allowing allocation of attentional resources toward multiple objects in the visual scene. These indexes also enable the perceptual system to represent objects as persistent across spatiotemporal gaps in the visual input, for example when objects are temporarily invisible due to occlusions (Scholl and Pylyshyn, 1999). Several theories for such an indexing mechanism have been proposed. One is the “fingers of instantiation” (FINST) model (Pylyshyn, 1989) which suggests that pointers or indexes are preattentive and automatically “stick” to the objects. Another is the “object files” model (Kahneman et al., 1992), which links object representations to higher level and effort-driven attentional processes. A more recent proposal is the multifocal attention model (Cavanagh and Alvarez, 2005) which posits parallel processing channels individuating and processing objects, where attention is constrained by the total bandwidth available to be divided between these channels. Further, such an indexing mechanism has been proposed to be dependent on the parietal lobes (Cusack et al., 2010). An extreme example of a disability to individuate and simultaneously attend multiple objects is simultanagnosia (Laeng et al., 1999), one of the core deficits in Bálint's syndrome, which is typically associated with dorsal parietal lesions (Moreaud, 2003; Rizzo and Vecera, 2002). Also, stroke patients with parietal lesions show tracking deficits for the contralesional visual hemifield (Battelli et al., 2001).

Imaging studies of MOT in the intact brain have reported widespread activations along the dorsal frontoparietal cortex, including the anterior and posterior parts of the intraparietal sulcus (IPS), the superior parietal lobule (SPL) and the frontal eye fields (FEF). While these core areas of the dorsal attention network (Corbetta et al., 2008) show both a main effect of tracking, as well as load-dependent blood oxygenation level (BOLD) increases with the number of tracked targets (Alnæs et al., 2014; Culham et al., 2001; Jovicich et al., 2001), the differential functional roles that these areas serve during tracking remain largely unknown. A few studies have attempted to disentangle the functional role of these cortical regions specifically during attentive tracking. In one of these studies (Culham et al., 2001), the authors contrasted model fits for different attentional response profiles during MOT, differentiating regions driven mainly by a task component (e.g., area MT and movement) and those driven mainly by the load component during tracking, showing that the load component was significantly greater than the task component in the IPS, while the inverse was found for the SPL and FEF. That is, while displaying strong task activations, these areas displayed less pronounced load dependence compared to the IPS. Howe et al. (2009) reported that FEF, aIPS, SPL and pIPS were differentially activated when attentively tracking objects, while the pIPS also increased activation when attending stationary objects. Further, based on an analysis of functional connectivity (FC) between these core nodes in the tracking network, Howe et al. (2009) identified aIPS as a hub in the tracking network. They proposed that pIPS contains the index of which objects are the targets, regardless of movement, while the aIPS is engaged during tracking, communicating with SPL and FEF, supposedly in order to suppress eye movements so as to track objects covertly.

Studies investigating the functional specialization of the parietal cortex suggest that sustained endogenous attention and endogenously driven shifts of attention depend on different parts of the dorsal frontoparietal network. In particular the IPS have been suggested to be important for individuating perceptually identical items over time (Cusack et al., 2010), by indexing their locations, whereas the SPL is involved in initiating shifts of attention (Serences and Yantis, 2007). Vandenberghe et al. (2012) have proposed a functional neuroanatomical model of attentional processes in the parietal lobe in which the middle segment of the IPS is hypothesized to be important for the compilation of spatial priority maps (Koch and Ullman, 1985), while the posterior segment is involved in attentional enhancement based on attentional weights for relevant stimuli in the contralateral visual hemifield. SPL, on the other hand plays a role in spatial shifting and displacement of these attentional weights. Thus, it is the IPS that would seem to possess the functional properties required to index objects during attentive tracking as proposed by Howe et al. (2009).

While most functional imaging studies of attention have focused on BOLD signal changes to probe the cortical mechanisms in attention, attentional processes also depend on the dynamic coupling of separate functional systems in the brain (Breckel et al., 2013; Madden and Parks, 2013), driven by task goals (Chadick and Gazzaley, 2011) and resource limitations or cognitive effort (Kitzbichler et al., 2011). Importantly, a network approach to functional imaging data differs from traditional task-fMRI by characterizing the role or importance of a brain area in terms of its relational properties with other brain areas (nodes) forming a network or a graph, rather than based on its activity level in isolation. Assuming that the engagement of IPS and SPL during MOT reflects two separate attentional processes—with IPS driving the generation attention priority maps, allowing attention to connect target objects while inhibiting distractor objects, and the SPL with a role in spatial attention shifts—we would expect these areas to show differential functional connectivity (FC) with other brain regions during a task requiring continuous attention toward target objects.

In the current study we investigate the roles of the IPS and the SPL in attentive tracking, by combining a continuous version of the MOT task with an analysis technique known as eigenvector centrality mapping (ECM). Centrality is a graph measure reflecting the importance of a node in a network. In ECM, a voxel wise approach is used to assign to each voxel a value reflecting its centrality in context of the network of all voxels measured in the brain. A voxel is given a high eigenvector centrality value if that voxel (node) shows high correlation with other nodes, which themselves are highly central in the network. Thus, a node with only a few connections to another highly connected node may thus be assigned a higher eigenvector centrality compared to a node with a greater number of connections, but to less connected nodes (Lohmann et al., 2010), thus ultimately identifying “computational hubs” in the brain (Bullmore and Sporns, 2009). An increased “hubness” of a brain node would thus indicate increased information flow trough this brain area to and from other areas of the brain. Previous studies have investigated changes in resting-state ECM induced by transcranial magnetic stimulation (Wink et al., 2012), altered states of consciousness (Hove et al., 2015) as well as to subjective states of hunger and satiety (Lohmann et al., 2010). Also, ECM has previously been used to investigate task-induced changes in brain connectivity for emotions elicited by music (Koelsch and Skouras, 2014), perception of food in patients with obesity (García-García et al., 2015), as well as for language production (Kim et al., 2011). To our knowledge no previous studies have used ECM to investigate selective attention during attentive tracking of objects.

Specifically, we reasoned that if the IPS is involved in object indexing, allowing attention to connect to target objects during attentive tracking, this area would increase its centrality, as measured with ECM, during a continuous tracking task, compared to a period with no attentional demands (rest). Since MOT requires such a connection to target objects to be sustained to enable attentional pursuit of targets, rather than attentional shifts between objects, we hypothesize that the SPL will show the opposite pattern, showing decreased centrality during task engagement. Further, we hypothesize that the increased centrality of the IPS is a result of increased connectivity to both prefrontal brain regions and visual cortex; possibly reflecting integration of goal-driven attentional signals with bottom-up visual sensory information during the tracking task. Finally, in this study, we included a blocked MOT version in order to investigate the BOLD signal changes during attentive tracking.