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Intraparietal regions play a material general role in working memory: Evidence supporting an internal attentional role

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ABSTRACT

Determining the role of intraparietal sulcus (IPS) regions in working memory (WM) remains a topic of considerable interest and lack of clarity. One group of hypotheses, the internal attention view, proposes that the IPS plays a material general role in maintaining information in WM. An alternative viewpoint, the pure storage account, proposes that the IPS in each hemisphere maintains material specific (e.g., left – phonological; right – visuospatial) information. Yet, adjudication between competing theoretical perspectives is complicated by divergent findings from different methodologies and their use of different paradigms, perhaps most notably between functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). For example, fMRI studies typically use full field stimulus presentations and report bilateral IPS activation, whereas EEG studies direct attention to a single hemifield and report a contralateral bias in both hemispheres. Here, we addressed this question by applying a regions-of-interest fMRI approach to elucidate IPS contributions to WM. Importantly, we manipulated stimulus type (verbal, visuospatial) and the cued hemifield to assess the degree to which IPS activations reflect stimulus specific or stimulus general processing consistent with the pure storage or internal attention hypotheses. These data revealed significant contralateral bias along regions IPS0-5 *regardless* of stimulus type. Also present was a weaker stimulus-based bias apparent in stronger left lateralized activations for verbal stimuli and stronger right lateralized activations for visuospatial stimuli. However, there was no consistent stimulus-based lateralization of activity. Thus, despite the observation of stimulus-based modulation of spatial lateralization this pattern was bilateral. As such, although it is quantitatively underspecified, our results are overall more consistent with an internal attention view that the IPS plays a material general role in refreshing the contents of WM.

1. Introduction

The neural underpinnings of short-term or working memory (WM) remain a source of intense research interest. A host of converging evidence from various methodologies implicates the intraparietal sulcus (IPS) in WM (fMRI: Cowan, 2011; Majerus et al., 2007, 2014, 2006; Song and Jiang, 2006; Todd and Marois, 2004; Xu and Chun, 2006; but see: Mitchell and Cusack, 2007; EEG: Klaver et al., 1999; Vogel and Machizawa, 2004; MEG: Mitchell and Cusack, 2011; Palva et al., 2010; neurostimulation: Herwig et al., 2003; and neuropsychology, reviewed in: Berryhill, 2012; Olson and Berryhill, 2009). However, although there is general agreement supporting IPS involvement in some aspect of WM, the nature of these contributions remains unclear. It is important to clarify this question to adjudicate between different theoretical accounts.

Perhaps the best known account reflects the Multicomponent Model's view that short-term memory for verbal information requires the phonological loop, whereas visuospatial information relies on the visuospatial sketchpad for maintenance of visuospatial information and any multimodal maintenance depends on the episodic buffer (Baddeley, 1986, 2000; Baddeley and Hitch, 1974; Repovs and Baddeley, 2006). These components have been attributed to cortical locations based largely on patient work and functional neuroimaging data such that the left supramarginal gyrus is linked with the phonological loop, the right parietal lobe as a putative location for the visuospatial sketchpad, and the angular gyrus as the episodic buffer (Baddeley, 2003; Chein et al., 2003; Vilberg and Rugg, 2008). This view, that the IPS is engaged in a material specific role in WM, can be considered a *pure storage* account. Lateralized IPS activity would reflect the nature of the contents of WM, with unilateral left IPS activity for verbal stimuli and unilateral right IPS activity for visuospatial stimuli, rather than

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the spatial location at encoding of the to-be-remembered stimuli. Under the pure storage account, bilateral activations would not be expected for stimulus specific WM tasks and a contralateral bias would be dependent on the nature of the stimuli in use rather than their spatial location.

A competing perspective suggests that IPS activity represents a domain general process reflecting the storage and attentional refreshing of items in WM (Berryhill et al., 2011; Chein and Fiez, 2010; Chein et al., 2003; Kiyonaga and Egner, 2013; Lewandowsky et al., 2009; Majerus et al., 2014). In essence, the IPS is thought to keep elements in WM active by returning them to the focus of attention. The *internal attention* view predicts that bilateral IPS involvement reflects the attentional refreshing of items held in WM, regardless of the task demands (e.g., verbal or visuospatial). This attentional role could be covert and coincident with more explicit rehearsal strategies that are stimulus specific, such as subvocal rehearsal of verbal stimuli. Importantly, therefore, it does not prohibit the emergence of a stimulus-dependent hemispheric asymmetry due to the usage of additional rehearsal strategies. This interpretation is consistent with attentional models of WM (e.g., Barrouillet and Camos, 2009; Cowan, 1999; Unsworth and Engle, 2007).

Although these predictions regarding the IPS may seem straightforward, we quickly encounter a thicket of seemingly inconsistent findings from different research fields. Within each experimental approach there is general agreement regarding the nature of IPS activity during WM, but disagreement across experimental approaches. For example, the fMRI literature reliably identifies *bilateral* IPS activity reflecting the number of items currently maintained in WM (Song and Jiang, 2006; Todd and Marois, 2004; Xu, 2007; Xu and Chun, 2006; for a recent meta-analysis see: Rottschy et al., 2012). Importantly, the amplitude of these activations increases until it asymptotes at an individual's WM capacity limit (Todd and Marois, 2005). It is worth noting that these types of fMRI investigations use centrally placed visual stimulus arrays and identify bilateral activations along the lateral IPS.

In contrast, the EEG literature focuses on a slow component from posterior electrode sites that emerges during WM maintenance (Gao et al., 2009; Ikkai et al., 2010; Jolicoeur et al., 2008; Klaver et al., 1999; McCollough et al., 2007; Vogel and Machizawa, 2004; reviewed in Drew et al., 2006). It is known by two names: the sustained posterior contralateral negativity (SPCN) and the contralateral delay activity (CDA, the term used throughout this manuscript). In these studies, participants maintain central fixation and are cued to covertly attend to visual stimuli presented in either the left or right hemifield. Here, the CDA is derived from electrodes positioned over posterior parietal sites and a pattern emerges during WM maintenance showing greater activity for stimuli presented contralaterally compared to stimuli presented ipsilaterally. Again, the increase in amplitude corresponds to an individual's behavioral WM capacity limit (Anderson et al., 2011; Vogel et al., 2005). The source of this slow component is thought to be in the IPS (Mitchell and Cusack, 2011).

These conflicting findings might appear to be a simple issue of differing conventions across techniques. A few studies have focused on resolving discrepancies between the data from different methodologies (Bray et al., 2015; Cutini et al., 2011; Robitaille et al., 2010; Sheremata et al., 2010), but they have reached different conclusions. For example, Sheremata and colleagues cued covert attention to oriented bars in one or both visual fields. They reported a contralateral bias in the left IPS, particularly in posterior portions, but no such contralateral bias in the right IPS. However, using a different spatial WM task Bray et al. (2015) compared IPS activity as a function of hemifield and observed a general contralateral bias for WM maintenance that became bilateral when maintenance demands required manipulation (Bray et al., 2015). In contrast, Robitaille and colleagues recorded fMRI, MEG and EEG data in the same participants while they performed a visuospatial WM task in a cued visual hemifield. Unexpectedly, they found bilateral IPS activity when looking at the fMRI data, but different components of the MEG data revealed both contralaterally driven and bilateral signals from posterior sites. They concluded that fMRI and EEG/MEG signals reflect different underlying neural processes. Cutini and colleagues reached a similar conclusion using a functional near-infrared spectroscopy (fNIRS) approach. They observed bilateral activations at detectors above the IPS even when unilateral encoding cues were provided. In summary, even when researchers have tried to assimilate the fMRI and EEG findings they have not achieved a consistent explanation.

An additional relevant consideration arises from the vision and attention literatures regarding what is represented in IPS regions. Visual attention relies on balanced activity in bilateral IPS regions; when one hemisphere is damaged this balance is disrupted and attentional deficits such as neglect or extinction emerge (e.g., Kinsbourne, 1977). The fact that hemispatial neglect more often follows right hemisphere lesions has lead to the hemispatial attention hypothesis, under which the right hemisphere controls attention to the full visual field whereas the left hemisphere controls attention to the right visual field alone (Heilman and Van Den Abell, 1980; Mesulam, 1981). However, fMRI studies have revealed that both the left and right IPS contain a set of topographic regions (IPS0-5) defined by their contralateral attentional or perceptual bias (Konen and Kastner, 2008; Schluppeck et al., 2005; Sereno et al., 2001; Silver et al., 2005; Swisher et al., 2007); reviewed in: (Silver and Kastner, 2009). In other words, for visual attention tasks various IPS regions show a clear contralateral bias and this bias permits the mapping of IPS regions of interest. Furthermore, disrupting the IPS using transcranial magnetic stimulation (TMS) predictably shifts the corresponding behavioral bias farther toward the ipsilateral side (Battelli et al., 2009; Brighina et al., 2002; Fierro et al., 2000; Plow et al., 2014; Pourtois et al., 2001; Szczepanski and Kastner, 2013). Thus, to address the mechanism of IPS in WM using fMRI it seems essential to cue the relevant visual hemifield (Sheremata et al., 2010) lest the WM responses be confounded by the bottom-up representation.

Incorporating the attended hemifield into consideration produces different predictions from the pure storage and internal attention classes of models. An internal attention model of WM can account for a contralateral bias in the IPS because it is stimulus general. The presence of contralateral bias is not strongly a function of the type of stimuli (verbal or visuospatial) to be remembered but rather a function of where the attended stimuli were located during encoding. A contralateral bias would pose a greater challenge for the pure storage view. This is because the pure storage model hypothesizes a material specific hemispheric lateralization revealing left IPS activity for verbal stimuli and right IPS activity for visuospatial stimuli. Thus, a unilateral contralateral bias would strongly depend on the stimulus category. The consequence for behavior would be that the pure storage account would predict significantly worse verbal WM performance for stimuli presented on the left and worse visuospatial WM performance for stimuli on the right.

To adjudicate between the pure storage and internal attention accounts, we investigated whether IPS activity during WM reflects a stimulus specific or a stimulus general process. A stimulus specific process consistent with the pure storage view predicts hemispheric lateralization solely as a function of stimulus type (left: verbal; right: visuospatial), regardless of where the stimulus is located on the display (left or right hemifield). In contrast, a stimulus general mechanism consistent with the internal attention view predicts bilateral activation regardless of stimulus type and location. To summarize, contralateral IPS activation after cueing