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Functional connectivity between ventral and dorsal frontoparietal networks underlies stimulus-driven and working memory-driven sources of visual distraction.

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Abstract

We investigate the neural basis of two routes to visual distraction: salient stimuli capture attention in a bottom-up fashion, and the reappearance of task-irrelevant items that are being actively maintained in working memory can lead to distraction via top-down, but automatic, guidance of attention. Bottom-up, stimulus-driven distraction has typically been associated with a ventral network incorporating the inferior frontal gyrus and temporoparietal junction. A dorsal network including the superior frontal gyrus, superior parietal cortex and intraparietal sulcus is known to underlie the voluntary, top-down control of attention. Here we show that the ventral attention network may be modulated in a top-down manner by task-irrelevant memory signals. Furthermore, we delineate how the biasing of attention by these bottom-up and top-down sources of visual distraction is modulated by changes in connectivity among critical nodes of ventral and dorsal frontoparietal regions. The findings further our understanding of the neural circuitry that mediates the control of human visual attention.

Keywords

Visual attention; fMRI; dorsal and ventral networks; top-down; bottom-up

1. Introduction

Human attention is a limited resource which operates to select behaviourally relevant stimuli from the constant stream of competing objects and events. A number of systems interact to control the allocation of attention to particular elements of the visual environment. Attention can be captured in a bottom-up fashion by the appearance of salient items (Theeuwes, 1991, 1992); this has obvious evolutionary advantages, allowing quick reactions to potentially dangerous events, but the accompanying distractibility may impede the performance of goal-directed tasks. Crucially, then, this process interacts with and is influenced by top-down cognitive control, which attempts to wrest attention away from salient but irrelevant aspects of the environment in order to focus on achieving specific goals (Folk and Remington, 1998; Folk et al., 1992; Kiss and Eimer, 2011; Muller et al., 2009; Proulx and Egeth, 2006). Attentional control is largely achieved by the biased selection of percepts that match some internal representation; for example, when searching for a yellow apple in a supermarket, items that are the wrong colour (e.g. a red apple) or the wrong shape (e.g. a banana) are filtered out in favour of items that are both round and yellow. Clearly this top-down system relies heavily on the relationship between attention and memory, as the contents of working memory (WM) bias the selection process. A great deal of evidence indicates that information held in WM (e.g. a colour) may draw visual attention automatically if it reappears in a subsequent search display, resulting in speeded response to a target which is surrounded by that colour or a slowed response if the colour in memory matches an irrelevant item (Carlisle and Woodman, 2011; Downing, 2000; Soto et al., 2005; Soto et al., 2008; Soto and Humphreys, 2009). Despite its top-down nature, this process is largely automatic and is observed even when it is detrimental to performance – for instance, by drawing attention away from the target towards known distracters matching the WM

content (Olivers et al., 2006; Soto et al., 2008).

There are therefore at least two routes to visual distraction; a bottom-up response to novel or unexpected salient stimuli and the top-down capture of attention by the contents of WM under circumstances where the memorised item is irrelevant for behaviour. Bottom-up detection of salient stimuli recruits a ventral frontoparietal network, including the right inferior frontal gyrus (IFG) and temporoparietal junction (TPJ; Corbetta and Shulman, 2002). The ventral network has been shown to be activated by unexpected stimuli which share some features with the target (Indovina and Macaluso, 2007; Natale et al., 2010). The right TPJ has been implicated in spatial reorienting{Chang, 2013 #1129} and in computing the behavioural relevance of salient signals (Geng and Mangun, 2011), while the IFG appears to play a 'gating' role, suppressing response to unexpected distracting or irrelevant items (Downar et al., 2001; Shulman et al., 2009).

We asked whether and how this ventral attention network is modulated by the additional presence of top-down memory signals during a visual search task. These signals may carry irrelevant or even misleading information for ongoing selection processes (Olivers et al., 2011; Soto et al., 2008). Top-down control of attention for goal-relevant targets recruits a dorsal frontoparietal network including the superior frontal gyrus, superior parietal cortex and intraparietal sulcus (Cabeza et al., 2008; Corbetta and Shulman, 2002). While voluntary, goal-directed top-down guidance of attention can modulate response to bottom-up cues in the ventrolateral prefrontal cortex (Reeck et al., 2012) and in visual cortex (McMains and Kastner, 2011; Melloni et al., 2012), it is unclear to what extent activation within the ventral attention network may be influenced by *automatic* top-down guidance from search-

irrelevant items held in WM (Olivers et al., 2011; Soto et al., 2008). To address this issue we employed a visual attention task that varied memory and saliency signals in an orthogonal manner. Crucially, both bottom-up and top-down sources of attentional capture always acted as distractors and were irrelevant to task performance. Increased functional connectivity within the dorsal frontoparietal attention network has been shown to modulate conscious awareness of peripheral stimuli (Chica et al., 2012), and coupling between regions of the ventral and dorsal attention networks appears to underlie response to unexpected salient onsets or stimulus change (Weissman and Prado, 2012). This led us to formulate a number of hypotheses: (1) the presence of salient distractors would activate ventral frontoparietal regions; (2) both top-down and bottom-up sources of distraction - arising from working memory signals and from salient stimulus onsets respectively - would modulate functional connectivity within the ventral network; (3) connectivity between the dorsal and ventral networks would be altered by memory-driven top-down guidance of attention to irrelevant stimuli.

2. Materials and methods

2.1 Participants

21 healthy participants (14 male, age range: 18-32 years), with normal or corrected-to-normal vision, were recruited by means of an advertising campaign and were paid £20 for their participation. No participant reported prior history of neurological or neuropsychiatric disorders. Participants were all naïve with regard to experimental aims and hypotheses. Approval for this study was granted by the West London Research Ethics Committee.

2.2 Experimental Procedure

The experiment consisted of two block types, hereafter referred to as the 'WM' and 'Priming' blocks. Each trial began with four white placeholder circles on a black background, presented in four onscreen quadrants. Each quadrant contained two possible stimulus locations around a clock face, namely, at 1 and 2 o'clock for quadrant 1, at 4 and 5 o'clock for quadrant 2, at 7 and 8 o'clock for quadrant 3 and at 10 and 11 o'clock for quadrant 4. The stimulus location within each quadrant was randomly selected on every trial. After 1000 ms, a coloured circle was presented at fixation for 200 ms. The colour of this circle was randomly selected from five possible colours: red, green, yellow, blue and pink. Participants were instructed to remember the colour of the central cue (WM blocks) or simply to look at it but not commit it to memory (Priming blocks). After a 500 ms delay, the placeholder circles were replaced by coloured circles containing white lines. Participants were instructed to search for the target – a white line, tilted 30° to either right or left - and indicate its orientation. The search display remained onscreen for 175 ms. On 50% of trials – referred to as 'match' trials - the cued colour reappeared in the display, though it never surrounded the target line. In addition, on 50% of trials one of the distractors and its surrounding circle

shifted position to the alternate stimulus location within the same quadrant 100 ms after initial presentation of the display, giving the appearance of a sudden stimulus onset. In the interests of brevity, we will refer to these trials as 'onset trials' although we acknowledge that the stimulus is technically not a new onset. Critically, this onset or stimulus change is an attention-grabbing event of the type shown to activate the ventral attention network. The presence or absence of the memory-matching item, and the presence or absence of the sudden stimulus onset were varied on a trial-by-trial basis. This led to a balanced 2 (memory context) x 2 (match condition) x 2 (onset condition) design, with 24 trials in each experimental cell (see Figure 1).

In order to ensure that participants were maintaining the cue colour in WM, 6 trials on each WM block were 'catch' trials in which the search array was followed by a memory probe, presented for 1500 ms. An equal number of catch trials were presented in the Priming blocks to ensure attention to the display. In these trials, a grey circle was presented in place of the initial colour cue, and participants were instructed not to respond to the subsequent search task. The inter-trial interval was jittered between 4 - 8 seconds, with a pseudo-exponential distribution (50% of ITIs were 2s, 25% of ITIs were 5s, 13% were 6 s, 6% were 7s and 6% were 8s) in order to facilitate the independent estimation of BOLD responses across trials (Ollinger et al., 2001). Participants performed 6 blocks of 38 trials, split across three fMRI runs (one WM and one Priming block per run, in random order). Several training blocks were completed prior to scanning until the level of search accuracy was above 90%, and participants were instructed not to move their eyes during the task. The short search duration was used to further discourage eye movements.

2.3 Image acquisition/scanning parameters

MRI scanning was conducted using a Siemens Magnetom Verio 3T MRI scanner and a 32-channel head coil. Following a brief localizer scan to determine the orientation of the subject's head within the field, 176 T1 weighted anatomical sagittal images were acquired with an FOV of 220 x 220mm, TR of 1900 ms, TE of 2.48 ms and slice thickness of 1mm, leading to a voxel resolution of 1x1x1 mm. Three functional runs of T2* weighted echo planar imaging were conducted to obtain 38 contiguous sagittal slices covering the whole brain. Each run contained 350 volumes which were acquired with an FOV of 222x222mm, TR of 2200 ms, TE of 30 ms and slice thickness of 3 mm. The resulting voxel resolution was 2.4x2.4x3.0 mm.

2.4 Imaging data analysis

fMRI data processing was carried out using FEAT (fMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). The first 6 volumes of the EPI scan were removed from each scanning session to account for T1 equilibrium effects, leaving 344 scans per run. The following pre-statistics processing was applied: non-brain removal using BET (Smith, 2002); motion correction using MCFLIRT (Jenkinson et al., 2002); 66 seconds high-pass temporal filtering and spatial smoothing using a Gaussian kernel of FWHM 5.0mm. Time-series statistical analysis was carried out using FILM (FMRIB's Improved Linear Model) with local autocorrelation correction (Woolrich et al., 2001) for each individual run. The different trial types were modelled as boxcar functions convolved with the hemodynamic response function. Each event began with the onset of the memory cue and had 875 ms duration (including cue exposure, cue-search delay and search exposure time). Explanatory variables (EVs) included the onset times for match and no-

match trials with and without stimulus onset separately for the WM blocks (4 EVS) and Priming block (4 EVs). Additional regressors of no interest included memory catch trials, errors and the motion realignment parameters. The temporal derivative of the haemodynamic response function was also added to the model for each explanatory variable in order to account for latency differences between slice acquisitions. Subsequently, we carried out cross-run individual analyses using fixed-effects to derive Z statistic images for all conditions and then performed group-level analyses using FLAME (FMRIB's Local Analysis of Mixed Effects) stage 1+2 as implemented in FEAT. We report maps of BOLD responses thresholded using clusters determined by a voxelwise Z threshold of 2.3 and a corrected cluster significance threshold of $p=0.05$, unless otherwise noted. Each individual's EPI scans were registered to high-resolution structural images using FLIRT, and were then co-registered and transformed to standard (Montreal Neurological Institute) space.

2.5 Psychophysiological Interaction (PPI) Analysis

We implemented functional connectivity analyses using the gPPI (generalized form of context-dependent PPI) method (McLaren et al., 2012). Pre-processing, registration and statistical analysis of the original variables were carried out using the same methods described above. An additional physiological regressor was added to the model which contained the timecourse of a specified spherical region of interest (with a radius of 3mm) for each participant. The seed region's timecourse was deconvolved from the haemodynamic response function using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>) prior to its inclusion in the model. Interaction regressors, consisting of the interaction between each psychological variable of

interest and the physiological regressor, were also included. Contrasts at the higher level were defined with reference to these interaction contrasts and thresholded using clusters determined by a voxelwise Z threshold of 2.3 and a (corrected) cluster significance threshold of $p=0.05$.

3. Results

3.1 Behavioural results

Median search reaction time (RT) was calculated for correct search trials only. No significant difference in RT was observed between the WM and Priming conditions, however main effects of the match and onset conditions were observed such that RT was slowed when the cued colour matched a search distractor relative to the no-match trials ($F_{1,20}=11.59$, $p<.05$). Search RTs were also slowed in the presence of a sudden stimulus onset ($F_{1,20}=22.34$, $p<.001$). These effects were qualified by an interaction between match and memory context (WM vs. Priming). The effect of match condition was enhanced in WM blocks relative to Priming blocks ($F_{1,20}=5.43$, $p<.05$), as RTs were further slowed by the presence of a matching object when the item had been held in memory. There was also an interaction between memory context and onset condition, with a greater effect of onset observed in WM blocks relative to Priming blocks ($F_{1,20}=6.64$, $p<.05$). This indicated that attentional capture by a sudden stimulus onset was increased in the WM condition relative to the Priming condition (note that this effect was independent of the matching factor). See Figure 2A for an illustration. There was no significant interaction between match condition and onset condition, and no 3-way interaction. Search accuracy (Figure 2B) did not change as a function of memory context ($F_{1,20}=.001$, $p>.05$) or match condition ($F_{1,20}=2.804$, $p>.05$), however mean accuracy was reduced in the onset condition relative to the no-onset condition ($F_{1,20} = 16.11$, $p<.001$).

3.2 Imaging results

As expected, the presence of an onset (main effect: onset > no-onset) activated the ventral frontoparietal network including bilateral TPJ, right IFG and bilateral posterior parietal and

lateral occipital cortices (see Figure 3 and Table 1). Our first hypothesis was therefore supported.

[Insert Table 1 here]

There were no main effects of memory context (i.e. WM > Priming and vice versa) at this threshold, however the absence of a memory effect could be due to the relatively low WM load (as only one item was maintained over the course of each trial). Examination of the uncorrected memory effects, thresholded at $Z=2.3$, showed a main effect of memory context (WM > Priming) in small bilateral regions of frontal cortex (including the MFG, SFG and frontal pole), bilateral posterior PPC including the intraparietal sulcus (IPS) and the left hippocampus. We observed a cluster in the left visual cortex that showed attenuated response during match trials relative to no-match trials, consistent with neural repetition suppression (Henson and Rugg, 2003; Sayres and Grill-Spector, 2006). No responses to the opposite contrast were detected at this threshold, but uncorrected analysis ($Z=2.3$) revealed enhanced response in right superior frontal cortex, the paracingulate gyrus and bilateral temporal pole when a memory-matching item was present in the display.

There was no initial evidence that neural repetition effects were modulated by memory context. We then performed analysis with a behavioural covariate to assess whether neural responses were related to inter-individual variability in how attention was captured by the WM contents during the task. We introduced the difference in RT between match and no-match trials (calculated separately for the WM onset, WM no-onset, PR onset and PR no-onset conditions) as covariates in the higher-level fMRI analysis. This difference is a measure

of the degree of attentional capture exerted by stimuli which match the colour of the cue stimulus. Covariate analysis showed that the interaction contrast between memory context and match presence (i.e. WM: match > no-match & Priming: match < no-match) revealed regions in bilateral lateral occipital cortex (LOC) and left temporoparietal regions, including the middle temporal gyrus and TPJ, whose activity covaried with the degree of attentional capture by matching trials in WM blocks. Further analysis confirmed that the effects of the RT covariate during this analysis were restricted to the WM condition and were not observed in the Priming condition. In other words, neural response to memory-matching stimuli was enhanced in those participants who also showed increased behavioural response to memory-matching stimuli, suggesting that variability in distractibility modulated response to top-down guidance of attention in the ventral attention network (see Figure 4 and Table 2). The absence of an overall interaction between memory and match conditions may therefore be due to individual differences in attentional capture.

[Insert Table 2 here].

3.3 Functional connectivity results

Our main aim was to investigate how functional connectivity from ventral frontoparietal regions, namely TPJ and IFG, was modulated by the presence of top-down (i.e. matching to irrelevant WM contents) and bottom-up (i.e. new stimulus onset) sources of attentional capture. PPI analyses were conducted from seed regions with a radius of 3mm. Both ventral seeds, in the TPJ (MNI coordinates: 64 -44 12, derived from the Harvard-Oxford Cortical Structural Atlas as the junction of the superior temporal gyrus, supramarginal gyrus and angular gyrus - see Tsakiris, Costantini & Haggard (2008) and the IFG (pars triangularis

region, derived from the Harvard-Oxford Cortical Structural Atlas implemented in FSL; MNI coordinates: 52 32 8) were contained within the regions activated by the onset > no-onset contrast.

For comparison, we carried out two additional PPI analyses from seed regions within the dorsal frontoparietal network to assay the specific nature of functional connectivity across ventral and dorsal networks. The first dorsal seed was located in the superior frontal gyrus (SFG; MNI coordinates: 26 12 64; ROI derived from regions activated by the memory/match interaction contrast – i.e. WM: match>no-match & Priming: no-match>match, $Z=2.3$, $p=0.05$, uncorrected). The second dorsal seed was in the anterior intraparietal sulcus (IPS; MNI coordinates: 40 -60 46). These coordinates were taken from peak voxel of the uncorrected WM>Priming contrast, in an effort to select a region of the IPS likely to respond to the top-down memory/attention demands of our paradigm. This region of the IPS has been identified as a key component of the dorsal attention network (Shulman et al., 2010) and has been implicated in the top-down control of attention during memory tasks (Ciaramelli et al., 2008). Further, an automated meta-analysis of 491 studies on neurosynth.org (Yarkoni et al., 2011) shows that these coordinates are strongly associated with memory retrieval, with a Z score of 4.72, and a variety of studies have described working memory effects in this region of the IPS (Beck et al., 2010; Bor and Owen, 2007; Choo et al., 2005; Majerus et al., 2007).

The SFG and IPS form part of the dorsal frontoparietal attention network, as described by Corbetta and Shulman (2002). As the principal aim of this study was to assess the functioning of the ventral network in relation to memory-driven attentional capture, we

focused our connectivity analyses on interactions between memory context and match factors and between memory context and the presence or absence of a stimulus onset.

(i) Functional connectivity from TPJ and IFG is modulated by the interaction of memory context and matching to memory.

An interaction between memory context (WM/Priming) and match condition (match/no-match) influenced functional connectivity with the TPJ (see Figure 5A). The contrast specification WM: match>no-match & Priming: no-match>match revealed increased coupling between the TPJ and surrounding ventral temporal regions, the right PPC and bilateral visual cortex when a distractor matched the contents of WM. Critically, the same interaction modulated connectivity between the IFG and the superior frontal sulcus (Figure 5B). Coupling between this region, an essential node of the dorsal network, and the ventral IFG seed was enhanced in the presence of a distractor stimulus that matched the contents of WM.

(ii) Ventral connectivity is modulated by the interaction of memory context and onset condition.

As the ventral attention network was activated in the presence of a sudden stimulus onset, we also assessed how the interaction of memory context (WM vs. Priming) and onset condition affected functional connectivity in this network. Reduced connectivity in the presence of an onset was observed during WM blocks between the TPJ and the parietal cortex, specifically right superior and posterior parietal cortex and the left inferior parietal lobule, while the opposite pattern was seen during Priming blocks. Functional connectivity from the IFG was not influenced by the interaction of memory context and onset condition,

although the presence of a sudden stimulus onset (irrespective of memory context) led to decoupling between the IFG and the bilateral posterior cingulate and precuneus and the left PPC.

The findings documented so far show that while top-down distraction driven by the contents of WM increased coupling between regions of the ventral attention network – specifically, the TPJ, PPC and early visual cortex – and between the IFG and superior frontal sulcus, bottom-up sources of distraction reduced connectivity between TPJ and PPC, an effect which was mainly observed in the WM condition. These findings provide support for our second hypothesis, that functional connectivity within the ventral network is modulated by both top-down and bottom-up sources of distraction, and for our third hypothesis, that top-down distraction modulates connectivity between the dorsal and ventral networks.

(iii) Functional connectivity from the dorsal network is modulated by the interaction of memory context and onset condition.

Two further connectivity analyses were conducted in order to determine whether the interactions described above - between memory context and match condition and between memory context and onset condition - were specific to the ventral network. Changes in functional connectivity during the task were assessed from two seed regions within the dorsal attention network, typically associated with voluntary control of attentional deployment (Corbetta and Shulman, 2002). To pre-empt the results, functional connectivity from the dorsal seeds was not modulated in a top-down manner by the interaction of memory context and match condition. An interaction between onset condition and memory context did however influence connectivity from both seeds.

The appearance of a salient onset, regardless of whether that colour had been cued at the start of the trial, resulted in a decrease in coupling between the right SFG and a network of right-hemisphere ventral regions - including the frontal pole and frontal medial cortex, the lingual gyrus and the superior temporal sulcus - during WM blocks, but not during Priming blocks (see Figure 5C). Functional connectivity between the right IPS (Figure 5D) and regions of the dorsal attention network, including the right PPC, precuneus and superior and middle frontal gyri, as well as the bilateral caudate nucleus, was similarly influenced by the interaction between memory context and onset condition (irrespective of the presence or absence of a match to the cued colour). Coupling between these regions decreased in the presence of an onset during WM blocks but not during Priming blocks. Taken together, these results indicate that coordinated activity *within* the dorsal network and *between* the ventral and dorsal networks was disrupted by salient distractors to a greater degree when WM was loaded relative to the Priming condition.

In summary, behavioural response to a visual attention task was impaired by both top-down and bottom-up sources of distraction, and their appearance modulated neural response in the ventral 'bottom-up' network. Bottom-up attentional capture disrupted functional connectivity within the dorsal attention network, and, crucially between the dorsal and ventral networks. Note that this effect was enhanced under conditions of WM load. In contrast, top-down capture of attention by WM contents enhanced connectivity within the ventral network, and between crucial nodes of the dorsal and ventral networks.

4. Discussion

Performance of day-to-day tasks can be hampered by distracting stimuli that may be related in some way to behavioural goals or may be perceptually salient but entirely irrelevant to the task at hand. We set out to examine the neural foundations of top-down and bottom-up sources of distractibility. In a replication of previous studies (Olivers et al., 2011; Soto et al., 2005; Soto and Humphreys, 2007, 2009), response time data revealed automatic top-down biases of attention towards the contents of WM. The presence of a distracter in the search array matching the memory cue led to slower search responses relative to a no-match condition, and this effect was stronger when the cue was held in WM relative to when it was merely attended. Bottom-up capture of attention by irrelevant stimuli was also observed as response latencies increased when the search display included a distracter in the form of a salient stimulus onset; these stimulus-driven effects were partially modulated by top-down control as the onset effect was enhanced when participants were holding a pre-cued colour in WM. Hence, reduced availability of WM led to increased distraction (Lavie et al., 2004). We found no interaction between the onset (bottom-up) and colour match (top-down) variables, suggesting that their effects were additive (Sternberg, 1998). In fact, the longest response times – indicative of greatest distractibility – were observed during matching onset trials when both top-down and bottom-up forms of attentional capture were present.

As expected, the presence of a salient stimulus onset activated a network of ventral frontoparietal regions including the bilateral TPJ and right IFG. We also found a significant repetition suppression effect in the left visual cortex which was independent of the memory context. The attenuation of responses during match trials relative to no-match trials is

suggestive of facilitated neural processing of matching items relative to non-matching items (Grill-Spector et al., 2006; Henson and Rugg, 2003). Initial analyses did not reveal any regions showing enhanced response to the presence of a match, and there was also no overall interaction between memory context and match condition. However, behavioural covariate analysis of the memory-capture effect on search performance did show that variability in the size of the WM-matching effect on search performance was associated with BOLD response in the ventral attention network. This is consonant with a number of previous studies that have described neural response patterns consistent with a modulation of repetition effects by memory context. These studies indicate that when items are held in WM their reappearance triggers enhanced neural response relative to non-matching items, while the opposite pattern (i.e. neural repetition suppression) is typically found for items that have merely been primed (Desimone, 1996; Greene and Soto, 2012; Miller and Desimone, 1994; Soto et al., 2012; Soto et al., 2007).

Crucially, the interaction between memory context (i.e. whether the cue was held in WM or merely attended), the matching between cue and search arrays and the presence of salient bottom-up signals strongly modulated functional connectivity within and between the dorsal and ventral attention networks. Below we discuss how the interplay between these factors is reflected in distinct patterns of connectivity.

Firstly, responses within the ventral network previously associated with bottom-up or stimulus-driven selection (i.e unexpected items; cf. Corbetta and Shulman, 2002) are also modulated by top-down sources of distraction. The reappearance of an irrelevant memory-matching stimulus is a very distracting event and can capture attention (Olivers et al., 2011;

Soto et al., 2008). This was evidenced here by increased search response latencies when such an item is present in the search display. The reappearance of a WM distracter in the search boosted functional connectivity within the ventral attention network: the TPJ displayed tighter coupling with surrounding regions of temporoparietal and occipital cortex in response to a previously cued item during WM blocks relative to Priming blocks. Top-down attentional capture driven by the contents of WM also enhanced connectivity between certain crucial nodes of the ventral and dorsal networks, specifically the IFG and the superior frontal sulcus. Recent data has indicated that the right IFG is crucial to the integration of top-down and bottom-up information and the resolution of competition between goal-directed and stimulus-driven sources of attentional capture (DiQuattro and Geng, 2011; Dodds et al., 2011). Here we demonstrate that inferior frontal contributions to attentional control may operate via enhanced connectivity with more dorsal brain regions under conditions of increased top-down control from WM.

A second novel finding was that bottom-up capture of attention by salient, but irrelevant stimuli disrupted functional connectivity within the dorsal attention network, reducing coupling between the IPS and right frontoparietal regions including the superior frontal gyrus and PPC. Interestingly, this effect was dependent on the availability of WM. Functional disconnection between dorsal frontoparietal regions in the presence of a salient onset increased during WM blocks relative to Priming blocks, independently of whether the colour of the onset matched the cued colour. A similar effect was observed in the behavioural data; attentional capture by salient distractors, indexed by slowed responses to the target, was enhanced during WM blocks when participants were actively engaged in memory maintenance. This suggests that the strain of maintaining information in WM while

performing an unrelated task reduces cognitive control, allowing the distracting stimulus to exert more influence on behaviour. Indeed, a body of research has demonstrated the effect of WM load in cognitive control; here we demonstrate this effect with a slight increase in WM load of only 1 item, in contrast with previous work using much more strenuous cognitive loads (de Fockert et al., 2001; Kelley and Lavie, 2011; Lavie and De Fockert, 2005; Lavie et al., 2004). The present results further indicate that this general WM load effect may come about through a reduction in coordinated activity within the goal-oriented dorsal network.

In addition to modulating connectivity within dorsal regions, the presence of distracting stimuli in the form of sudden salient onsets can also alter the connectivity between the dorsal and ventral networks. For example, Weissman and Prado (2012) describe a reduction in coupling between the IFG and the posterior parietal cortex during attentional capture by salient stimuli, namely a target appearing at an uncued or unexpected location. Here we further document how connectivity between critical nodes of the ventral and dorsal networks is altered by the presence of irrelevant memory distracters under conditions of varying memory load. In particular we report decoupling between the TPJ and bilateral superior and posterior parietal cortex, and between the SFG and ventral frontal and temporal regions in the presence of a sudden stimulus onset, but more critically, we show that these changes in functional connectivity between dorsal and ventral frontoparietal networks are further modulated by the availability of WM processing (i.e. intensified during WM blocks relative to Priming blocks). The ventral network, including the TPJ and IFG, has been conceptualised as a circuit breaker for the dorsal network which controls the current focus of attention, redirecting attention away from the current item or location in a

stimulus-driven (bottom-up) fashion (Astafiev et al., 2006; Corbetta and Shulman, 2002). We observed an overall reduction in coupling between the dorsal and ventral networks in response to a bottom-up source of attentional capture, as the top-down modulation of attention by the dorsal network was over-ridden by the sudden onset of a salient distractor. This decoupling was exacerbated under conditions of increased WM load, leading to further reduction in cognitive control.

5. Conclusions

The findings presented here demonstrate that interplay between critical nodes of the dorsal and ventral attention networks governs the effects of bottom-up and top-down, memory-driven sources of distraction, thus highlighting the importance of studying functional connectivity to further our understanding of the neural circuitry supporting the capture of human visual attention.

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Figures

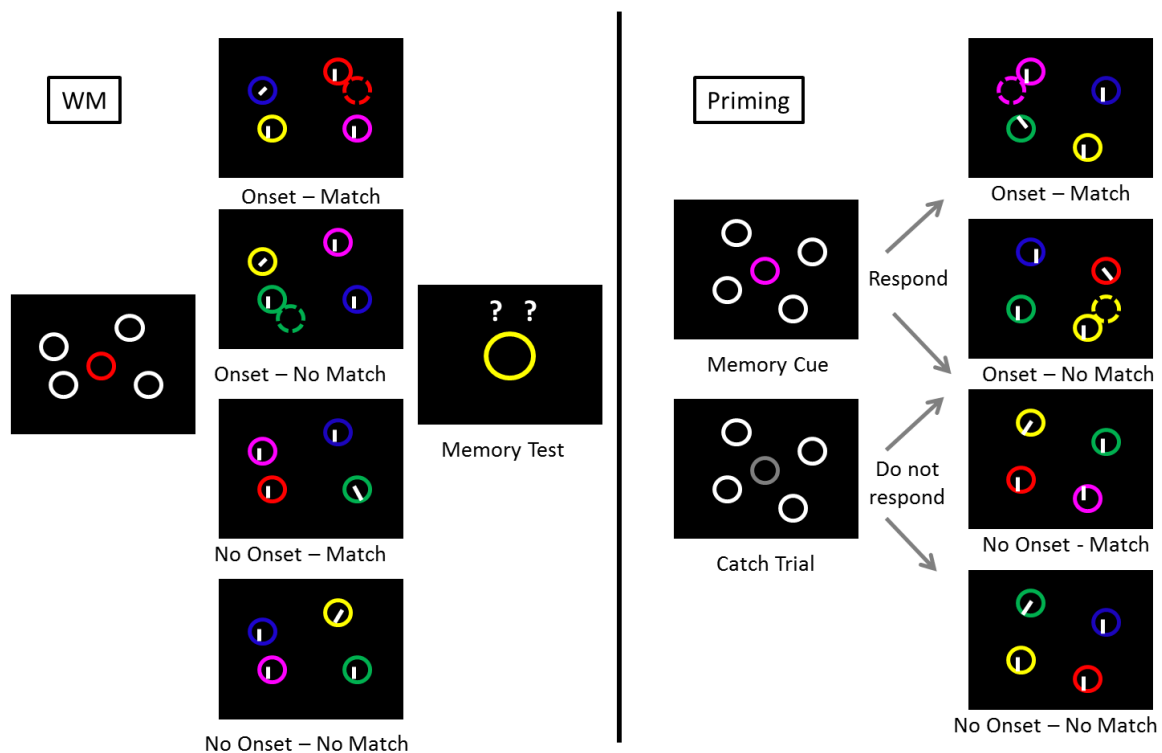


Figure 1. Trial procedure for WM and Priming blocks. Participants were first presented with a colour cue, which they were required to memorise (WM blocks) or simply look at (Priming blocks). A grey colour cue presented during Priming block 'catch' trials was the signal to withhold response to the remainder of the trial. A search display containing 4 coloured circles surrounding white lines was then presented. Participants were instructed to search for the tilted line (target) and indicate its orientation. During 'match' trials the colour cue reappeared in the search display, surrounding a distractor. Solid circles indicate original positions of the colour stimuli. During 'onset' trials one of the distractor stimuli moved to a new position, indicated by the dashed circles. A memory test was presented at the end of some WM block trials, in which the colour of a test stimulus was compared against the original cue colour.

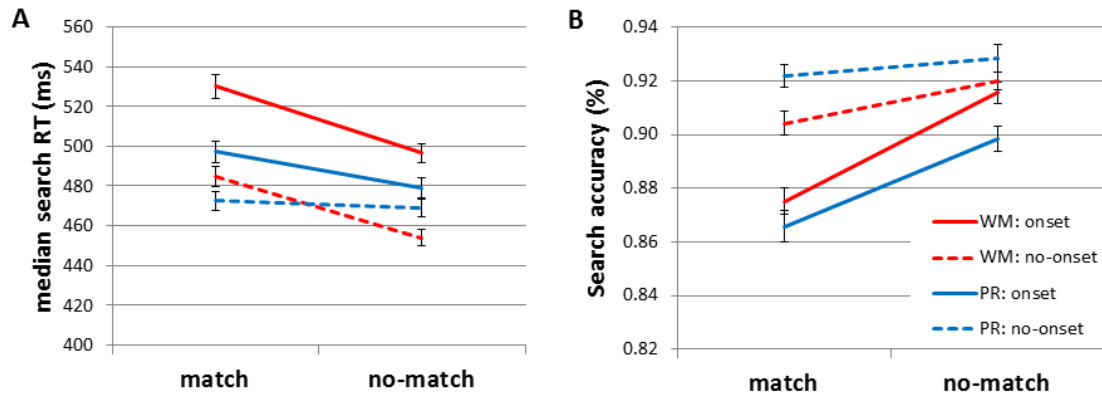


Figure 2. (A) Median search reaction time and (B) search accuracy as a function of memory, match and onset conditions. Error bars represent standard errors of the mean.

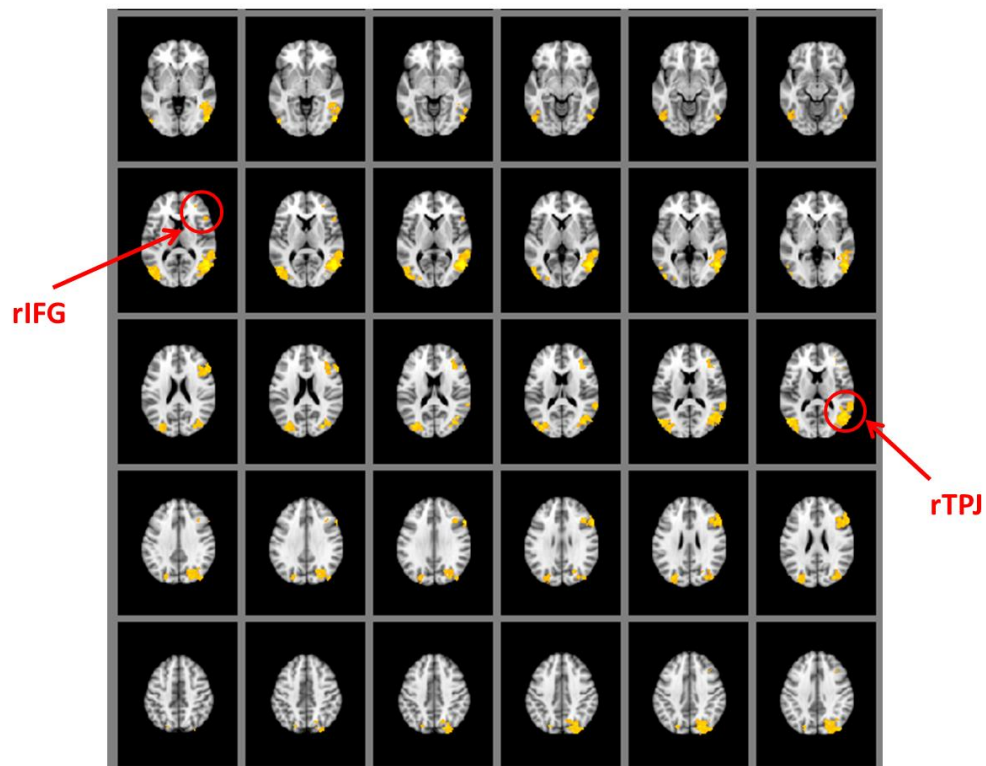


Figure 3. Regions displaying increased BOLD signal in the presence of an onset. This contrast activates regions typically associated with the ventral attention network, including the inferior frontal gyrus and temporoparietal junction. Image is in neurological orientation (R=R).

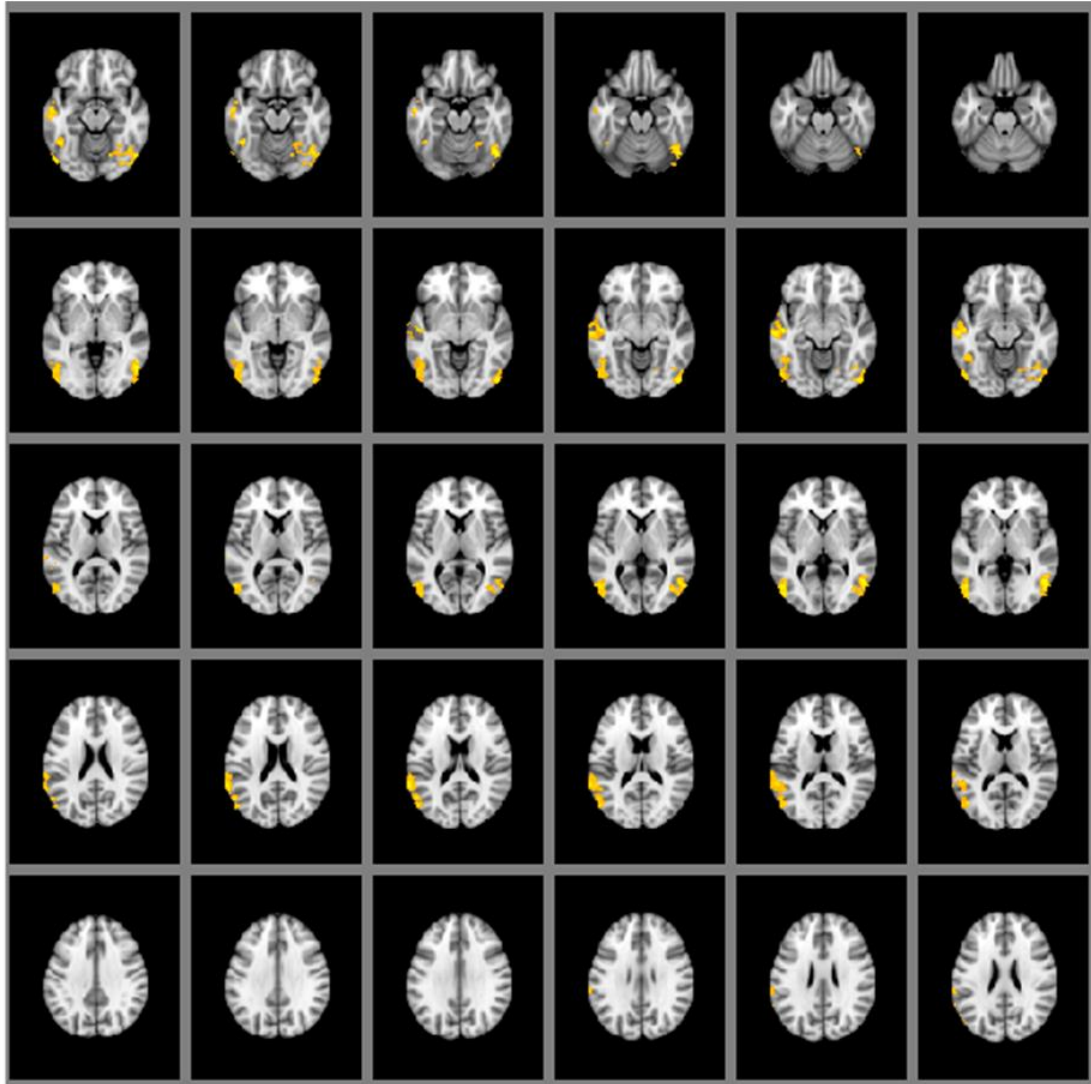


Figure 4. Regions whose activity covaried with the difference in reaction times between ‘match’ and ‘no-match’ trials during assessment of memory/match interaction. This interaction effect – whereby the effect of match trials was greater during WM blocks than Priming blocks – was enhanced in those participants who displayed increased behavioural distractibility. Image is in neurological orientation (R=R).

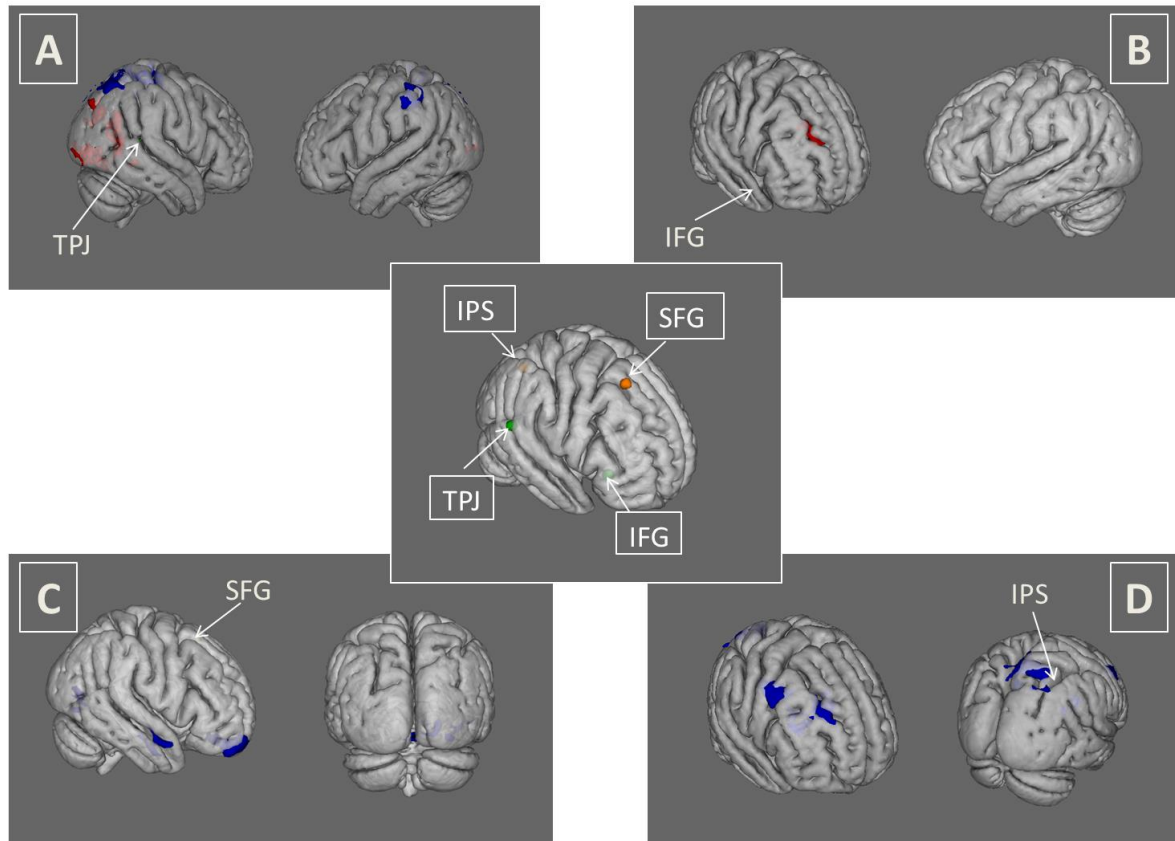


Figure 5. Functional connectivity from (A) right temporoparietal junction (B) right inferior frontal gyrus (C) right superior frontal gyrus and (D) right intraparietal sulcus. Blue voxels: regions displaying reduced connectivity with the seed region in the presence of a salient onset during WM blocks, and the opposite pattern during Priming blocks. Red voxels: regions displaying increased coupling with the seed region in the presence of a matching item during WM blocks relative to Priming blocks. The central panel illustrates the location of all four seed regions; dorsal seeds are depicted in orange while ventral seeds are depicted in green.