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Directing spatial attention in mental representations: Interactions between attentional orienting and working-memory load

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Orienting spatial attention to locations in the extrapersonal world has been intensively investigated during the past decades. Recently, it was demonstrated that it is also possible to shift attention to locations within mental representations held in working memory. This is an important issue, since the allocation of our attention is not only guided by external stimuli, but also by their internal representations and the expectations we build upon them. The present experiment used behavioural measures and event-related functional magnetic resonance imaging to investigate whether spatial orienting to mental representations can modulate the search and retrieval of information from working memory, and to identify the neural systems involved, respectively. Participants viewed an array of coloured crosses. Seconds after its disappearance, they were cued to locations in the array with valid or neutral cues. Subsequently, they decided whether a probe stimulus was presented in the array. The behavioural results indicated that orienting of spatial attention within working memory attenuates the well-known effect of decreasing performance when memory load is increased. So "internal" spatial orienting seems to highlight information or facilitate search within working memory, which leads to advantages in retrieval. Imaging enabled the separation of brain areas supporting spatial orienting functions from those sensitive to working-memory load. Orienting of spatial attention to the contents of working memory activated posterior parietal cortex bilaterally, the insula, and lateral and medial frontal cortices.

Keywords: Spatial orienting; Attention; Mental representations; Working memory; fMRI; Parietal; Frontal

Introduction

Attention can be directed voluntarily to locations in the extrapersonal world, highlighting some aspects while neglecting others, and thus biasing our perception and action in the environment. This cognitive process of spatial orienting has been extensively studied during the past decades, using a wide range of paradigms and methods. Recently, Griffin and Nobre (2003) and Nobre et al. (2004) demonstrated that it is also possible to orient spatial attention in the "internal world" in a comparable manner, i.e., to shift attention within mental representations, for instance, to locations held in working memory. This is an important issue, since internalised, mnemonic representations play a significant role in guiding our perception and action.

The demonstration of the ability to orient attention to locations in working memory extends our knowledge about the interplay between attentional orienting and working memory. Previously, several links between these two cognitive domains have been established (e.g., Baddeley, 1993; Cowan, 1988; Desimone and Duncan, 1995; Smith and Jonides, 1999). For instance, it has been proposed that the contents of working memory can direct attention spatially (Downing, 2000), that spatial attention can support rehearsal in spatial working memory (Awh et al., 1998, 1999, 2001; Postle et al., 2004), and that working memory can serve to suppress interference from distractors enabling the focussing of attention (DeFockert et al., 2001). Furthermore, several studies have reported that attention and working memory are supported by largely overlapping networks, including regions around the intraparietal sulcus and the frontal eye fields (e.g., LaBar et al., 1999; McCarthy, 1995; Pollmann and von Cramon, 2000).

This new line of research shows that it is also possible and advantageous to voluntarily orient spatial attention to locations held *within* working memory. Direct comparisons of external and internal spatial orienting of attention revealed striking similarities, at the behavioural as well as the neural level. Using a traditional experimental paradigm to investigate orienting of attention in the extrapersonal world (Posner, 1980), attention was oriented to a spatial location by an informative cue *before* a target stimulus appeared (pre-cueing). In contrast, cues presented *after* the disappearance of an array of items that has to be remembered, oriented attention to a spatial location within internal representations, i.e., the cue pointed to a location of an item held in working memory (retro-cueing). If participants were required to decide whether a probe stimulus was present in the array, a pattern of

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shorter reaction times (RTs) and higher accuracy was found if a spatial cue correctly indicated the position of an item that matched the probe (valid cue). The behavioural effects were equivalent to those obtained with pre-cueing toward upcoming arrays (Griffin and Nobre, 2003).

However, it remains unclear what processes are enhanced by attentional orienting in the working-memory domain. Orienting retro-cues may provide a shortcut for the search within working memory, enhancing the maintenance and/or selection of the attended item and leading to advantages in its retrieval. Inhibition of distracting items at irrelevant locations is also possible. Response-related factors may also come into play, though a previous behavioural experiment (Griffin and Nobre, 2003, experiment 2) showed that spatial orienting to working memory was not simply a consequence of changes in response biases.

When investigated with event-related functional magnetic resonance imaging (efMRI), activity in extensively overlapping neural networks was observed for directing attention to locations in the external world and to their representation in the internal world. In addition to a common set of activations, cues that oriented attention to working memory also engaged a number of prefrontal regions selectively (Nobre et al., 2004). The findings suggest that spatial cognition in both domains shares common neural substrates to a large extent. Prefrontal areas may contribute additional functions to task performance when working-memory representations are involved.

However, the specific functions contributed by prefrontal areas during spatial orienting to working-memory arrays remain unclear. These could have contributed directly to the spatial orienting effect, for example, by providing the source of the top–down biasing signal when working memory was involved (Desimone and Duncan, 1995; Downing, 2000). Conversely, they could have contributed other functions not specifically related to spatial orienting, but instead more general functions afforded by the task in those types of trials. For example, retro-cues enabled participants to select the target item from the array and to inhibit distractor stimuli, but pre-cues did not.

In addition, the comparisons between retro-cues and pre-cues might have been confounded by memory load. Nobre et al. (2004) investigated orienting processes by analysing brain activity evoked by the cue stimuli. Pre-cues were always presented at the beginning of a trial before an upcoming array and did not require memorisation of any information, whereas the retro-cues were presented after the array had to be memorised. That is, retro-cueing always occurred in the context of working memory, whereas pre-cueing did not. If the measures of brain activity elicited by the cue were partly contaminated by activity during the preceding intervals, then activity related to retro-cueing could also reflect in part load within working memory.

The present experiment was designed to address these questions by investigating the interaction between retro-cueing and working-memory load with efMRI. We adopted the experimental task used in previous studies (Griffin and Nobre, 2003; Nobre et al., 2004) and introduced the additional factor of working-memory load, by varying the number of items in the array (see Fig. 1 for a schematic of the task). This manipulation enabled us to separate the effects of memory load from the effects of spatial orienting within working memory, and to disentangle the contributions from the largely overlapping neural networks supporting these processes.

Furthermore, if spatial orienting improves the search or selective retrieval of information held in working memory, there should be an interactive effect between spatial orienting and

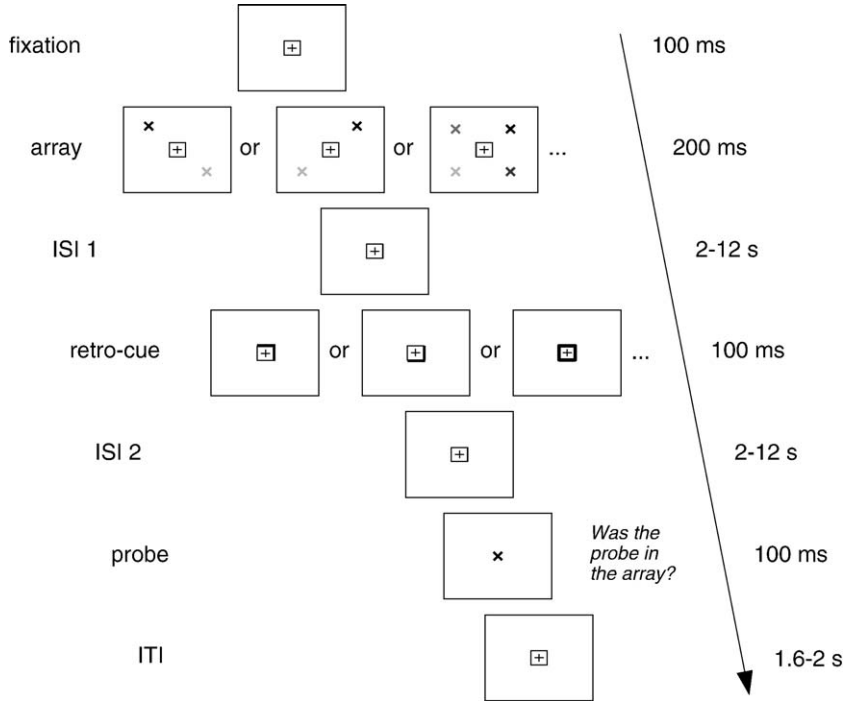

Fig. 1. Schematic outline of the task. An array of two or four differently coloured crosses was presented (the colours could be any out of the following: yellow, green, ash, blue, cyan, orange, red or pink), followed by a retro-cue, which either validly indicated the position of the cross matching the probe or gave no information (40% neutral trials). Afterwards, participants had to indicate with a forced-choice response whether or not the probe stimulus was present in the array (chance was 50% probability). The intervals varied pseudo-randomly within the given limits. On average, one trial lasted for 12.5 s. See Methods section for details. (Abbreviations: ISI = inter-stimulus interval; ITI = inter-trial interval.)