



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.

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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 and Humphreys, 2009; Soto et al., 2005, 2008). 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 et al., 2013) 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;

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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., 2013), 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; and (3) connectivity between the dorsal and ventral networks would be altered by memory-driven top-down guidance of attention to irrelevant stimuli.

Materials and methods

Participants

21 healthy participants (14 males, 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.

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 the 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) × 2 (match condition) × 2 (onset condition) design, with 24 trials in each experimental cell (see Fig. 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 and 8 s, with a pseudo-exponential distribution (50% of ITIs were 2 s, 25% of ITIs were 5 s, 13% were 6 s, 6% were 7 s and 6% were 8 s) 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.

Image acquisition/scanning parameters

MRI scanning was conducted using a Siemens Magnetom Verio 3 T MRI scanner and a 32-channel head coil. Following a brief localiser 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 × 220 mm, TR of 1900 ms, TE of 2.48 ms and slice thickness of 1 mm, leading to a voxel resolution of 1 × 1 × 1 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 222 × 222 mm, TR of 2200 ms, TE of 30 ms and slice thickness of 3 mm. The resulting voxel resolution was 2.4 × 2.4 × 3.0 mm.

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 s high-pass temporal filtering and spatial smoothing using a Gaussian kernel of FWHM 5.0 mm. 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

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