BRAIN RESEARCH

Research Report

Cognitive control of attention in the human brain: Insights from orienting attention to mental representations

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ABSTRACT

In this review, we summarize a new line of experimentation showing that attentional orienting can bias information processing in the working memory domain as well as in the perceptual domain to optimize goal-directed behavior. A new experimental paradigm was developed, which revealed that spatial orienting cues that appear after perceptual events (retro-cues), when these have been internalized into working memory representations, can retrospectively enhance performance to a similar degree as spatial precues appearing before perceptual events. As part of their facilitatory action, retro-cues diminish the costs of retrieving items from increasing loads within working memory. Hemodynamic and electrophysiological brain imaging experiments show a high degree of overlap between brain areas and dynamics involved in spatial orienting in the working memory domain compared to the perceptual domain. In addition, functional magnetic resonance imaging points to the selective involvement of frontal areas during spatial orienting in the working memory domain. The roles of different frontal areas remain to be clarified but may include both early roles in guiding spatial shifts occurring within a mnemonic context as well as selection of memorized targets amidst distracting stimuli. Experiments have also begun to reveal the ability to orient attention selectively to object-based representations in working memory and suggest that the neural representations of objects in working memory can be directly modulated by this process. The findings bolster contemporary notions of a strong theoretical relationship between attentional orienting and working memory, suggesting that these two cognitive functions interact in more ways and directions than previously considered.

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Attentional orienting is the major set of psychological functions that dynamically guide and optimize our perception and action through the bombardment of information that hits us through every sensory modality and at every level. It can be defined as the selective biasing of information processing towards specific attributes of events based on changing motivation, volition, or expectation.

Research so far has mainly investigated attentional orienting in the perceptual domain, that is, orienting to attributes of perceptual stimuli, based on perceptual cues. Striking examples in this field are the research on orienting to spatial locations (Posner, 1980) and objects (Duncan, 1984), but it is also possible to orient attention to other attributes like time (Coull and Nobre, 1998; Nobre, 2001a; Griffin and Nobre, 2005), intentions and actions (Lau et al., 2004; Rushworth et al., 1997, 2001, 2003), semantic associations (Cristescu et al., 2003a,b; Moores et al. 2003), and more. The use of brain imaging techniques during the last decades has contributed to the

dominant view of a large-scale network built around a critical parietal–frontal axis, which modulates information processing from early stages of perceptual analysis through top-down influences (Nobre, 2004b; Mesulam et al., 2005; Kastner and Ungerleider, 2000).

Despite the unquestionable progress of research on attentional orienting, it has left out one important aspect of our cognitive experience. As humans, much of our world is based on mental representations that are constructed from our experiences and interactions with the external world. We constantly build, retrieve, and update these mnemonic representations. Although intuition suggests that we should also be able to orient our attention to the selective attributes of our mental representations, this possibility has remained relatively unexplored.

The current article reviews the first steps in a research program that investigates the ability to orient attention selectively to the contents of mental representations maintained in working memory. As a shorthand nomenclature, we refer to these as "internal" representations to signify that they are mnemonic in nature and independent of the persistence of external visual stimulation. We contrast the ability to bias access to or retrieval from these internal representations to the ability to bias the processing of perceptual representations triggered by external input. We refer to the latter type of representation as "external" to emphasize their dependence on external stimulation. (We do not mean to imply by this nomenclature that perceptually driven representations lack a concomitant "internal" or mental counterpart.) We put forth a simple experimental paradigm with which to investigate selective attentional orienting toward the contents of working memory and review results from experiments using complementary brain imaging methodologies investigating the neural basis of this process.

1. Experimental paradigm

The first aim of the research program was to ascertain if it is possible to orient attention voluntarily to the contents of working memory representations in a similar way to how we orient our attention to perceptual stimuli in the external world and thereby improve behavior.

To answer this question, Griffin and Nobre (2003) developed a new paradigm, which joined the traditional cueing paradigm to investigate visual spatial orienting (Posner, 1980) with the partial-report paradigm (Sperling, 1960; Averbach and Coriel, 1961) used to probe specific aspects of iconic memory traces of briefly presented visual arrays (Fig. 1). In the basic experimental task, participants viewed a stimulus array and were later asked to determine whether a probe stimulus had been present or absent within the array (50% probability). Spatial cues shown before the array (precues) and predicting the likely location of the probe stimulus in these search conditions have been known to improve performance relative to when a neutral, uninformative precue is provided (e.g., Posner, 1980; Jonides, 1981). In the new and critical condition, spatially informative cues were presented seconds after the presentation of a stimulus array (retro-cue), indicating retrospectively the location where a relevant stimulus was present. The principal question was whether spatially predictive retro-cues could optimize behavior based on an internalized representation of the array that existed only within working memory. The behavioral benefits and costs of precue and retro-cue conditions were assessed within subjects using accuracy and reaction time measures when cues were spatially informative (80% validity) or neutral.

In contrast to previous research using exogenous cues to probe the contents of iconic memory (Dixon et al., 1997), these new experiments used endogenous cues to orient attention voluntarily to spatial locations of representations maintained in working memory. Whereas previous research has investigated how the validity of exogenous spatial cues can impact upon the transfer of contents into working memory (Vogel et al., 2005; Schmidt et al., 2002), the new experiments asked whether access to or retrieval from working memory is itself under voluntary control. Finding that retro-cues can significantly alter behavioral performance in these working memory search conditions would strongly argue against the established dogmatic position that retrieval from working memory follows an automatic serial process (Sternberg, 1966, 1975). In
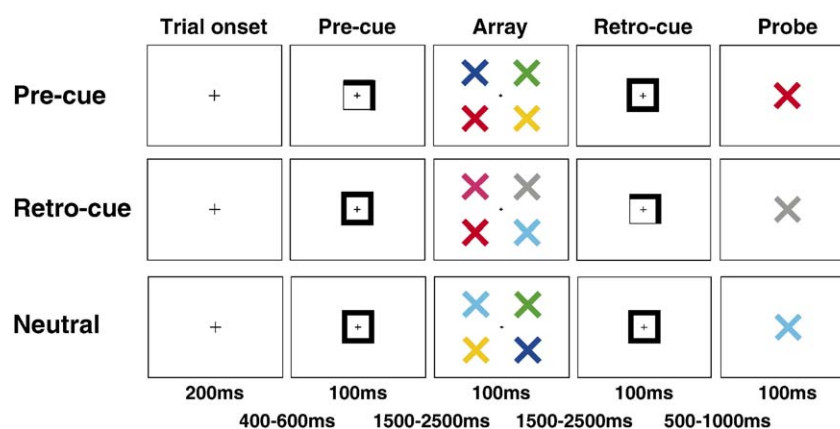
Fig. 1 – Retro-cueing paradigm. In all trials a precue, an array of four differently colored crosses, a postcue and a probe were presented. Informative cues indicated the relevant location in the array with a validity of 80%. In neutral trials, the cues were not spatially informative. In all trials, participants indicated if the probe had been present or absent in the array (50% probability).

the experiments reviewed, the number of items presented in the array was presumed to fall within the limits of working memory capacity (Luck and Vogel, 1997; Vogel et al., 2001; Wheeler and Treisman, 2002). In addition, the intervals between the presentation of the array and the retro-cue in the presented experiments were chosen to be long enough to ensure that selective attention operated within the domain of working memory and not during the iconic memory period (see Coltheart, 1980; Sperling, 1960).

The behavioral results showed that being validly cued retrospectively to a particular location within the working memory representation led to significant accuracy and reaction time benefits compared to having no information about which location would be probed (neutral cue) (Fig. 2). Invalid retro-cues made accuracy of performance significantly worse. These results strongly suggested that retrieval from working memory is not a fully automatic process (Sternberg, 1966). Interestingly, the cueing effects found with retro-cues were highly comparable to those conferred by precues. These, in turn, replicated the well-known effects of orienting spatial attention to upcoming visual arrays (Posner, 1980; Jonides, 1981; Müller and Findlay, 1987; Müller and Rabbit, 1989). A follow-up experiment in which the memory of each location of the array was probed separately showed that the effects did not simply result from differential response biases to cued versus uncued locations (Griffin and Nobre, 2003; Experiment 2). Instead, the findings pointed to improved quality of the representation of the relevant item within working memory or improved access to it, such as through an optimized search operation.

2.   Neural control

Inspired by the striking behavioral similarities between spatial orienting to an internal versus external representation, event-related functional magnetic resonance imaging (fMRI) and event-related potentials (ERPs) were used to investigate and compare the cortical substrate of both processes.

As mentioned above, numerous studies have investigated the brain areas coordinating spatial orienting to external events with fMRI (e.g., Corbetta et al., 1993; Nobre et al., 1997, 2001b, 2004; Gitelman et al., 1999; Corbetta and Shulman, 2002a;

Kastner and Ungerleider, 2000; Yantis et al., 2002; Giesbrecht and Mangun, 2005) and ERPs (Nobre et al., 2000; Harter et al., 1989, Yamaguchi et al., 1994; Van Velzen and Eimer, 2003; Hopf and Mangun, 2000), but spatial orienting to internal events has remained relatively unexplored. However, several lines of research have emphasized the close interplay between attentional orienting and working memory: reporting overlapping neural networks (McCarthy, 1995; LaBar et al., 1999; Pollmann and von Cramon, 2000), demonstrating functional similarities (Awh and Jonides, 2001; see also Downing, 2000; DeFockert et al., 2001), and positing a close link at the theoretical level (Desimone and Duncan, 1995; Baddeley, 1993). These proposed commonalities between the mechanisms of spatial attention and working memory suggest that a scene in working memory can be scanned in a spatial fashion, similarly to a perceptual scene. In addition, reports from patients with hemispatial neglect indicate impairments in the spatial representation of or access to mental representations (Bisiach and Luzzatti, 1978; Bisiach et al., 1979). This type of neglect involving internal representations can, in some cases, be dissociable from neglect for the extrapersonal space (Ortigue et al., 2001; Beschin et al., 2000; Coslett, 1997; Guariglia et al., 1993), suggesting that the neural mechanisms for orienting attention to internal versus external representations may differ partly in terms of the necessary brain areas or connections.

2.1.   Functional magnetic resonance

A simplified version of the retro-cueing paradigm was developed for investigation with fMRI (Nobre et al., 2004a). Participants were asked to decide whether the final probed item corresponded to the item in the location that had been cued before or after the presentation of the array. The cues were therefore imperative and forced an obligatory shift of attention to one location in the array. Long and jittered intervals (2–15 s) were interposed between the events of each trial in order to de-correlate their hemodynamic responses and to avoid temporal expectations (Griffin and Nobre, 2005). Brain areas supporting spatial orienting to external or internal events were identified by comparing spatial versus neutral precues and retro-cues, therefore minimizing the contribution of unspecific processing of cue stimuli, such as perceptual analysis, alerting, or interpretation of their meaning.
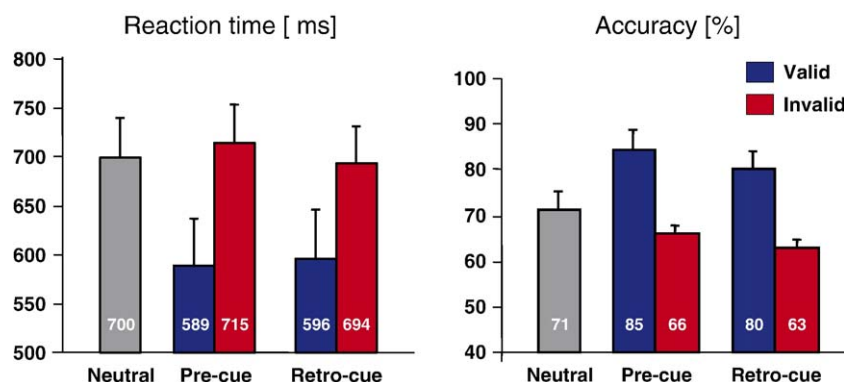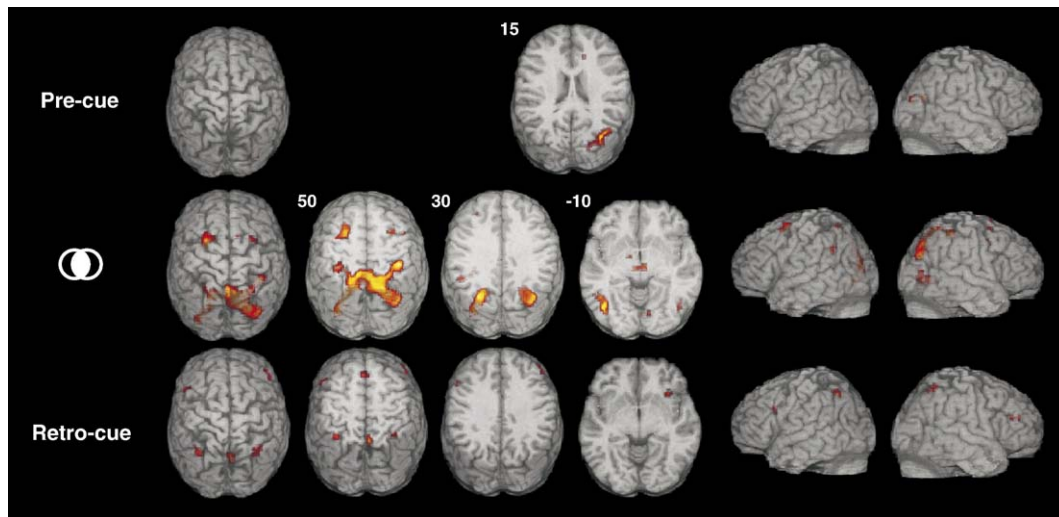

Fig. 2 – Behavioral results. Mean (±SEM) reaction time and accuracy measures (target present responses only). (N = neutral; V = valid; I = invalid; numbers indicate reaction times in milliseconds and accuracies in percent, respectively).

Fig. 3 – fMRI results. The top row shows brain areas selectively active for pre- over retro-cues, and the bottom row brain areas selectively engaged for retro- over precues. The middle row shows the results of a conjunctions analysis revealing regions commonly activated by both precues and retro-cues. The numbers indicate the location of the axial slice in MNI space.

Spatial precues and retro-cues both trigger a shift in spatial attention, operating in the working memory and perceptual domains, respectively. A strong overlap in the pattern of activation, including recruitment of the parietal–frontal circuit identified to control spatial shifts in the perceptual domain (Vandenberghe et al., 2001a; Yantis et al., 2002), would therefore suggest that common mechanisms for spatial orienting could operate across both types of domain; whereas distinct patterns of activation would suggest that the system for spatial orienting was largely determined by the domain in which spatial shifts occur. However, in addition to the spatial shifts, precues and retro-cues also trigger other processes within the context of the task. Spatial shifts in the perceptual domain are anticipatory in nature, and occur in the absence of any given preexisting perceptual representation.[1] Precues may therefore also generate a sustained anticipatory biasing of task-relevant perceptual areas. Retro-cues operate upon preestablished working memory representations. The spatial shift can lead directly toward selection of the relevant item and/or concomitant filtering of distractor stimuli. Neither type of cue can lead to further decision-making processes, which are delayed until the appearance of the final probe stimulus.

Spatial orienting to internal and external representations both engaged a large network involving parietal, frontal, and visual cortices. Common activity covered large part of the posterior parietal cortex bilaterally, including precuneus, superior parietal lobule, and intraparietal sulcus (Fig. 3, middle). In the frontal cortex, activity occurred in the frontal eye fields (Paus, 1996; Luna et al., 1998) and more inferiorly in the lateral premotor cortex bilaterally. The extensive neuroanatomical overlap complements the highly comparable

behavioral effects found for precues and retro-cues and indicates that spatial orienting in both the perceptual and working memory domain share some common substrates. The areas of common activation were similar to those reported during visual spatial orienting (Yantis et al., 2002; Beauchamp et al., 2001; Hopfinger et al., 2000; Gitelman et al., 1999; Nobre et al., 2001b; Kastner and Ungerleider, 2000; Corbetta, 1998, Corbetta et al., 2000; Vandenberghe et al., 2001a). The findings suggest that the sensorimotor parietal–frontal circuits capable of coding events within spatial frameworks for action mediate spatial orienting in both the perceptual and working memory domains (Nobre, 2004b).

In line with the multiple functions or precues and retro-cues within the task, differences in activations were also observed. Precues preferentially activated the intersection of right parietal, temporal, and occipital cortices (Fig. 3, top). This area was speculatively proposed to maintain the spatial focus of attention and/or to provide top-down biases for more ventral visual areas (Vandenberghe et al., 2001b). Selective activations for retro-cues over precues occurred in several frontal regions, namely, the medial premotor areas, right middle frontal gyrus, right ventrolateral prefrontal cortex adjacent to anterior insula, and left posterior inferior frontal gyrus (Fig. 3, bottom). These prefrontal areas have commonly been reported in tasks involving working (D'Esposito et al., 2000; Haxby et al., 2000; Owen, 2000; Smith and Jonides, 1999; McCarthy et al., 1996) and tasks that involve executive processes to achieve behavioral goals (Duncan et al., 2000; Miller, 2000; Miller and Cohen, 2001).

There are several possible explanations for the role of these areas in retro-cueing. The first possibility is that frontal areas are selectively involved in generating spatial shifts when these occur within a mnemonic context. In this case, the spatial orienting networks would not be co-extensive in the perceptual and working memory domains; however, orienting in the working memory domain would additionally rely on some selective frontal signals. Alternatively, prefrontal activity could reflect

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[1] However, it is possible that mental imagery or memory is used to establish some kind of representation template upon which the spatial expectations can work in preparation for the perceptual input.

other functions triggered by retro-cues, such as selection of a target item among distractors (Thompson-Schill et al., 2002).

Some interpretations can be ruled out. Selective frontal activations by retro-cues cannot be explained by simply maintaining information in working memory, because (1) the activity related to retro-cues and not the delay-activity was analyzed, and (2) valid retro-cues were always compared against neutral retro-cues, thus equating any load-related maintenance activity. In addition, the design of the paradigm delayed decision making and response selection to the later probe presentation phase of the trial so that these processes also cannot account for the present activations.

Spatial retro-cues also enhanced activity in some commonly activated parietal regions, specifically along the middle aspect of the intraparietal sulcus bilaterally, and the medial superior parietal lobule and precuneus. These areas resemble those proposed to control the shifting of the spatial focus of attention in the extrapersonal world (Vandenberghe et al., 2001a; Hopfinger et al., 2001; Yantis et al., 2002; Beauchamp et al., 2001; Corbetta et al., 2002b). Research on posterior parietal cortex in nonhuman primates has revealed that some of these areas may show specialization for multiple functions related to spatial cognition. For example, activity in LIP is modulated by intended eye movements, attentional monitoring, and working memory (Colby et al., 1996). In addition, increased activity in the precuneus has been reported in tasks involving mental imagery (Ishai et al., 2000), a process which may play an important role during internal orienting, with retro-cues triggering the access/search through the mental images of the array in working memory.

In summary, this experiment demonstrated that orienting attention to both external and internal events activates a highly overlapping network of posterior parietal and frontal brain areas, suggesting strong commonalities of both processes. The selective involvement of frontal brain areas during spatial orienting to internal events points towards additional specific processes, either directly related to triggering or controlling "internal orienting" or related to target selection and distractor inhibition.

2.2. *Event-related potentials*

To gain further insights into the commonalities and differences of the neural processes involved in internal versus external orienting, the simplified retro-cueing task (as used for the fMRI study) was also adapted for investigation with event-related potentials (ERPs) (Griffin and Nobre, 2003; Experiment 3). The high temporal resolution of ERPs permits investigating the degree of overlapping mechanisms in real time. The findings again suggested a large degree of overlap between spatial orienting in perceptual and working memory domains (Fig. 4). Both types of orienting elicited directionally sensitive lateralized posterior followed by anterior potentials (Nobre et al., 2000; Harter et al., 1989; Yamaguchi et al., 1994; Van Velzen and Eimer, 2003; Hopf and Mangun, 2000). However, some early differences between spatial orienting in the two domains were also observed. Retro-cues selectively elicited early activity that was distributed over frontal regions of the scalp. Although

several difficulties plague the identification of the neural sources of components of ERPs, especially in complex cognitive tasks, the early frontal component supports the possibility that (some of) the prefrontal regions selectively engaged by spatial retro-cues in the fMRI experiment (Nobre et al., 2004a) may play an early role in triggering spatial orienting within the working memory domain.

Modulation of late potentials related to cognitive evaluation and response variables was also observed, in agreement with the additional different functions afforded by spatial precues and retro-cues.

The ERP results therefore further supported a high degree of overlap in the dynamics of brain activity during spatial orienting to perceptual and working memory arrays, as well as in the brain areas involved. The high temporal resolution of the method, however, also indicated that the processes are not equivalent, and that the early stages of spatial shifts in the working memory domain involve additional processes, reflected by a frontally distributed component. Further research will be required to clarify the contribution of prefrontal areas to this component, and the putative contribution of prefrontal areas in generating spatial shifts in the working memory domain.

The ERP results also indirectly address another very basic and important question concerning the nature of mental working memory representations. Intuitively, it is assumed that mental representations have some sort of analogue, pictorial instantiation, replicating the array presented before, which enables it to be searched in a spatial fashion. However, this assumption remained untested, and other forms of organization for such mnemonic representations are conceivable, including one that is only propositional in nature and bears no resemblance to any perceptual input. The lateralized differences in ERPs following leftward and rightward retro-cues and the similarity of these effects to those engaged when orienting toward a perceptual array suggest that spatial mechanisms can also be engaged to interact with mental representations, providing some support for the assumption that mental representations are spatially organized.[2]

3.   Putative mechanisms

The promise of these early findings prepared the ground for addressing the next series of questions, relating to the mechanisms by which attentional orienting can optimize working memory performance. Several possibilities come into mind: Most intuitively, orienting could optimize searching through the working memory representation by providing a spatial shortcut for search, such as by spatially biasing or directing the search. It is also possible that spatial orienting leads to a selective enhancement of a particular item or location within the representation, that is, an enhancement of the maintenance of the specific relevant information. Alternatively, orienting could enhance spatially specific retrieval

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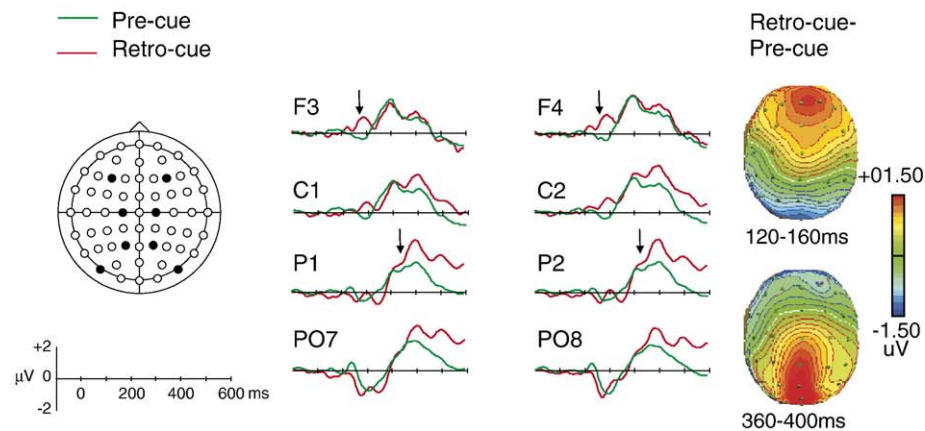[2] We thank one of the reviewers for this most interesting proposal.
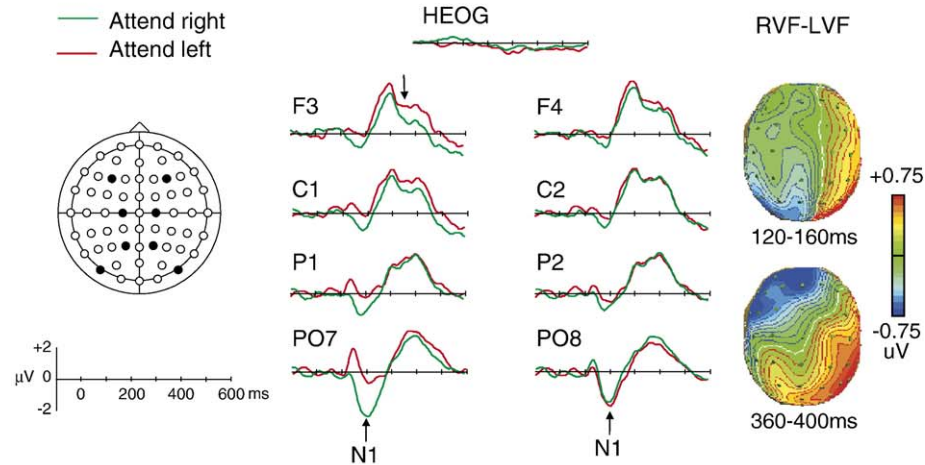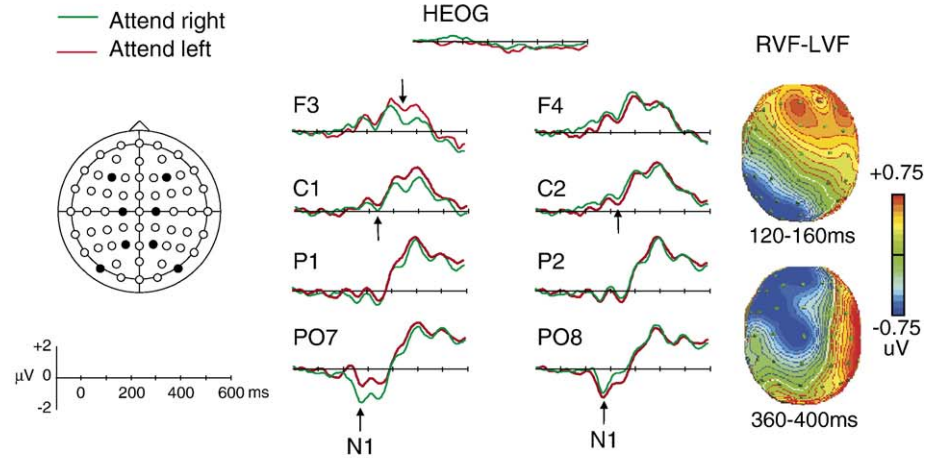
Fig. 4 – ERP results. Grand-averaged waveforms elicited by precues (top panel) and retro-cues (middle panel) when subject attended the left (red line) and right (green line) visual fields. The bottom panel shows grand-averaged waveforms elicited by precues (green) and retro-cues (red). To isolate the effects of spatial orienting, all waveforms have had the waveforms from the neutral cue that occurred at the same time point subtracted from them. The arrows indicate statistically significant effects. HEOG = horizontal eye channel; RVF = right visual field; LVF = left visual field.
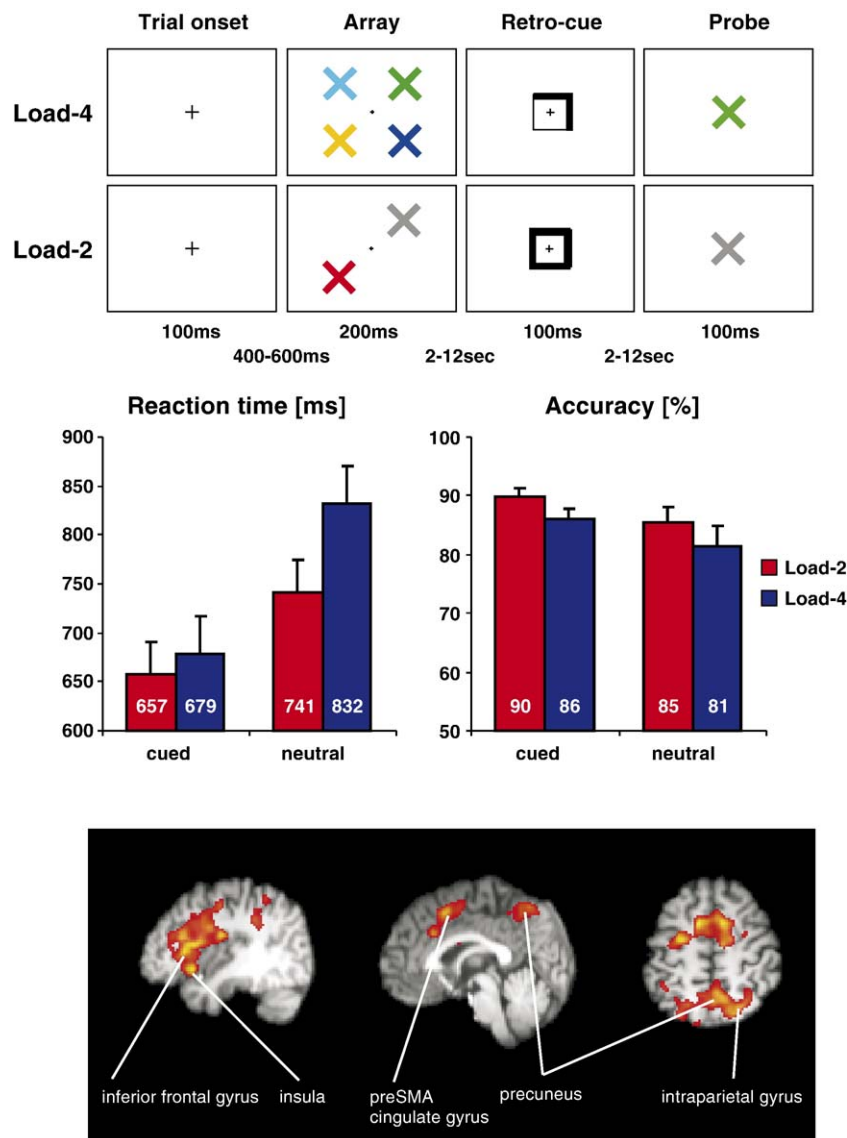
Fig. 5 – Interactions between attentional orienting and working memory load. The top panel shows a schematic of the experimental paradigm. The task resembles the basic retro-cueing paradigm, except using retro-cues with a validity of 100% (imperative cues) and neutral cues only. The intervals between the array and the retro-cue and the retro-cue and the probe were varied in a pseudo-randomized fashion in order to enable to separate activity related to different phases of the trial. To manipulate working memory load, the size of the array varied between two or four differently colored crosses. The middle panel shows mean (±SEM) reaction time and accuracy measures (target present responses only). The bottom panel reports brain areas showing a significant interaction of orienting spatial attention to locations stored in working memory and working memory load (see text for details).

mechanisms or inhibition of distracting information at irrelevant locations. Finally, participants could also develop response strategies by which they were more likely and/or faster to respond to items at the attended locations (Kinchla et al., 1995).[3] These different possibilities are by no means mutually exclusive, and the actual mechanism might be composed of a combination of them.

To investigate the mechanism of spatial orienting within working memory, Lepsien et al. (2005) introduced a working memory load manipulation into the retro-cueing paradigm in an fMRI study (Fig. 5, top). The specific aims of the experiment were (1) to separate unequivocally the effects of working memory load from the effects of spatial orienting; (2) to disentangle activity related to each of these processes within the largely overlapping neural networks; and, most importantly, (3) to investigate the interaction between spatial orienting and working memory load to shed some light on possible mechanisms involved.

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[3] Although previous experiments have ruled out response strategies as being the sole explanation (Griffin and Nobre, 2003; Experiment 2), differential response weighting may still contribute to the effects in an additive manner.

Increased working memory load typically leads to decreases in retrieval performance (Sternberg, 1966). However, if spatial orienting improves the search or selective retrieval of information held in working memory, this negative effect of load on the performance should be attenuated, and the performance should be less affected as the working memory load increases.

The behavioral results replicated both speed and accuracy benefits of valid retro-cueing for deciding whether the probe item was present in the array (Fig. 5, middle). In addition, the results showed a main effect of working memory load, replicating the classical pattern reported by Sternberg (1966), which has led to the common interpretation that working memory retrieval proceeds via a serial and exhaustive search mechanism, with each additional item adding a fixed time to the search process (Sternberg, 1975). However, the effect of load in the current study was diminished by orienting spatial attention to the array in working memory, as indicated by an interaction between cueing and load, especially in target-present trials. The increase in reaction times with higher levels of load was much smaller for cued as compared to neutral trials. A trend towards this pattern was also found for accuracy. These results challenge the standard view on the automaticity of working memory retrieval, indicating that an exhaustive and serial search is not obligatory, but that attention can facilitate the search through working memory, leading to advantages in retrieval.

The fMRI data were analyzed in a comparable fashion, that is, by investigating the interaction of spatial orienting and working memory load (contrast: [(cued/load-4-cued/load-2)-(neutral/load-4-neutral/load-2)]). The pattern of activation resembled the parietal–frontal activations reported for orienting attention following precues and retro-cues (Nobre et al., 2004a) (Fig. 5, bottom). In addition, extensive left frontal activations were observed, covering the anterior insula, and extending into frontal operculum and inferior frontal gyrus. The specific contrast used in the current study ensures unequivocally that the activations are not contaminated by any simple difference in working memory load. This clarifies that these same areas activated by spatial retro-cues relative to precues in the previous experiment (Nobre et al., 2004a) are not simply related to retro-cues appearing within a period involving maintenance of information in working memory. In the current study, the activity in these areas was driven by the spatial orienting to locations stored in working memory under increasing selection demands due to increasing levels of load. Together with the behavioral findings, this suggests that retrocues optimize the search and retrieval of the attended item. In this particular context, the frontal activations are most consistent with selective retrieval of target information and/or inhibiting irrelevant distractors. These regions show increased activity as the number of possible target locations (and therefore also distractors) increases. Previous studies have also suggested that the inferior frontal gyrus may be involved in selection of information among competing alternatives (Thompson-Schill et al., 1997), or in the guidance of controlled retrieval functions (Wagner et al., 2001; Thompson-Schill, 2003).

Although the current study makes some headway in revealing how spatial orienting may optimize retrieval functions in working memory, it does not address the possibility that the quality of the representation of selected items within working memory may be altered by attentional orienting. In the perceptual domain, several studies have shown that the response in specialized cortices is enhanced if attention is directed towards a location or stimulus feature that is represented therein (e.g., Moran and Desimone, 1985; Tootell et al., 1998; Corbetta et al., 1991; Le et al., 1998; Chawla et al., 1999; Giesbrecht et al., 2003; O'Craven et al., 1999; Serences et al., 2004). In other words, orienting attention influences the cortical representations of these stimuli. Conceptually extending this principle leads to the intriguing possibility that orienting attention in memory could have a comparable effect on mental representations. Attentional orienting could 'highlight' information in working memory by selectively enhancing activity associated with the maintenance of the relevant information.

This hypothesis was tested in a follow-up fMRI study (Lepsien and Nobre, 2005), which also investigated the ability to orient attention to the representation of objects held in working memory. The retro-cueing paradigm was adapted so that retro-cues presented during the retention interval-directed attention to one out of two objects held on-line in working memory. Pictures of faces and outdoor scenes were chosen as objects, capitalizing on the extensive research indicating that their perceptual analysis includes specialized regions in the posterior fusiform gyrus (faces), and the parahippocampal gyrus, respectively (scenes) (Allison et al., 1994; Puce et al., 1995; Kanwisher et al., 1997, Epstein and Kanwisher, 1998; Aguirre et al., 1998). In addition, these areas show sustained activity during the maintenance of faces and/ or scenes in working memory (Ranganath et al., 2004; Druzgal and D'Esposito, 2001; Postle et al., 2003), indicating their involvement in storing such stimuli. Measuring the activity in these areas following the presentation of retro-cues could therefore reveal if attentional orienting can enhance the mental representation of an object itself. The prediction was that maintenance-related activity in the fusiform and parahippocampal gyrus should increase when the mental representation of a face or scene is attended, respectively.

Behavioral results showed that object-based orienting led to improved working memory performance (Lepsien and Nobre, 2005). Measures of activation (parameter estimates) extracted from the fusiform and parahippocampal gyri during the delay period before the retro-cues replicated showed sustained and selective working memory activity in these areas, replicating previous results. The signal extracted from the delay period after the presentation of the retro-cue showed clear selective modulation depending on the relevance of the stimuli coded in that region. Fusiform activity increased when attention was oriented to the mental representation of the face in working memory. Accordingly, parahippocampal activity increased when attention was oriented to the representation of the scene (Fig. 6). The experiment therefore revealed that orienting attention to mental representations in working memory can change the representation itself, by enhancing selective portions of the maintenance-related activity.

4. Conclusions and implications

The line of research presented in this review supports the conceptualization of attentional orienting as a flexible
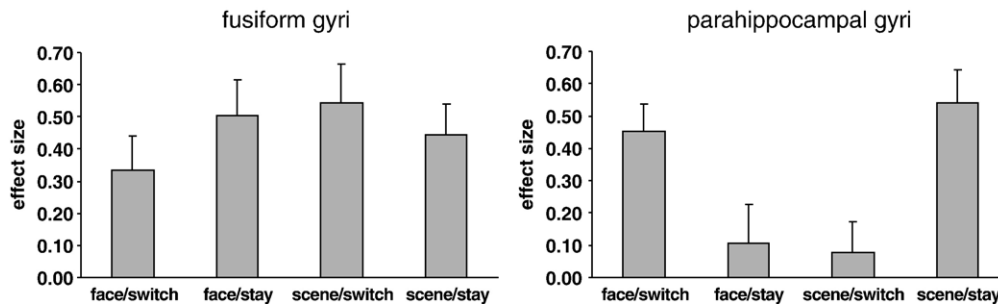
Fig. 6 – Modulation of maintenance-related activity. The bar plots show effects sizes (parameter estimates) extracted in the fusiform and parahippocampal gyri. The task required the subjects to memorize a face and a scene. A first cue indicated to orienting their attention either to mental representation the face or the scene in working memory (cue 1: face, scene), and a second cue instructed them to shift their attention from the currently attend representation to the other one, or to maintain the current focus of attention (cue 2: switch, stay). The effect sizes for the four different conditions face/switch, face/stay, scene/switch, and scene/stay were extracted from the retention interval following the second cue.

mechanism to optimize perception and action in the perceptual as well as mnemonic domain. The demonstration that it is not only possible to orienting attention to locations and objects in the extrapersonal world, but also to the internalized representations we build from these, adds a new aspect to the concept of attentional orienting. The direct comparison of both processes revealed striking similarities, both in terms of behavioral cueing effects, and highly overlapping networks.

There is broad consensus about the control of attention being implemented in a widespread network of parietal, frontal, and subcortical areas, with the core elements of posterior parietal cortex and the frontal eye fields. This has been confirmed using a variety of attentional orienting tasks and methodologies (Mesulam, 1981, 1999). Current research has started to characterize the functional specializations in the different subregions within the network, in terms of the different types of expectations they can support (e.g., spatial locations and temporal intervals) (Coull and Nobre, 1998), and the types of functions they can perform within a set of expectations (e.g., shifting versus holding the spatial focus) (Vandenberghe et al., 2001a; Yantis et al., 2002). Undoubtedly, there is much fine-grained heterogeneity still to be revealed within this parietal–frontal network.

Recent research has suggested that additional brain areas with relevant functional specialization join the core network depending on the actual context in which attention is oriented. For example, in the case of orienting to temporal intervals in tasks requiring speeded motor responses additional left-hemisphere parietal and premotor areas involved in motor preparation become involved (Nobre, 2001a, 2004). In the case described here, of orienting attention to mental representation in working memory, prefrontal areas join the core network, pointing towards additional control functions involved in orienting to mental representations. Orienting attention in the perceptual as well as in the working memory domain both involve top-down biases to select relevant information and/or suppress distractors to enhance perception and action. However, unsurprisingly, the processes of orienting attention to external versus internal events also differ in their cognitive demands. The former typically requires sustained attention after the orienting cue in anticipation of the stimulus array. In contrast, the latter requires maintenance and selective retrieval of information from a preexisting working memory representation. The result that both types of orienting attention are supported by highly comparable networks is all the more exciting in light of these substantive differences in cognitive demands.

This line of research has also crossed the boundaries between investigations of attentional orienting and working memory. These two major cognitive domains have been mostly studied in isolation, although a number of studies have stressed a strong relationship between them (e.g., Baddeley, 1993; Cowan, 1988; Desimone and Duncan, 1995; LaBar et al., 1999; Pollmann and von Cramon, 2000; Downing, 2000; DeFockert et al., 2001). Recent models of working memory suggest that the maintenance of information is accomplished by directing attention to the representations of this information, stored in posterior brain areas (for recent reviews see Curtis and D'Esposito (2003), Ranganath and D'Esposito (2005)), and that spatial attention supports rehearsal in spatial working memory, by means of focal shifts of spatial attention to the memorized location, respectively (Awh et al., 1999, Awh and Jonides, 2001; Postle et al., 2004; see also Jha, 2002).

The studies presented in this review support and further extend the contemporary view of a strong interconnection between attention and working memory. They demonstrate that the focus of attention can also be altered dynamically after perception, when items are already being maintained in working memory, depending on changing expectations or volition during goal-directed behavior. Moreover, they show that attentional orienting within working memory can retroactively influence maintenance-related activity in functionally specialized posterior areas, as well as engaging selective retrieval functions. In summary, the present studies show that the interplay between attention and working memory is bidirectional, and even more prevalent and flexible than previously proposed.

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