

Episodic memory for spatial context biases spatial attention

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Abstract The study explores the bottom-up attentional consequences of episodic memory retrieval. Individuals studied words (Experiment 1) or pictures (Experiment 2) presented on the left or on the right of the screen. They then viewed studied and new stimuli in the centre of the screen. One-second after the appearance of each stimulus, participants had to respond to a dot presented on the left or on the right of the screen. The dot could follow a stimulus that had been presented, during the study phase, on the same side as the dot (congruent condition), a stimulus that had been presented on the opposite side (incongruent condition), or a new stimulus (neutral condition). Subjects were faster to respond to the dot in the congruent compared to the incongruent condition, with an overall right visual field advantage in Experiment 1. The memory-driven facilitation effect correlated with subjects' re-experiencing of the encoding context (*R* responses; Experiment 1), but not with their explicit memory for the side of items' presentation (source memory; Experiment 2). The results indicate that memory contents are attended automatically and can bias the deployment of attention. The degree to which memory and attention interact appears related to subjective but not objective indicators of memory strength.

Keywords Memory · Retrieval · Attention

I (MM) became aware of Giovanni Berlucchi's work very early in my career. Having published my first short paper on laterality in what essentially was a vanity press journal (Moscovitch and Catlin 1970), a paper I was sure was the equivalent of placing a note in a bottle and floating it out to sea, I was surprised and delighted to see it cited as a footnote in Brain in a paper on laterality by an Italian group to which Giovanni belonged (Rizzolatti et al. 1971). It did not matter at all to me that it was cited under my first name rather than my last. All I cared about is that someone had found the bottle and read the note. That was the beginning of a long association. Giovanni, Giacomo Rizzolatti, and Carlo Umiltà were the first people to invite me to present my work at a university outside North America. I still remember fondly how graciously Giovanni and his wife hosted me. The elegance, intelligence, and deep authority of his work reflects the man. What it does not capture is his generosity and kindness (or his fast, but assured, handling of cars which may not be unusual for Italian drivers, but which impressed me, and sometimes made me catch my breath). Giovanni and his collaborators promoted me and my work. Through them I developed an Italian connection which lasts to this day. I met Elisabetta Ladavas on that first visit to Italy and she came to work as a post-doctoral fellow with me. And now, more than a quarter century later, Elisabetta's student, Elisa Ciaramelli, is my post-doctoral fellow. It is fitting that she is the primary author of this paper in honour of Giovanni with whom my Italian connection began. The paper even has a laterality component, though one arising from the interaction of episodic memory with attention, which is its main concern.

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Introduction

An interesting question for cognitive psychology is whether memory retrieval processes require attention for their operation. One approach that has been extensively used to address this question is to reduce attentional resources during memory tasks, for example by having subjects divide their attention between the memory task and a concurrent task, and see whether memory suffers. While numerous studies have shown that dividing attention at encoding causes consistent detrimental effects on later memory performance, the effects that the same manipulation has on memory retrieval are more subtle, and depend crucially on the type of memory task examined (e.g., Baddeley et al. 1984; Craik et al. 1996). If the memory task makes heavy demands on controlled processes during retrieval, such as those needed to initiate a strategic search (e.g., recall from categorized word lists, list discrimination), then interference effects of dividing attention on memory are observed (Moscovitch 1992, 1994; Park et al. 1989; Jacoby et al. 1989; Kane and Engle 2000). In contrast, divided attention during retrieval has little, if any, impact on more direct memory tasks, such as recognition or recall of uncategorized words, which benefit little from strategic search processes (e.g., Baddeley et al. 1984; Craik et al. 1996; Fernandes and Moscovitch 2000; Naveh-Benjamin et al. 1998). This finding has led some researchers to suggest that memory retrieval, once initiated, is an automatic process that runs almost obligatorily (Craik et al. 1996).

Additional evidence, however, has indicated that even in relatively automatic memory tasks the attentional costs and needs of memory retrieval are in fact detectable. Fernandes and Moscovitch (2000, 2002) found that recall of a list of unrelated words was disrupted when participants concurrently performed a word-based distracting task, although it was not if they performed a picture-based distracting task. This finding suggests that memory retrieval may compete with ongoing processing for reactivation of content representations. Moreover, although memory performance does not normally suffer from divided attention at retrieval, memory retrieval does inflict costs on the distracting task (e.g., Naveh-Benjamin et al. 2005; Craik et al. 1996; Fernandes and Moscovitch 2000; Ciaramelli et al. 2008a). This finding indicates that, even when mandatory, episodic memory retrieval usurps attentional resources from ongoing processes.

The interest in the relation between memory retrieval and attention has been revived by the recent observation from electrophysiology (Rugg and Curran 2007) and functional neuroimaging (fMRI; e.g., Wagner et al. 2005) that the posterior parietal cortex shows consistent retrieval success effects (i.e., larger activity for studied items correctly identified as old compared to new items correctly rejected). Previous research has shown that the posterior parietal cortex supports distinct attentional systems, which mediate

different attentional processes. According to one prominent theory (Corbetta and Shulman 2002), the superior parietal lobe (SPL) allocates top-down attention to specific aspects of the environment, whereas the inferior parietal lobe (IPL) mediates the bottom-up capture of attention by salient environmental stimuli. Thus, the involvement of posterior parietal cortex in memory retrieval not only supports the notion that attention is needed for episodic memory retrieval, but also raises the question of whether different attentional systems would make separate contributions to this process.

We have hypothesized that the SPL and the IPL would play conceptually analogous roles during perception and episodic memory retrieval. According to the attention-to-memory (AtoM) hypothesis (Ciaramelli et al. 2008b; Cabeza 2008), the SPL is implicated in allocating top-down attention to memory retrieval during strategic retrieval tasks, whereas the IPL mediates the automatic, bottom-up attentional capture by retrieved memory contents. Preliminary support for this proposal comes from recent reviews of fMRI studies of recognition memory showing that the SPL is consistently active when retrieval is effortful and therefore the need for top-down attentional resources is maximal, e.g., for items endorsed with low versus high confidence. In contrast, the IPL is consistently active when the attentional capture by memory contents is supposedly maximal, e.g., for salient memories accompanied by contextual details versus memories that are merely familiar (Ciaramelli et al. 2008b; Vilberg and Rugg 2008).

A dual-process conceptualization of the interplay between attention and memory may account for the behavioral evidence reviewed above. On the one hand, memory retrieval seems to need top-down attention to be carried on. This is most apparent when the operations required along the memory task are strategic, as revealed by the interference effects on memory performance from dividing attention during retrieval (e.g., Moscovitch 1994; Jacoby et al. 1989). On the other hand, the costs inflicted by the memory task on the secondary tasks (Naveh-Benjamin et al. 1998; Ciaramelli et al. 2008a) could reflect the fact that the output of memory retrieval (whether it was strategic or automatic) captures attention in a bottom-up fashion.

The aim of the present study was to investigate further the relation between attention and memory retrieval, focusing on the bottom-up component of the model. While the interference of attentional deprivation on memory performance has been object of many investigations, no study has thus far focused on the attentional consequences of memory retrieval (but see Naveh-Benjamin and Guez 2000). If memory retrieval captures attention, then it should affect ongoing attentional decisions. The decrements observed in the secondary task during divided attention manipulations suggest that this is indeed the case. However, since in previous studies the secondary task was run continuously throughout the retrieval

task, the degree to which the to-be-attended items in the secondary task overlapped with the to-be-recognized items was not controlled. By the same reasoning, in such studies it is hard to tell which specific aspect of retrieval interfered with the attentional task (e.g., endorsement of targets, rejection of distracters), or whether factors modulating retrieval also influenced its attentional consequences. We designed two experiments using a sequential paradigm to examine the effect of automatic memory retrieval on upcoming attentional decisions. The logic behind the experiments is explained below.

Experiment 1

In the first experiment, individuals studied words presented either on the left or on the right of the screen. After study, they were represented with the studied words, this time appearing in the centre of the screen, intermixed with new words. One-second after the appearance of each word, a dot was presented on the left or on the right of the screen, and participants' task was to respond to its appearance by pressing a left or a right key, respectively. If memory contents are attended automatically, then the mere view of stimuli originally studied on one side should induce an automatic shift of attention to that side, thereby facilitating response to dots appearing on the same (congruent condition) compared to the opposite side (incongruent condition) (see also Fischer et al. 2003; Tlauka and McKenna 1998; Hommel 2002). To the extent that this facilitation effect is driven by subjects' re-accessing the spatial features of studied items, we expected it to increase with the degree to which participants reported having re-experienced the encoding context at retrieval. That is, the effect should depend on recollection rather than familiarity (Tulving 1985; Yonelinas 2002).

Methods

Subjects

Thirty undergraduate students (13 males; age range 18–25, mean age 19.11 years) from an introductory course at the University of Toronto received course credit for their participation. All participants were right-handed and had normal or corrected-to-normal vision. Participants gave written informed consent for the study, which was approved by the ethics committee of the University of Toronto.

Materials

Ninety-six words (mean frequency 31, SD 34; mean imagery 4.8, SD 1.2), between 4 and 8 letters long, were selected from the Kucera and Francis (1967) pool. Forty-

eight words were studied. The other 48 words were not studied but served as distracters during the “attentional phase” or during the recognition phase. The assignment of words to the different task phases was counterbalanced across participants. The experimental task was created in E-prime (Schneider et al. 2002). Words appeared in black 20-point Arial font. Viewing distance was approximately 60 cm.

Procedure

The experimental session was comprised of a study phase, an “attentional” phase, and a recognition phase. During the study phase, participants viewed 48 words, 24 appearing on the left and 24 on the right side of the screen. Each stimulus was presented for 4 s and followed by a 500-ms blank screen. Participants were instructed to memorize the words for a later memory test. Immediately after, participants underwent the attentional phase. During this phase, the 48 studied words were presented again, one at time, intermixed with 24 new words, in random order. Words appeared in the centre of the screen. Participants were instructed to maintain fixation on the centre of the screen. One-second after the appearance of each word, a dot (0.5° in diameter) appeared either on the left or on the right of the screen. Participants' task was to respond to the appearance of the dot, by pressing the “z” key (on the left of the keyboard), with the left index finger, if the dot appeared on the left, and the “/” key (on the right of the keyboard), with the right index finger, if the dot appeared on the right. The word and the dot stayed on the screen until a response to the dot occurred, or until 2 s had elapsed. The attentional phase was designed such that one-third of the dots were preceded by a word that had been presented, during the study phase, on the same side as the dot (*congruent condition*), one-third of the dots were preceded by a word that had been presented on the opposite side (*incongruent condition*), and one-third of the dots were preceded by a new word (*neutral condition*). Figure 1 depicts the different conditions of the attentional phase.

During the recognition phase, which followed immediately, participants were presented again with the 48 studied words, together with 24 new words (different from those used in the attentional phase), in random sequence. Words appeared in the centre of the screen. For each word, participants decided if it was old or new, by using the “1” and “2” keys. The assignment of response keys to the “old” and “new” responses was counterbalanced across participants. Each stimulus stayed on the screen until a response occurred, or until 3 s had passed. For words classified as “old”, participants were additionally asked to make a decision about the subjective experience of retrieval (i.e., Remember/Know judgement; Tulving 1985). They were

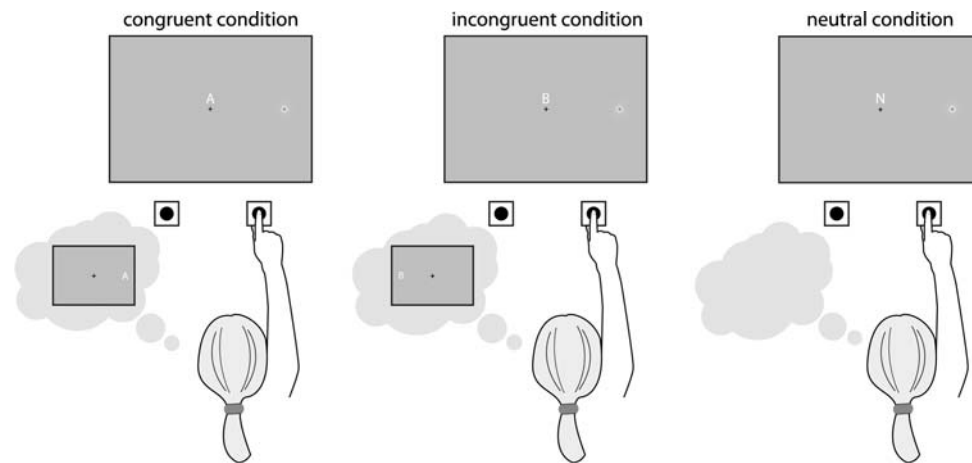


Fig. 1 A representation of the “attentional phase”. Letters stand for *words* in Experiment 1 and *pictures* in Experiment 2. Subjects had to detect a dot appearing on the left or the right side of the screen by pressing a left or a right key, respectively. In the congruent condition, the dot was preceded by a stimulus (A) that had been presented, during the

study phase, on the same side as the dot. In the incongruent condition, the dot was preceded by a stimulus (B) that had been studied on the opposite side. In the neutral condition, the dot was preceded by a new stimulus (N)

instructed to classify the endorsed item as “remembered” (R response) when recognition engendered clear recollection of the item and the contextual details surrounding it, and as “known” (K response) if it triggered merely a feeling of familiarity, without awareness of the context in which it appeared (Tulving 1985; Gardiner 1988).

Results and discussion

Figure 2 shows reaction times (RTs) for responding to the dot by side (left, right) and condition (congruent, incongruent, neutral) in the “attentional phase”. As is evident, the congruent condition is favoured regardless of side, with an overall advantage for dots appearing in the right visual field. Table 1 shows recognition memory accuracy associated with R and K responses for words studied on the left and on the right in the “recognition phase”. Here, no side is favoured, though R responses were more accurate than K responses.

Attentional phase

The above impressions were confirmed by ANOVA on RTs for responding to the dot, with dot presentation (left vs. right), and word presentation (left presentation, right presentation, no presentation) as within-subject factors. The analysis yielded an effect of dot presentation [$F(1, 29) = 6.15, P < 0.05$], such that subjects responded more quickly to dots presented on the right than on the left (370 vs. 389 ms; $P < 0.05$), and a significant dot presentation \times word presentation interaction [$F(2, 58) = 7.17, P < 0.05$]. Post hoc comparisons revealed that subjects responded

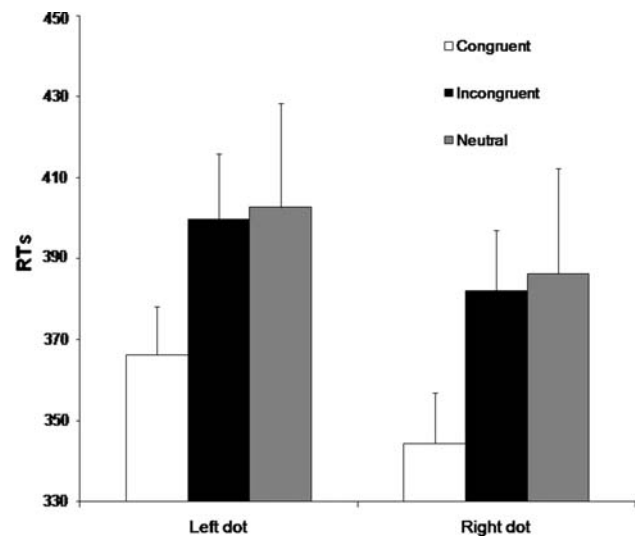


Fig. 2 Reaction times for responding to the dot by side (*left, right*) and condition (congruent, incongruent, neutral) in Experiment 1. Bars represent standard errors of the mean

more quickly to dots presented on the left preceded by words that were studied on the left (congruent condition) compared to words that were studied on the right (incongruent condition; 366 vs. 399 ms; $t(29) = -2.67; P < 0.05$; see Fig. 2). No difference in RTs emerged between the incongruent and the neutral condition ($P > 0.4$). Similarly, RTs were shorter for responding to dots presented on the right that were preceded by words studied on the right (congruent condition), compared to words studied on the left (incongruent condition; 344 vs. 382 ms; $t(29) = -2.93; P < 0.01$; see Fig. 2). Again, no difference in RTs emerged between the incongruent and the neutral condition ($P > 0.4$).

Table 1 Recognition accuracy by response type and side of presentation of words in Experiment 1

	Recognition accuracy		
	Remember	Know	Total
Left words	0.60 (0.04)	0.21 (0.04)	0.81 (0.03)
Right words	0.56 (0.04)	0.21 (0.03)	0.77 (0.03)

Values in parenthesis represent standard errors of the mean

Accurate trials were $\geq 98\%$ across conditions. The same ANOVA conducted on accuracy showed no significant effect of dot presentation ($P = 0.13$), word presentation ($P = 0.79$), or dot presentation \times word Presentation interaction ($P = 0.34$).

Recognition phase

Memory performance was high, and comparable for words studied on the left and on the right. An ANOVA on accuracy scores (hit rates – false-alarm rates), with Memory response (R vs. K) and word presentation (left vs. right) as within-subject factors, yielded an effect of Memory response [$F(2, 29) = 41.11, P < 0.01$]: Accuracy associated with R responses (0.58) was higher than accuracy associated with K responses (0.21; $P < 0.05$). No significant effect of word presentation ($P = 0.06$) or word presentation \times memory response interaction emerged ($P = 0.55$).

Our interest in this section was to investigate whether participants advantage in responding to dots in the congruent compared to the incongruent condition, i.e., facilitation effect, was modulated by the degree to which participants felt they were re-accessing the items' study context. The results showed that this was indeed the case. The facilitation effect for responding to dots presented on the left correlated with the frequency of R responses to words studied on the left ($r_{\text{Pearson}} = 0.42, P < 0.05$; see Fig. 3). It was not related to overall hit rates (i.e., collapsed across R and K responses, $P = 0.84$), and correlated negatively with the frequency of K responses ($r_{\text{Pearson}} = -0.47, P < 0.05$; see Fig. 3). Analogously, the facilitation effect for responding to dots presented on the right correlated with the frequency of R responses to words studied on the right ($r_{\text{Pearson}} = 0.40, P < 0.05$), but not with overall hit rates ($P = 0.23$), or with the frequency K responses ($r_{\text{Pearson}} = -0.35, P = 0.06$).

In summary, the results of this experiment showed that viewing an item originally studied on one side causes an automatic shift of attention to that side, facilitating response to stimuli presented on the same compared to the opposite side. This memory-driven facilitation effect correlated with individuals' *subjective* impression that they were re-accessing items' encoding context, as measured by the proportion of R responses they gave during recognition. We

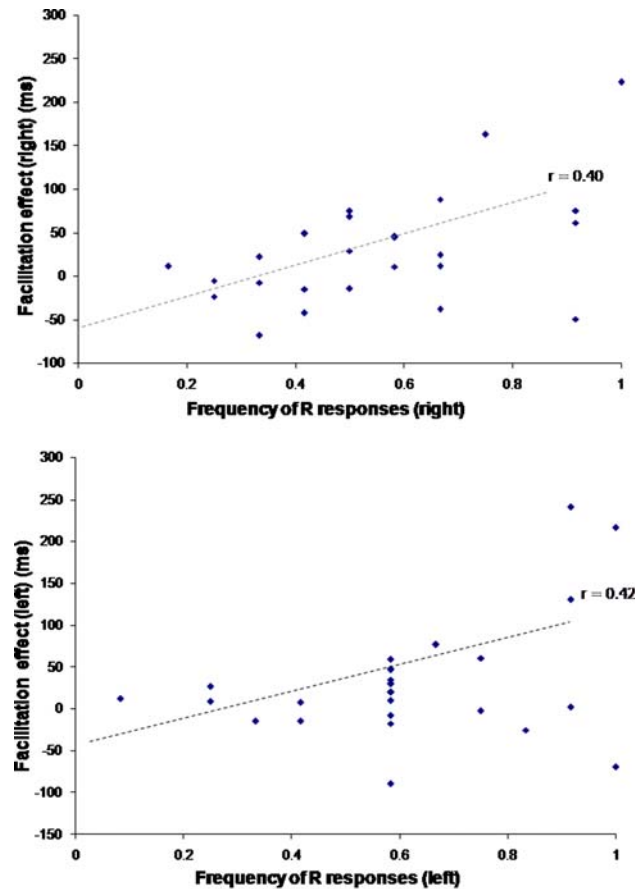


Fig. 3 Scatterplots of the correlation between the memory-driven facilitation effect (i.e., difference in RTs for responding to the dot in the incongruent versus congruent condition) and recollection levels. The *upper panel* displays the facilitation effect for dots presented on the *right* and the frequency of remember responses for words studied on the right. The *lower panel* displays the facilitation effect for dots presented on the left and the frequency of remember responses for words studied on the left

note that there was an overall advantage for responding to dots appearing on the right compared to the left visual field. Possibly, processing words in the attentional phase activated the left hemisphere, which, in turn, biased attention to the right hemifield (Kinsbourne 1970).

Experiment 2

In the second experiment we investigated whether the relation between the facilitation effect and recollective experience found in Experiment 1 was driven by subjects' *objective* remembering of the side where the memory stimuli had been studied. Thus, we asked subjects to recall the spatial location (left vs. right) of recognized items (i.e., source memory), instead of providing Remember responses. Though not the main purpose of the experiment, we also wanted to determine whether the right field advantage

observed in Experiment 1 would be eliminated using pictures as stimuli. Because pictures can be represented verbally and non-verbally (Moscovitch 1979, 1986), there should be no hemispheric advantage in processing them, and so no visual field advantage should emerge.

Method

Subjects

Thirty undergraduate or graduate students (15 males; age range 20–28, mean age 22.17 years) of the University of Toronto, different from those that had participated in Experiment 1, took part in this experiment. Participants were right-handed and had normal or corrected-to-normal vision. Participants received course credit or a 10\$ compensation. They gave written informed consent for the study, which was approved by the ethics committee of the University of Toronto.

Materials

Three hundred and twenty pictures (mean familiarity 2.45; range 1–4.75; see Snodgrass and Vanderwart 1980) were selected. One hundred and sixty pictures were presented at study whereas the other 160 served as distracters either in the attentional phase or in the recognition phase. The assignment of pictures to the different task phases was counterbalanced across participants. The experimental task was created in E-Prime. Viewing distance was approximately 60 cm.

Procedure

As in Experiment 1, the experimental session was comprised of a study phase, an “attentional” phase, and a recognition phase. The study phase and the attentional phase were not conceptually different from those in Experiment 1, except they used a different type and number of stimuli. During the study phase, participants viewed 160 pictures, 80 appearing on the left and 80 on the right side of the screen. Each stimulus was presented for 4 s and followed by a 500-ms blank screen. Participants were instructed to memorize the pictures. During the attentional phase, the 160 studied pictures and 80 new pictures appeared one at time in the centre of the screen. One-second after the picture’s appearance, a dot appeared either on the left or on the right of the screen. As in Experiment 1, dots could be preceded either by a picture that was originally studied on the same side (congruent condition), or on the opposite side (incongruent condition), or by a new picture (neutral condition; see Fig. 1). Again, participants responded to the

appearance of the dot by pressing the “z” and the “/” keys for dots appearing on the left or on the right, respectively. The picture and the dot stayed on the screen until a response to the dot occurred, or until 2 s had elapsed.

The recognition test differed slightly from that in Experiment 1. Participants viewed the 160 studied pictures together with 80 new pictures, in random sequence. For each picture, they decided if it was old or new, by pressing the “1” or “2” keys. For pictures endorsed as “old”, participants additionally indicated whether the item at study had been presented on the left or on the right of the screen.

Results and discussion

Figure 4 shows reaction times (*RTs*) for responding to the dot by side of presentation (left vs. right) and condition (congruent vs. incongruent vs. neutral). As in Experiment 1, there was an advantage in the congruent condition in both visual fields, but no overall advantage for one field over the other. Table 2 shows recognition and source memory accuracy for words presented on the left and on the right, with no difference between fields.

Attentional phase

The above impressions were confirmed by ANOVA on *RTs* for responding to the dot, with dot presentation (left vs. right), and Picture presentation (left presentation, right presentation, no presentation) as within-subject factors. There was no effect of dot presentation ($P = 0.94$) or picture

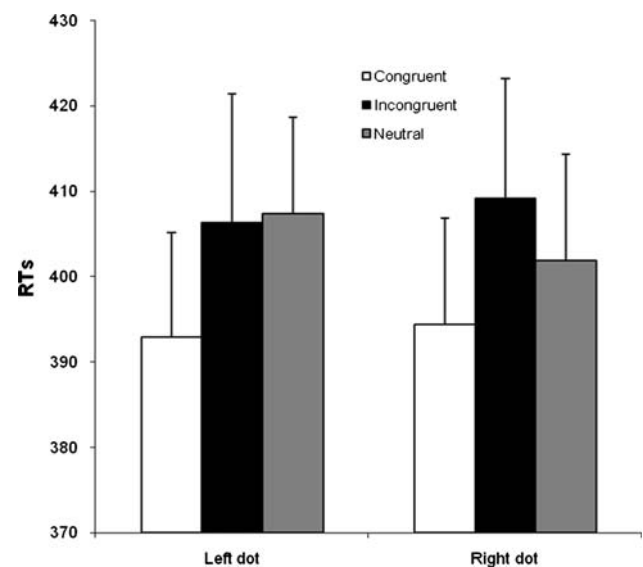


Fig. 4 Reaction times for responding to the dot by side (*left, right*) and condition (congruent, incongruent, neutral) in Experiment 2. *Bars* represent standard errors of the mean

Table 2 Recognition and source accuracy by side of presentation of pictures in Experiment 2

	Recognition accuracy	Source accuracy
Left pictures	0.89 (0.02)	0.79 (0.02)
Right pictures	0.88 (0.02)	0.77 (0.03)

Values in parenthesis represent standard errors of the mean

presentation ($P = 0.79$), but a significant dot presentation \times picture presentation interaction [$F(2, 58) = 4.56, P < 0.05$]. Post hoc comparisons revealed that subjects responded more quickly to dots presented on the left preceded by pictures studied on the left (congruent condition) compared to pictures studied on the right (incongruent condition; 393 vs. 406 ms; $t(29) = -2.56; P < 0.05$). No difference in RTs emerged between the incongruent and the neutral condition ($P > 0.18$). As well, RTs were shorter for responding to dots appearing on the right and preceded by pictures studied on the right (congruent condition) vs. the left side of the screen (incongruent condition; 394 vs. 409 ms; $t(29) = -2.48; P < 0.01$). Again, no difference in RTs emerged between the incongruent and the neutral condition ($P > 0.22$). Accurate trials were $\geq 99\%$ across conditions. The same ANOVA conducted on accuracy showed no significant effect of dot presentation ($P = 0.13$), picture presentation ($P = 0.33$), or dot presentation \times picture presentation interaction ($P = 0.63$).

Recognition phase

Recognition and source accuracy were quite high, for both pictures presented on the left and on the right. T_{student} tests confirmed no difference either in recognition accuracy ($P = 0.34$) or in source accuracy ($P = 0.44$) between pictures presented on the left and on the right.

In this section we investigated whether the memory-driven facilitation effect was related to participants' objective memory for the position of the pictures at study. We therefore analysed separately RTs to dots preceded by pictures whose position had been correctly recalled in the recognition phase (collapsed across left and right) and RTs to dots preceded by pictures whose position was not remembered (collapsed across left and right). We excluded from the analysis 6 subjects who attained a source accuracy ≥ 0.90 , thereby precluding examination of items characterized by source retrieval failures. An ANOVA on RTs for responding to dots, with condition (congruent vs. incongruent) and source accuracy (accurate vs. inaccurate) as within-subject factors, yielded an effect of condition [$F(1, 23) = 14, P < 0.01$], confirming that subjects responded more quickly to dots in the congruent compared to the incongruent condition ($P < 0.05$), but no effect of source

accuracy ($P = 0.65$), or condition \times source accuracy interaction ($P = 0.63$). Indeed, both the facilitation effect (17 vs. 12 ms), and the relative facilitation effect, i.e., $(RT_{\text{incongruent}} - RT_{\text{congruent}})/RT_{\text{congruent}}$, were comparable between the correct and the incorrect source conditions (0.04 vs. 0.05; $P > 0.6$ in both cases). Moreover, no correlation emerged between the facilitation effect and source accuracy, neither for stimuli presented on the left nor on the right ($P > 0.68$ in both cases).

In summary, as in Experiment 1, viewing an item originally studied on one side biased spatial attention to the same side. The memory-driven facilitation effect, however, was not related to participants' objective (source) memory for the side in which pictures were presented at study. As predicted, no visual field advantage emerged in this experiment, consistent with the notion that no hemispheric advantage should exist for processing nameable pictures.

General discussion

In the present study, we examined the attentional consequences of episodic memory retrieval. Subjects were tested in a choice reaction time task in which they had to press a right or a left key depending on the position of a dot presented at random on the left or on the right side of the screen. In the congruent condition, the dot was preceded by a stimulus (a word in Experiment 1; a picture in Experiment 2) that had been studied, in a previous phase, on the same side of the dot. In the incongruent condition, the dot was preceded by a stimulus that had been studied on the opposite side. In the neutral condition, the dot was preceded by a new stimulus. In two experiments, we have shown that subjects responded more quickly to the dot in the congruent compared to the incongruent condition. That is, viewing a central stimulus that had been studied on the left facilitated response to dots presented on the left as compared to the right, whereas the opposite was found for stimuli studied on the right.

The results of the present study are consistent with the AtoM model of episodic memory retrieval (Ciaramelli et al. 2008b; Cabeza 2008). We argue that in our task viewing the central stimuli during the attentional phase triggered the recovery of the full, contextually-detailed memory for those stimuli via pattern completion, an hippocampally dependent process by which exposure to a subset of stimuli from an earlier event causes the reactivation of memory for the entire event (Norman and O'Reilly 2003; Eichenbaum 2000; Treves 2004). Regions in the IPL oriented attention to these salient events (Corbetta and Shulman 2002). Attending to episodic memories with spatial features clearly caused spatial shifts of attention in subjects, who benefited when responding to probes that appeared where

their attention had been biased by the memory event. Similar effects are observed in the semantic memory domain. For example, perceiving a digit induces attentional shifts to the region of space that is congruent to the position associated with that digit on a mental number line (Fischer et al. 2003; Casarotti et al. 2007; Galfano et al. 2006). Interestingly, in our study the memory-driven facilitation effect was related to participants' re-experiencing the study phase, but not to their ability to recall the side where the memory stimuli had been studied. This finding makes it unlikely that the effect was mediated through the assignment of a left–right code to memory stimuli by the subjects, and subsequent deliberate alignment of the attentional spotlight with the cued location (Posner 1980; Berlucchi et al. 1989). Rather, it suggests that the degree to which participants re-experienced (attended) the contextual details of their memories modulated their behaviour linearly, consistent with the AtoM model (Ciamelli et al. 2008b). There is an aspect of the results, however, that conflicts with our model. If retrieval success captures attention, then one should have observed a worse attentional performance following studied compared to unstudied stimuli. But this did not happen: Reaction times were comparable to dots preceded by studied and unstudied stimuli. Possibly, we were not able to observe retrieval success effects on attentional performance because the dot was presented relatively too late, i.e., 1 s after the presentation of the memory stimulus. Future studies manipulating the delay between the presentation of the memory stimulus and the dot might capture the desired effect.

Our results make contact with previous research showing memory-based spatial compatibility effects. For example, Tlauka and McKenna (1998) asked subjects to study a real or verbally described map, in which elements were located on the left or right side. Later, participants carried out choice responses to those elements, now centrally presented. Performance was better if the response side corresponded to the original location of the element on the map than if it did not (see also Chun and Jiang 1998). Similarly, Hommel (2002) showed that retrieving non-spatial information about a previewed object with spatial features facilitated responses that spatially corresponded to the object's features. Memory contents also influence oculomotor behaviour. Richardson and Spivey (2000), for example, had participants learn a series of verbal facts presented auditorily while an unrelated event was simultaneously visible in one of the quadrants of the computer screen. When later queried on each fact, subjects made more eye fixations towards the (now empty) region of space where the visual information had occurred during learning of that fact, compared to other locations. Moreover, differences in eye movement behavior are observed for novel versus repeated stimuli (Ryan et al. 2000), or intact versus rearranged

backgrounds (Hannula et al. 2007). Overall, these studies suggest that episodic memory representations contain information about the spatial relations among the elements composing the original event. Retrieval of the event entails the automatic re-activation of its spatial features, which can affect attention and action (see Hommel 2002; di Pellegrino et al. 2005; Ryan et al. 2000). The results also further strengthen the notion that similar mechanisms underlie attention shifts across mental products and the external space (Farah 1989; Savazzi et al. 2008).

A major novel finding of the present study is that the memory-driven facilitation effect correlated with recollection levels for studied stimuli, as assessed by the proportion of Remember responses they attracted. Remember responses reflect the subjective impression of re-experiencing the event surrounded by its contextual features (Tulving 1985). This finding suggests that the ability to influence bottom-up attention is a strong correlate of vividly recollected memories, in line with the AtoM model (Ciamelli et al. 2008b). Accordingly, patients with lesions in the IPL, who show deficits in detecting relevant contralesional information (i.e., *neglect*, Vallar et al. 2003; Corbetta and Shulman 2002), also provide fewer Remember responses during memory tasks (Davidson et al. 2008). Like percepts, memories in parietal patients do not capture attention automatically (i.e., *memory neglect*; Cabeza et al. 2008), leading them to report an absence of memory in severe cases (Berryhill et al. 2007), or diminished recollective experience when the deficit is less severe (Davidson et al. 2008). In contrast, subjects' memory for the side where words had been studied (i.e., source memory) did not predict the impact of memory retrieval on bottom-up attention in our study, or of eye-movements in Ryan et al.'s (2000) study. This finding provides additional support to the notion that subjective recollection and source memory, although both reflecting memory for contextual details surrounding an event, are two different facets of memory, with only the former having an impact on bottom-up attention. Consistently, IPL regions sensitive to bottom-up attention are more responsive to recollection than to source memory (Ciamelli et al. 2008b). Moreover, patients with lesions in the IPL, who produce fewer remember responses in memory task, are normally able to recall source information (Davidson et al. 2008; Simons et al. 2008).

It is worth noting that we obtained a laterality effect favoring the right visual field-left hemisphere in Experiment 1 when words were used but not in Experiment 2 in which nameable pictures were used. Though responses were only measured to dots, we speculated that it is likely that words activated the left hemisphere and biased attention to the right field (Kinsbourne 1970), whereas nameable pictures activated both hemispheres (Moscovitch 1986). Alternatively, it is possible that the laterality effect was

related to left–right scanning for words, as the dot in the right, but not left visual field, appeared in the location compatible with the scanning direction.

To conclude, we have shown that episodic memory retrieval captures attention automatically, and influences the deployment of spatial attention. Moreover, the results suggest that the degree to which memory and bottom-up attention interact is a function (or a predictor) of subjective but not objective indicators of memory strength.

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References

- Baddeley AD, Lewis V, Eldridge M, Thomson N (1984) Attention and retrieval from long-term memory. *J Exp Psychol Gen* 113:518–540
- Berlucchi G, Tassinari G, Marzi CA, Di Stefano M (1989) Spatial distribution of the inhibitory effect of peripheral non-informative cues on simple reaction time to non-fixated visual targets. *Neuropsychologia* 27:201–221
- Berryhill ME, Phuong L, Picasso L, Cabeza R, Olson IR (2007) Parietal lobe and episodic memory: bilateral damage causes impaired free recall of autobiographical memory. *J Neurosci* 27:14415–14423
- Cabeza R (2008) Role of parietal regions in episodic memory retrieval: the dual attentional processes hypothesis. *Neuropsychologia* 46:1813–1827
- Cabeza R, Ciaramelli E, Olson IR, Moscovitch M (2008) Parietal cortex and episodic memory: an attentional account. *Nat Rev Neurosci* 9:613–625
- Casarotti M, Michielin M, Zorzi M, Umiltà C (2007) Temporal order judgment reveals how number magnitude affects visuospatial attention. *Cognition* 102:101–117
- Chun MM, Jiang Y (1998) Contextual cueing: implicit learning and memory of visual context guides spatial attention. *Cogn Psychol* 36:28–71
- Ciaramelli E, Ghetti S, Borsotti M (2008a) Divided attention during retrieval suppresses false recognition in confabulation. *Cortex* (In press)
- Ciaramelli E, Grady CL, Moscovitch M (2008b) Top–down and bottom–up attention to memory: a hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia* 46:1828–1851
- Corbetta M, Shulman GL (2002) Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3:201–215
- Craik FIM, Govoni R, Naveh-Benjamin M, Anderson ND (1996) The effects of divided attention on encoding and retrieval processes in human memory. *J Exp Psychol Gen* 125:474–479
- Davidson P, Anaki D, Ciaramelli E, Cohn M, Kim A, Murphy KJ, Troyer AK, Moscovitch M, Levine B (2008) Does lateral parietal cortex support episodic memory retrieval? Evidence from focal-lesion patients. *Neuropsychologia* 46:1743–1755
- di Pellegrino G, Rafal R, Tipper SP (2005) Implicitly evoked actions modulate visual selection: evidence from parietal extinction. *Curr Biol* 15:1469–1472
- Eichenbaum H (2000) Cortical–hippocampal networks for declarative memory. *Nat Rev Neurosci* 1:41–50
- Farah M (1989) Mechanisms of imagery–perception interaction. *J Exp Psychol Hum Percept Perform* 15:203–211
- Fernandes MA, Moscovitch M (2000) Divided attention and memory: evidence of substantial interference effects at retrieval and encoding. *J Exp Psychol Gen* 129:155–176
- Fernandes MA, Moscovitch M (2002) Factors modulating the effect of divided attention during retrieval of words. *Mem Cognit* 30:731–744
- Fischer MH, Castel AD, Dodd MD, Pratt J (2003) Perceiving numbers causes spatial shifts of attention. *Nat Neurosci* 6:555–556
- Galfano G, Rusconi E, Umiltà C (2006) Number magnitude orients attention, but not against one’s will. *Psychon Bull Rev* 13:869–874
- Gardiner JM (1988) Functional-aspects of recollective experience. *Mem Cognit* 16:309–318
- Hannula DE, Ryan JD, Tranel D, Cohen NJ (2007) Rapid onset relational memory effects are evident in eye movement behavior, but not in hippocampal amnesia. *J Cogn Neurosci* 19:1690–1705
- Hommel B (2002) Responding to object files: automatic integration of spatial information revealed by stimulus–response compatibility effects. *Q J Exp Psychol* 55A:567–580
- Jacoby LL, Woloshyn V, Kelley CM (1989) Becoming famous without being recognized: unconscious influences of memory produced by divided attention. *J Exp Psychol Gen* 118:115–125
- Kane MJ, Engle RW (2000) Working-memory capacity, proactive interference, and divided attention: limits on long-term memory retrieval. *J Exp Psychol Learn Mem Cogn* 26:336–358
- Kinsbourne M (1970) The cerebral basis of lateral asymmetries in attention. *Acta Psychol* 33:193–201
- Kucera H, Francis WN (1967) Computational analysis of present-day American English. Brown University Press, Providence, RI
- Moscovitch M (1979) Information processing in the cerebral hemispheres. In: Gazzaniga MS (ed) *Handbook of behavioural neurobiology*, vol. 2. Neuropsychology. Plenum Press, New York, pp 379–446
- Moscovitch M (1986) Afferent and efferent models of visual perceptual asymmetries: empirical and theoretical implications. *Neuropsychologia* 14:91–114
- Moscovitch M (1992) Memory and working-with-memory—a component process model based on modules and central systems. *J Cognit Neurosci* 4:257–267
- Moscovitch M (1994) Cognitive resources and dual-task interference effects at retrieval in normal people: the role of the frontal lobes and medial temporal cortex. *Neuropsychology* 8:524–534
- Moscovitch M, Catlin J (1970) Interhemispheric transmission of information: measurement in normal man. *Psychon Sci* 18:211–213
- Naveh-Benjamin M, Guez J (2000) Effects of divided attention on encoding and retrieval processes: assessment of attentional costs and a componential analysis. *J Exp Psychol Learn Mem Cogn* 26:1461–1482
- Naveh-Benjamin M, Craik FIM, Guez J, Dori H (1998) Effects of divided attention on encoding and retrieval processes in human memory: further support for an asymmetry. *J Exp Psychol Learn Mem Cogn* 24:1091–1104
- Naveh-Benjamin M, Craik FI, Guez J, Kreuger S (2005) Divided attention in younger and older adults: effects of strategy and relatedness on memory performance and secondary task costs. *J Exp Psychol Learn Mem Cogn* 31:520–537
- Norman KA, O’Reilly RC (2003) Modeling hippocampal and neocortical contributions to recognition memory: a complementary-learning-systems approach. *Psychol Rev* 110:611–646
- Park DC, Smith AD, Dudley WN, Lafronza VN (1989) Effects of age and a divided attention task presented during encoding and retrieval on memory. *J Exp Psychol Learn Mem Cogn* 15:1185–1191
- Posner MI (1980) Orienting of attention. *Q J Exp Psychol* 32:3–25

- Richardson DC, Spivey MJ (2000) Representation, space and Hollywood Squares: looking at things that aren't there anymore. *Cognition* 76:269–295
- Rizzolatti G, Umiltà C, Berlucchi G (1971) Opposite superiorities of the right and left cerebral hemispheres in discriminative reaction time to physiognomical and alphabetical material. *Brain* 94:431–442
- Rugg MD, Curran T (2007) Event-related potentials and recognition memory. *Trends Cogn Sci* 11:251–257
- Ryan JD, Althoff RR, Whitlow S, Cohen NJ (2000) Amnesia is a deficit in relational memory. *Psychol Sci* 11:454–461
- Savazzi S, Mancini F, Marzi CA (2008) Interhemispheric transfer and integration of imagined visual stimuli. *Neuropsychologia* 46:803–809
- Schneider W, Eschman A, Zuccolotto A (2002) E-prime reference guide. Psychology Software Tool, Pittsburgh
- Simons JS, Peers PV, Hwang DJ, Ally BA, Fletcher PC, Budson AE (2008) Is the parietal lobe necessary for recollection in humans? *Neuropsychologia* 46:1185–1191
- Snodgrass JG, Vanderwart M (1980) A standardized set of 260 pictures: norms for name agreement, image agreement, familiarity, and visual complexity. *J Exp Psychol* 6:174–215
- Tlauka M, McKenna FP (1998) Mental imagery yields stimulus-response compatibility. *Acta Psychol* 98:67–79
- Treves A (2004) Computational constraints between retrieving the past and predicting the future, and the CA3–CA1 differentiation. *Hippocampus* 14:539–556
- Tulving E (1985) Memory and consciousness. *Can Psychol* 26:1–12
- Vallar G, Bottini G, Paulesu E (2003) Neglect syndromes: the role of the parietal cortex. *Adv Neurol* 93:293–319
- Vilberg KL, Rugg MD (2008) Memory retrieval and the parietal cortex: a review of evidence from a dual-process perspective. *Neuropsychologia* 46:1787–1799
- Wagner AD, Shannon BJ, Kahn I, Buckner RL (2005) Parietal lobe contributions to episodic memory retrieval. *Trends Cogn Sci* 9:445–453
- Yonelinas AP (2002) The nature of recollection and familiarity: a review of 30 years of research. *J Mem Lang* 46:441–517