Overlapping mechanisms of attention and spatial working memory

Edward Awh and John Jonides

Spatial selective attention and spatial working memory have largely been studied in isolation. Studies of spatial attention have provided clear evidence that observers can bias visual processing towards specific locations, enabling faster and better processing of information at those locations than at unattended locations. We present evidence supporting the view that this process of visual selection is a key component of rehearsal in spatial working memory. Thus, although working memory has sometimes been depicted as a storage system that emerges 'downstream' of early sensory processing, current evidence suggests that spatial rehearsal recruits top-down processes that modulate the earliest stages of visual analysis.

Working memory is a system that enables the temporary maintenance of limited information, where that information is kept on-line or available for immediate access by other cognitive processes. This kind of active maintenance is essential for a variety of tasks such as language comprehension and problem-solving[1,2]. An influential model of working memory was proposed by Baddeley and his colleagues[3] that included a separation between working memory for visuospatial versus verbal information. Subsequent research has yielded a further fractionation for visuospatial information, suggesting separate stores for visual and spatial working memory. For example, there are numerous studies that suggest there are dissociations of spatial and object working memory[4–8]. This division within the architecture for working memory mirrors the known organization of the mammalian visual system, in which separate pathways have been shown to process spatial and object visual features[9]. Although it has been productive to identify the independent components of the working memory system, the next step is to provide a functional description of how information is maintained within each system. The evidence reviewed in this article supports a specific hypothesis regarding the subcomponents of spatial working memory.

The maintenance of information in spatial working memory appears to recruit a network that includes occipital, dorsal parietal and superior frontal cortex. This article focuses on evidence relevant to a description of the cognitive mechanisms that are implemented by this neural network. Baddeley and colleagues[3] proposed the first specific hypothesis regarding the functional subcomponents of spatial working memory. They suggested that this system might rely upon implicit eye-movement programs, analogous to the way that verbal rehearsal involves a component of subvocal articulation. In support of this hypothesis, eye movements have been shown to disrupt the accurate maintenance of information in spatial working memory[10]. However, it has also been observed that spatially directed arm movements can interfere with spatial working memory[11], raising the possibility of a more-general mechanism for maintenance that might not be tied exclusively to the oculomotor system. Smyth and Scholey[12] proposed such an account when they argued that the short-term maintenance of spatial information involves covert shifts of attention. In line with this view, there is evidence that supports a specific hypothesis: the active maintenance of spatial information is accomplished by means of focal shifts of spatial attention to memorized locations. This argument hinges on a long line of research that has shown that orienting of spatial selective attention causes relative improvements in visual processing (independent of the direction of gaze) at attended relative to unattended locations in space[13]. There is compelling biological evidence that these processing improvements begin at the level of early sensory processing[14]. This mechanism might operate in the service of memory as well as perception, by providing a functional marker for location-specific representations in working memory. By this account, the frontal and parietal mechanisms involved in spatial working memory are an attention circuit that operates in the service of memory.

The plausibility of attention-based rehearsal is supported by a comparative analysis of the neuroanatomy of spatial working memory and spatial selective attention[15,16]. Both processes are driven by a right-hemisphere dominant network of frontal and parietal sites; this anatomical overlap suggests a functional relationship between attention and memory systems. Of course, one weakness in this analysis is that different behavioral paradigms have been used to assess the brain regions that participate in attention and working memory. Differences in the task demands, stimulus displays and overall difficulty of these disparate experiments places limits on what we can conclude from this analysis. Nevertheless, there is an apparent correlation between the brain circuits that mediate attention and working memory. But the strength of the overlap between the neural substrates recruited

Edward Awh*
University of Oregon,
1227 University,
Eugene, OR 97403, USA.
*e-mail: awh@
darkwing.uoregon.edu

John Jonides
University of Michigan,
525 E. University,
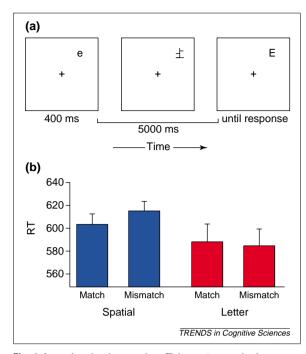Ann Arbor,
MI 48109, USA.

Fig. 1. Assessing visual processing efficiency at memorized locations. (a) The events in a single trial of the spatial and letter dual tasks. The choice reaction time stimulus that appeared during the retention interval allowed a direct comparison of visual processing efficiency at memorized and non-memorized locations. Subjects were required to fixate centrally throughout each trial, and compliance was verified by video monitoring. (b) Mean reaction times (RT) to the choice stimulus. Only in the spatial condition, were subjects faster to respond to choice stimuli that matched the location of the memory cue, suggesting that spatial attention is directed towards locations held in working memory. The failure to observe this effect in the letter condition rules out the stimulus display as the cause of this effect. Although reaction times appear to be faster on average in the letter condition, this reflects the responses of a single subject in the letter condition; thus, there was no reliable difference in choice reaction times between the spatial and letter conditions. The results would be unchanged if this subject were excluded.

in these tasks does not show that there are functional consequences to this overlap, as a hypothesis of attention-based rehearsal would claim. This article goes beyond the correlational evidence to present data of two sorts:
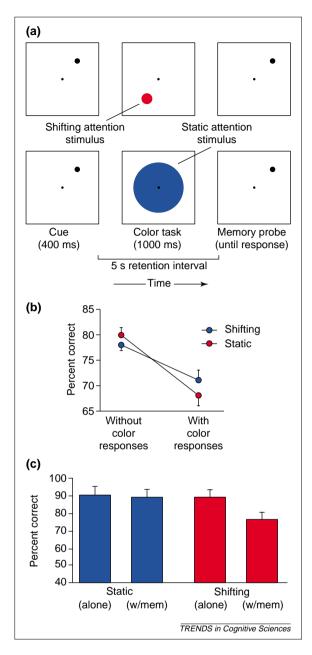
(1) Behavioral evidence shows us that visual processing at memorized locations is better than at non-memorized locations, consistent with the notion that visual attention is focused on the memorized locations[17]. Moreover, if subjects are forced to direct attention away from locations held in working memory, their ability to remember those locations is impaired[12,17,18]. This interference effect suggests that spatial orienting of attention is a necessary part of accurate spatial memory, rather than being merely a correlated phenomenon.

(2) Additional evidence from functional magnetic resonance imaging (fMRI) and event-related potentials (ERPs) reveals the cortical mechanisms that underlie spatial rehearsal effects. These data suggest that spatial rehearsal modulates early sensory processing in the visual areas that represent the memorized locations[19]. The time course and

cortical locus of these rehearsal effects are similar to those that are observed after explicit manipulations of spatial selective attention (Ref. 20; and A. Jha and G.R. Mangun, unpublished).

Behavioral evidence
If spatial selective attention is directed towards a location stored in working memory, then the typical effects of spatial attention – improved visual processing efficiency – should be observed at that location. Awh *et al.*[17] have provided a behavioral test of this prediction. Subjects were engaged in a simple memory task (see Fig. 1a), in which a letter (the cue) appeared in a specific location. Five seconds later, another letter (the probe) appeared on the screen and subject indicated whether the probe matched the information that they were holding in memory. Half of the subjects memorized the location of the cue, while the other half memorized the identity of the cue. During the retention interval, subjects made speeded key presses to indicate the shape of a letter-like character that appeared on the computer screen. In some trials, the choice stimulus appeared in the same location as the memory cue (choice match); in the other trials the choice stimulus appeared in other parts of the visual field (choice miss). The key prediction was that subjects' reaction times to the choice stimulus should be faster when it fell in the memorized location, but only when subjects were rehearsing the location of the initial memory cue. The letter memory condition served as a control for the stimulus display; if the predicted effect was a result of automatic orienting of attention[21] or the mere presence of a 25% correspondence between the location of the cue and the choice stimulus, then the same effects should have been observed in both the letter and the spatial conditions. Only in the spatial memory condition were reaction times reliably faster to choice-match stimuli than to choice-miss stimuli (see Fig. 1b). No trace of this effect was observed in the letter memory condition. These data suggest that spatial rehearsal – not the stimulus display – was responsible for the reaction time effects in the spatial memory condition.

This study demonstrates the predicted association between the focus of spatial attention and the memorized locations, but it did not address the stronger claim that spatial selective attention plays a functional role in working memory. That is, spatial attention might be directed towards the memorized locations without playing a beneficial role in the active maintenance of location information. This issue has been addressed by testing a simple prediction of attention-based rehearsal: if subjects are hindered in their ability to direct attention towards the memorized locations, then memory accuracy should decline. The first study to demonstrate this connection between spatial attention and spatial working memory was carried out by Smyth and

Fig. 2. Interference with spatial rehearsal by disrupting the focus of spatial attention. (a) Events in the shifting attention condition (top) and the static attention condition (bottom). Subjects were instructed to remember the location of the initial memory cue for 5 s. At the end of the trial, they indicated whether or not the probe was in the same location as the one they were remembering. Subjects classified the colors of the stimuli appearing during the retention interval. The shifting attention condition entailed shifts of attention away from the memorized location; the static attention condition did not. (b) Spatial memory accuracy. Subjects participated in four separate conditions: the shifting and static attention conditions (right side: 'with color responses'), and two control conditions during which color stimuli were presented, but only memory responses were required (left side: 'without color responses'). As predicted by attention-based rehearsal, memory performance was worse in the shifting attention condition than in the static attention condition. In order to rule out the explanation that the color task was simply more difficult in the shifting attention condition, the static attention stimuli were made more difficult to discriminate (the colors were more similar) than the shifting attention stimuli. (c) Accuracy of color discriminations in the shifting attention condition and the static attention condition. Subjects were equally accurate when the color tasks were performed without the accompanying spatial memory task – the 'alone' condition (but recall that reaction times were slower in the static attention condition, because the colors were more difficult to discriminate). However, the addition of the spatial memory task (the 'w/mem' condition) caused significant impairment of color responses in the shifting attention condition, but color responses in the static attention condition were unaffected.

interval of a memory task for a single location (see Fig. 2a). There were two types of color task. One task required the color classification (e.g. red or blue) of a small stimulus that was randomly positioned on the computer screen, a task that required a shift of attention to accomplish because of the size and eccentricity of the stimulus (the shifting-attention condition)[22]. The other task required a similar color judgment, but the stimuli were large enough to occlude all potential memorized locations – thus, attention shifts were not required for the color discrimination (the static-attention condition). The prediction was that memory performance should be worse in the shifting-attention condition than in the static-attention condition, because shifts of attention to non-memorized locations should be incompatible with attention-based rehearsal. The results (shown in Fig. 2b) confirmed this prediction; the shifting-attention task caused greater decrements in memory performance than did the static-attention task. The responses to the color stimuli were also informative. When the color tasks were performed alone (i.e. without the memory task) accuracy was equal between the shifting- and static-attention conditions. However, when the memory task was added, color responses became far less accurate in the shifting-attention condition but were unaffected in the static-attention condition (see Fig. 2c). This result underscores the fundamental incompatibility between accurate maintenance of information in spatial working memory and a secondary task that requires shifts of spatial attention. The results from these interference studies are a crucial aspect of the behavioral evidence, because they demonstrate that spatial attention plays a beneficial functional role in the active maintenance of location information (but see Box 1 for further discussion).

Scholey[12]. They studied performance on a traditional measure of spatial memory span, the Corsi Blocks test. Subjects viewed an array of boxes on a computer screen while a subset of these boxes was indicated one at a time. After a 12.5 s retention interval, the subjects were required to recall the spatial sequence by touching the appropriate boxes in the correct order. The results showed that if subjects were engaged with secondary tasks requiring shifts of attention during the retention interval, memory performance declined. A subsequent study showed that this result obtained when subjects were required to maintain fixation throughout the delay interval[18], showing that the secondary tasks interfered with shifts of attention, not shifts of gaze.

Awh *et al.*[17] have also addressed this issue using a dual-task interference paradigm. Subjects performed a color discrimination task during the retention

Box 1. Examining the motor-rehearsal hypothesis

Although we argue that covert shifts of attention play a role in spatial rehearsal, careful consideration should be given to the potential role of implicit motor programs in these tasks. This hypothesis suggests that representations in spatial working memory could be maintained by the selection of spatially specific motor responses towards the memorized locations[a,b]. Even in the absence of overt motor responses, it would be possible for motor programs to serve as an engram for spatial memory. Evidence has been reported from a variety of paradigms that show covert orienting towards the memorized locations, but these data do not contradict the motor-rehearsal account because they show only an association between covert orienting and the stored location. The experiments that address the functional role of attention more directly are those that show a deficit in spatial memory accuracy when subjects are prevented from maintaining an attentional focus at locations held in working memory[c,d]. However, these data might be reconciled with a motor rehearsal account, because the tasks used to hinder covert orienting towards the locations in working memory might have also had the effect of disrupting spatially specific motor programs. Moreover, the issue is complicated by the fact that there are strong links between spatially directed movements and covert shifts of attention (see, for example, Ref. e). While these links may or may not be obligatory[f–h], they are a challenge for attempts to disentangle the contributions of motor programming and spatial attention in working memory with behavioral evidence. Despite this ambiguity, we note that the clearest evidence for motor-based rehearsal has come from tasks that required subjects to recall the positions via motor movements to the memory locations; but evidence of attention-based rehearsal has been observed with tasks that do not require spatially directed motor movements.

Perhaps some of the strongest pieces of evidence against a pure motor-rehearsal account are findings that dissociable neural substrates appear to mediate motor-programming and spatial rehearsal. Carlson *et al.* recorded single-unit activity from the prefrontal cortex of monkeys and found three classes of neurons: (1) those active during the delay period; (2) those active during both delay and movement periods; and (3) those active only during movement periods[i]. The most relevant finding for the present purposes was that 70% of the delay-related neurons did not fire in relation to movement or the sensory stimuli used in the experiment. So, mnemonic coding cannot be explained solely in terms of spatially specific motor programs. Similar evidence has also been observed in humans. Petit *et al.* used fMRI to observe a within-subject dissociation between superior frontal regions active during spatial working memory delays, and a more posterior frontal region that was active during saccadic eye movements[j]. These data suggest a mnemonic code in spatial working memory that is independent of motoric codes, but it seems nonetheless likely that both attention-based and motor-based processes are important for spatial rehearsal. An important goal for future research is to identify the factors that elicit different modes of rehearsal in visuospatial working memory.

References
a Schneider, W.X. (1999) Visual-spatial working memory, attention, and scene representation: a neuro-cognitive theory. *Psychol. Res.* 62, 220–236
b Chieffi, S. *et al.* (1999) Hand-centred coding of target location in visuo-spatial working memory. *Neuropsychologia,* 37, 495–502
c Awh, E. *et al.* (1998) Rehearsal in spatial working memory. *J. Exp. Psychol. Hum. Percept. Perform.* 24, 780–790
d Smyth, M.M. and Scholey, K.A. (1994) Interference in immediate spatial memory. *Mem. Cognit.* 22, 1–13
e Heiner, D. *et al.* (1998) Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Visual Cognit.* 5, 81–107
f Klein, R. (1980) Does oculomotor readiness mediate cognitive control of visual attention? In *Attention and Performance* (Vol. 8) (Nickerson, R.S., ed.), pp.259–276, Erlbaum
g Rafal, R. *et al.* (1989) Saccade preparation inhibits reorienting to recently attended locations. *J. Exp. Psychol. Hum. Percept. Perform.* 15, 673–685
h Reuter-Lorenz, P.A. and Fendrich, R. (1992) Oculomotor readiness and covert orienting: differences between central and peripheral precues. *Percept. Psychophys.* 52, 336–344
i Carlson *et al.* (1997) Dissociation of mnemonic coding and other functional neuronal processing in the monkey prefrontal cortex. *J. Neurophysiol.* 77, 761–774
j Petit *et al.* (1998) Sustained activity in the medial wall during working memory delays. *J. Neurosci.* 18, 9429–9437

The cortical substrate of spatial rehearsal effects

Neuroimaging studies of spatial working memory and spatial selective attention have supported the hypothesis of attention-based rehearsal in two ways. First, there is a clear overlap in the brain regions that have been implicated in these processes[15,16]. A variety of neuroimaging studies, using a diverse range of stimulus materials and task requirements converge upon the view that spatial rehearsal elicits activity in a right-hemisphere dominant network of frontal and parietal sites[5–7]. In line with this finding, neuroimaging studies of spatial selective attention reveal activity in a strikingly similar constellation of brain regions[23–25]. However, as we noted earlier, this kind of correlational evidence can offer only indirect support for the idea that spatial rehearsal has a close functional relationship with spatial selective attention. The remainder of this article focuses on studies that suggest spatial rehearsal and spatial selective attention also have similar functional
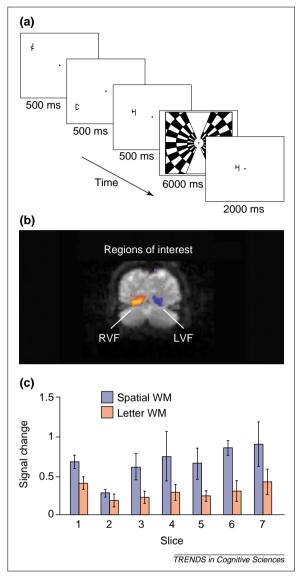
Fig. 3. Spatial rehearsal modulates early visual activity. (a) A single trial in the spatial memory condition. Memory cues had a 300 ms interstimulus interval. The flickering checkerboard was presented 500 ms after the offset of the third memory cue, and the memory probe appeared 500 ms after the offset of the checkerboard. During scanning, subjects were presented with blocks of memory trials that alternated between the right and left visual field. In the letter memory condition, the timing and placement of stimuli were identical, but Geneva font letters were presented instead of false fonts. (b) Examples of the regions of interest (ROIs) that were used to compare right and left hemisphere visual activations in a single subject (RVF, LVF; stimulus presented to right and left visual fields, respectively). The yellow–orange areas show the brain regions that responded to the right side of the flickering grid, and the blue–purple areas depict visual areas responsive to the left visual field. Talairach transformations of these data suggest that the functionally defined ROIs are restricted to Brodmann areas 17, 18 and 19. (c) The mean level of contralateral visual activation (expressed in percent signal change) observed in the spatial and letter working memory (WM) tasks. These measurements represent the total amount of contralateral visual activation observed within each of the seven coronal slices (5 mm thick and contiguous, starting at the occipital pole and moving forwards) that showed visually responsive voxels. From slices 1–7, the coronal slices move in the anterior direction. The reliable evidence of visual activity in the letter condition provides a baseline estimate of the stimulus-driven visual activity in these tasks. Thus, the significantly greater levels of contralateral visual activity in the spatial condition suggest the influence of spatial selective attention during rehearsal in spatial working memory.

consequences. In particular, spatial rehearsal has a clear impact on the quality of early visual processing, and these visual modulations mirror those that have been previously documented in studies of spatial selective attention.

The behavioral studies document changes in visual processing efficiency at memorized locations, as predicted by the hypothesis of attention-based rehearsal. However, they leave unanswered questions regarding the precise nature of these spatial rehearsal effects. For example, there is a growing body of biological evidence regarding the timing and anatomical locus of spatial attention effects. These studies have revealed that spatial attention causes modulations of visual processing in early visual areas contralateral to the attended regions of space[26–32], and that these effects begin within the first 100 ms of the onset of visual information[33–36]. Does spatial rehearsal elicit similar modulations of early sensory processing?

In order to learn about the cortical locus of these spatial rehearsal effects, Awh *et al.*[19] conducted an fMRI study that measured posterior visual activations while subjects performed a spatial working memory task. The purpose of this study was to observe whether activations appeared contralateral to memorized locations – as they do to attended locations. The task (illustrated in Fig. 3a) required subjects to memorize three locations (marked by false-font characters) in either the left or right visual field for 7 s. During this retention interval, a bilateral flickering grid occluded all possible memorized locations. By observing the independent visual responses to the left and right sides of the flickering grid, it was possible to assess whether or not sensory responses to the grid were amplified contralateral to the memorized locations. For example, during right visual field memory trials, attention-based rehearsal would predict greater visual responses to the right side of the flickering grid (i.e. in the left hemisphere visual areas). One pitfall of this procedure was that there were unilateral presentations of memory stimuli. Thus, the encoding of the memory display alone might have resulted in some visual activation contralateral to the memorized locations. In order to assess the contributions of encoding versus rehearsal effects, the same subjects were given a non-spatial memory condition. This task employed the same timing and placement of memory stimuli as the spatial one, but letters were presented instead of false fonts, and subjects were instructed to remember the identity, rather than the location, of these letters. This condition provided a direct assessment of the contralateral visual activations that arose owing to encoding of these stimulus displays. (Note that in these experiments, the use of a functional criterion to identify visual areas in each subject acknowledges the recent demonstrations of substantial between-subject
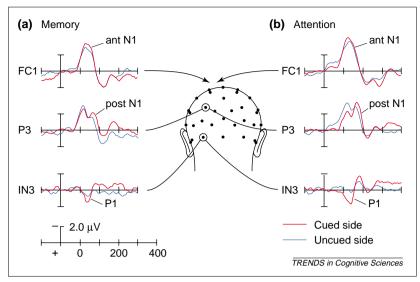
Fig. 4. Phasic visual modulations due to spatial rehearsal event-related potential waveforms elicited by the behaviorally irrelevant probes at locations FC1, P3 and IN3. The modulations appeared during the delay period of the memory task (a) and during the target detection period of the attention task (b). This figure shows responses to probes in the right visual field. Evoked responses were larger in amplitude at memorized locations; these modulations were very similar to those observed at attended locations. Abbreviations: ant N1, anterior negativity; post N1, posterior negativity; P1, positivity. (Modified from Ref. 20.)

variability in the functional morphology of early visual areas[37]. That is, although the regions of interest could have been created by means of Talairach normalization, the present within-subject approach is a more reliable way of identifying visually responsive brain regions.)

The results (depicted in Fig. 3c) showed that spatial rehearsal did elicit the predicted visual modulations. There were consistent increases in activation in the visual areas contralateral to the memorized locations, a result similar to previous neuroimaging studies of spatial attention[26–32]. Contralateral visual activations were also observed in the letter memory task (consistent with the unilateral presentation of memory stimuli), but these effects were significantly smaller than those observed in the spatial condition. Thus, the modulations of visual responses to stimulation in the memorized locations could not be explained just by the encoding of the stimulus display. Instead, these effects support the idea that spatial attention is oriented towards the memorized locations, leading to amplified visual responses contralateral to those locations.

The timing of the visual modulations induced by spatial rehearsal

The previous study reveals a cortical locus for changes in visual processing efficiency at memorized locations, as observed in the behavioral work. However, none of the studies provides evidence regarding the time course of these visual modulations. In particular, one would like to know whether the temporal profile of the visual modulations associated with spatial rehearsal mimics that associated with spatial attention.

An ERP study by Awh *et al.*[20] has provided information about the time course of spatial rehearsal effects to address this issue. Subjects engaged in two experimental conditions. One was a spatial memory condition similar to the fMRI study described above. The other condition used the same stimulus parameters to observe visual evoked responses after explicit manipulations of spatial attention. These parallel conditions set the stage for a strong test of the overlap between spatial rehearsal in working memory and spatial attention. The memory condition required subjects to remember three locations in either the right or left visual field for 8.7 s. At the end of the trial, subjects indicated whether a single memory target occupied one of the locations stored in memory. During the delay period, a series of behaviorally irrelevant probes (patterned rectangles that occluded all potential memory locations in one visual field) were flashed over memorized and non-memorized locations, and the evoked visual responses to these probes were analyzed as a function of whether they overlapped the memorized locations or not. The key question was whether spatial rehearsal elicits phasic modulations of visual responses over memorized locations. During the other experimental condition, subjects performed an explicit spatial attention task. The stimulus display was virtually identical, except that small targets that were difficult to detect appeared during the retention interval, interspersed between the behaviorally irrelevant probes. The cues at the beginning of the trial directed subjects to attend to either the right or left side of the display to detect these targets. Thus, a direct comparison could be made between the effects of spatial rehearsal and spatial attention on ERPs to identical visual stimuli. Consistent with previous electrophysiological studies of spatial attention[36], the evoked visual responses were significantly larger in amplitude at memorized than at non-memorized locations[20] (Fig. 4). Furthermore, very similar modulations were observed in the spatial attention condition when subjects were explicitly instructed to direct attention to the left and right visual fields. These experiments provide another marker of the functional overlap between spatial working memory and spatial selective attention, the phasic modulation of visual responses, beginning only 100 ms after stimulus onset.

Isovoltage contour maps can be derived that show the mean amplitude of the visual modulations observed in the memory and attention task (during the latency window of the P1, anterior N1 and posterior N1 components) (Fig. 5). The scalp topography of these visual modulations further highlights the striking similarity between the effects of spatial rehearsal and spatial attention. The P1 modulations were focused at posterior occipitotemporal electrode sites, contralateral to the evoking stimuli. The anterior N1 modulations were broadly distributed over frontal electrode sites, with no clear laterality effect in either task. The posterior N1 effects were at occipitotemporal
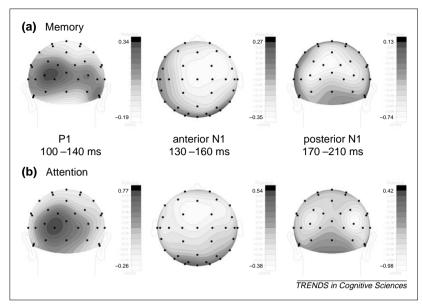
Fig. 5. Scalp topography of spatial rehearsal effects. Isovoltage contour maps of the mean amplitude of the positivity (P1), anterior negativity (N1) and posterior negativity (N1) modulations for right visual field stimuli. The topography of these visual modulations was very similar across the memory and attention conditions. Notice the contralateral (i.e. left hemisphere) scalp distribution of the P1 modulations. (Modified from Ref. 20.)

electrode sites, extending more centrally than the P1 modulations. In all three latency windows, the topography of the visual modulations is highly similar across the memory and attention conditions.

Jha and Mangun also studied the time course of the visual modulations due to spatial rehearsal (A. Jha and G.R. Mangun, unpublished). They observed phasic modulations of the P1 component, with higher amplitude responses at memorized locations. In addition, analyses of the early and late phases of the retention interval showed that these visual effects were sustained throughout the retention interval, consistent with the hypothesis that these modulations are due to spatial rehearsal. Thus, there are two similar reports showing phasic modulations of visual responses during spatial rehearsal in working memory. Furthermore, a direct comparison of the evoked visual responses during spatial rehearsal in working memory and spatial selective orienting reveals strong overlap in the latency and scalp topography of the modulations in the two tasks.

Conclusions

We have reviewed three classes of results about the relationship of spatial attention and working memory.

First, measurements of reaction time, hemodynamic responses and visually evoked brain potentials all suggest location-specific changes in visual processing at memorized locations – a result that is consistent with the known effects of spatial attention. Second, if these shifts of attention to memorized locations are interrupted, memory accuracy declines. Finally, studies that address the cortical substrate of these effects reveal modulations of activity in the early visual areas contralateral to memorized locations, beginning during the earliest stages of visual processing. Thus, both the neural locus and timing of these rehearsal effects further corroborate a role for spatial selective attention.

These data converge on a single view: there is a functional overlap in the mechanisms of spatial working memory and spatial selective attention. By our account, mechanisms of spatial attention are recruited in the service of a rehearsal-like function to maintain information active in working memory. This recruitment is cognitively economical, in that it makes handsome use of a system specialized for processing real space in order to maintain an on-line representation of remembered space. We suspect that the recruitment of mechanisms of sensory processing in the service of memory is not isolated to spatial material. There is evidence, for example, of the involvement of inferotemporal processing in working memory for objects as well[38,39], leading to the possibility of a sensory–memory alliance for this material. Future research could well benefit from examining other memory systems to determine whether sensory systems play an important role in memory more generally.

References

1 Carpenter, P.A. *et al.* (1990) What one intelligence test measures: A theoretical account of the processing in the Raven Progressive Matrices Test. *Psychol. Rev.* 97, 404–431
2 Newell, A. (1990) *Unified Theories of Cognition*, Harvard University Press
3 Baddeley, A.D. (1986) *Working Memory*, Oxford University Press
4 Tresch, M.C. *et al.* (1993) Double dissociation of spatial and object visual memory: Evidence from selective interference in intact

human subjects. *Neuropsychologia* 31, 211–219
5 Smith, E.E. *et al.* (1995) Spatial vs. object working memory: PET investigations. *J. Cogn. Neurosci.* 7, 337–356
6 Courtney, S.M. *et al.* (1996) Object and spatial visual working memory activate separate neural systems in human cortex. *Cereb. Cortex* 6, 39–49
7 McCarthy, G. *et al.* (1996) Activation of human prefrontal cortex during spatial and nonspatial working memory tasks measured by functional MRI. *Cereb. Cortex* 6, 600–611

8 Mecklinger, A. and Muller, N. (1996) Dissociations in the processing of "what" and "where" information in working memory: An event-related potential analysis. *J. Cogn. Neurosci.* 8, 453–473
9 Ungerleider, L.G. and Mishkin, M. (1982) Two cortical visual systems. In *Analysis of Visual Behavior* (Ingle, D.J. *et al.*, eds), pp.549–586, MIT Press
10 Baddeley, A.C. and Lieberman, K. (1980) Spatial working memory. In *Attention and Performance* (Vol. 8) (Nickerson, R.S., ed.), pp. 521–539, Erlbaum

11 Smyth, M.M. and Pelky, P. (1992) Short term retention of spatial information. *Br. J. Psychol.* 83, 359–374

12 Smyth, M.M. and Scholey, K.A. (1994) Interference in immediate spatial memory. *Mem. Cognit.* 22, 1–13

13 Posner, M.I. (1980) Orienting of attention. *Q. J. Exp. Psychol.* 32, 3–25

14 Mangun, G.R. *et al.* (1987) The spatial orienting of attention: Sensory facilitation or response bias? In *Current Trends in Event-related Potential Research* (Johnson, R., Jr *et al.*, eds), pp. 118–124, Elsevier

15 Awh, E. *et al.* (1995) Human rehearsal processes and the frontal lobes: PET evidence. *Ann. New York Acad. Sci.* 769, 97–119

16 Awh, E. and Jonides, J.(1998) Spatial Selective Attention and Spatial Working Memory. In *The Attentive Brain* (Parasuraman, R., ed.), pp 353–380, MIT Press

17 Awh, E. *et al.* (1998) Rehearsal in spatial working memory. *J. Exp. Psychol. Hum. Percept. Perform.* 24, 780–790

18 Smyth, M.M. (1996) Interference with rehearsal in spatial working memory in the absence of eye movements. *Q. J. Exp. Psychol.* 49A, 940–949

19 Awh, E. *et al.* (1999) Rehearsal in spatial working memory: evidence from neuroimaging. *Psychol. Sci.* 10, 443–437

20 Awh, E. *et al.* (2000) The role of spatial selective attention in working memory for locations: evidence from event-related potentials. *J. Cogn. Neurosci.*12, 840–847

21 Jonides, J. (1981) Voluntary vs. automatic control over the mind's eye movement. In *Attention and Performance IX* (Long, J.B. and Baddeley, A.D. eds), pp. 187–203, Erlbaum

22 Tsal, Y. and Lavie, N. (1993) Location dominance in attending to color and shape. *J. Exp. Psychol. Hum. Percept. Perform.* 19, 131–139

23 Corbetta, M, *et al.* (1993) A PET study of visuospatial attention. *J. Neurosci.* 13, 1202–1226

24 Gitelman, D.R. *et al.* (1996) Functional imaging of human right hemispheric activation for exploratory movements. *Ann. Neurol.* 39, 174–179

25 Coull, J.T. *et al.* (1998) Monitoring for target objects: activation of right frontal and parietal cortices with increasing time on task. *Neuropsychologia* 36, 1325–1334

26 Gratton, G. (1997) Attention and probability effects in the human occipital cortex: An optical imaging study. *NeuroReport* 8, 1749–1753

27 Heinze *et al.* (1995) Combined temporal imaging of brain activity during visual selective attention in humans. *Nature* 372, 543–546

28 Moran, J. and Desimone, R. (1984) Selective attention gates visual processing in the extrastriate cortex. *Science* 229, 782–784

29 Petersen, S.E. *et al.* (1994) PET studies of parietal involvement in spatial attention: comparison of different task types. *Can. J. Exp. Psychol.* 48, 319–338

30 Brefczynski, J.A. and DeYoe, E.A. (1999) A physiological correlate of the 'spotlight' of visual attention. *Nat. Neurosci.* 2, 370–374

31 Gandhi, S.P. *et al.* (1999) Spatial attention affects brain activity in human primary visual cortex. *Proc. Natl. Acad. Sci. U. S. A.* 96, 3314–3319

32 Tootell, R.B. *et al.* (1998) The retinotopy of visual spatial attention. *Neuron, 21,* 1409-1422.

33 Eason, R. *et al.* (1969) Effects of attention and arousal on visually evoked cortical potentials and reaction time in man. *Physiol. Behav.* 4, 283–289

34 Harter, M.R. and Anllo-Vento, L. (1991) Visual-spatial attention: Preparation and selection in children and adults. In *Event-related Potentials of the Brain* (Brunia, C.H.M. *et al.*, eds), pp. 183–194, Elsevier

35 Hawkins, H.L. *et al.* (1990) Visual attention modulates signal detectability. *J. Exp. Psychol. Hum. Percep. Perform.* 16, 802–811

36 Mangun, R.G. *et al.* (1993) Electrocortical substrates of visual selective attention. In *Attention and Performance XIV* (Meyer, D. and Kornblum, S., eds), pp. 219–243, MIT Press

37 Sereno, M.I. *et al.* (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science* 268, 889–893

38 Miller, E.K. *et al.* (1996) Neural mechanisms of visual working memory in prefrontal cortex of the macaque. *J. Neurosci.* 16, 5154–5167

39 Desimone, R. *et al.* (1995) Multiple memory systems in the visual cortex. In *The Cognitive Neurosciences* (Gazzaniga, M.S., ed.), pp. 475–486, MIT Press

Trends Guides and Supplements questionnaire

Trends Guides and supplements are supplementary publications produced in association with the Trends journals. The aim of these Guides and Supplements is to provide our readers with emerging information on a topical area of research, in a single focused issue.

Trends Guides and supplements can be found online at www.journals.bmn.com and are distributed FREE to subscribers of relevant Trends journals.

We want to know what you think of these Guides and supplements.

- Are they useful to you?

- Did you enjoy reading these publications?

- Are there any changes you would like to suggest?

- Would you like to propose a topic for coverage in a Trends Guide?

Enclosed in the April issue of *TICS* there will be a looseleaf questionnaire. We would be extremely grateful if you could spare a few minutes to fill in this questionnaire and return it to us using the reply-paid envelope provided.

Alternatively, you will also find this questionnaire online at http://www.bmn.com/questionnaire?questionnaire=trendsguides

Thank you for your help.