



FOCUS ARTICLE

A systematic review and meta-analysis of memory-guided attention: Frontal and parietal activation suggests involvement of fronto-parietal networks

Manda Fischer | Morris Moscovitch | Claude Alain

Department of Psychology, Rotman Research Institute, University of Toronto, Toronto, ON, Canada

Correspondence

Manda Fischer, Department of Psychology, Rotman Research Institute, University of Toronto, Toronto, ON, Canada.

Email: manda.fischer@mail.utoronto.ca

Funding information

Natural Sciences and Engineering Research Council of Canada, Grant/Award Numbers: A83470, RGPIN-2016-05523

Abstract

Prior knowledge and long-term memory can guide our attention to facilitate search for and detection of subtle targets embedded in a complex scene. A number of neuropsychological and experimental studies have investigated this effect, yet results in the field remain mixed, as there is a lack of consensus regarding the neural correlates thought to support memory-guided attention. The purpose of this systematic review and meta-analysis was to identify a common set of brain structures involved in memory-guided attention. Statistical analyses were computed on functional magnetic resonance imaging (fMRI) studies that presented participants with a task that required them to detect a target or a change embedded in repeated and novel complex visual displays. After a systematic search, 10 fMRI studies met the selection criteria and were included in the analysis. The results yielded four significant clusters. Activity in right inferior parietal (Brodmann area [BA] 9) and right superior parietal (BA 7) lobes suggests involvement of a fronto-parietal *attention* network, while activity in left mid-cingulate cortex (BA 23) and right middle frontal gyrus (BA 10) suggests involvement of a fronto-parietal *control* network. These findings are consistent with the notion that fronto-parietal circuits are important for interfacing retrieved memories with attentional systems to guide search.

This article is categorized under:

Psychology > Memory

Psychology > Learning

Psychology > Attention

KEYWORDS

fronto-parietal network, long-term memory, medial temporal lobe, memory-guided attention

1 | INTRODUCTION

Everyday activities, such as navigating a webpage, require us to search for objects in complex environments. For example, the amount of time it takes to find the “login” button depends not only on how eye-popping the button is on the website, but also on a person’s prior experience. Extracting patterns from the environment and capitalizing on these

long-term associations is thought to aid perception during real-time search. Several brain regions have been identified that may underlie this effect, yet there remains a lack of consensus in the field. In this article, we define memory-guided attention as “expectation for perception”, whereby the memory of a familiar stimulus contains predictive information about an association that is used to influence a perceptual decision. In order to qualify as memory-guided attention, there must be a long-term association that influences a perceptual decision.

Memory-guided attention can be examined in two stages: (a) The procedural learning stage, at which repeated exposure to a configuration and embedded target enables learning of the configuration-to-target location association and (b) The memory-guided selective attention stage, at which the learned associations are *used* to facilitate target detection (Voss, Galvan, et al., 2011; Voss, Gonsalves, et al., 2011; Voss, Warren, et al., 2011; Wang & Voss, 2014). This systematic review and meta-analysis focusses on the second stage, in which learned associations are used to guide attention toward an anticipated target location. We suggest that this stage isolates the effect of interest, as it captures the unique quality of *expectation for perception*. Examining memory-guided attention at a specific stage is critical in order to identify its neural substrates. Therefore, the aim of this review and meta-analysis is to elucidate what conditions and processes are implicated in memory-guided attention, consider the behavioral consequences, and identify the neural substrates mediating it.

2 | NEURAL CORRELATES UNDERLYING MEMORY-GUIDED ATTENTION

In this section, we review a set of brain structures and networks that have been identified as being important for memory-guided attention.

2.1 | The medial temporal lobe

To date, there is a lack of consensus regarding the role of the medial temporal lobes (MTLs), particularly the hippocampus, in memory-guided attention. The MTLs are thought to be involved in memory-guided attention because of their involvement in associative learning (Córdova, Turk-Browne, & Aly, 2019; Goh et al., 2004; Hannula & Ranganath, 2009; Henke, 2010; Hirsh, 1974; Konkel & Cohen, 2009; Olsen, Moses, Riggs, & Ryan, 2012; Schacter, Dobbins, & Schnyer, 2004). In memory-guided attention tasks, the making of target-to-context associations appears to be critical in order to guide attention. Therefore, if associative learning, supported by the hippocampus, is necessary in order to bias attention, memory-guided attention should be affected by MTL damage.

Chun and Phelps (1999) found support for the involvement of the hippocampus in memory-guided attention. In their study, amnesic patients with hippocampal and extended MTL damage were impaired on a spatial contextual cueing task. Park, Quinlan, Thornton, and Reder (2004) administered doses of midazolam, a central nervous system depressant that causes a temporary anterograde amnesia, to induce temporary amnesia pharmacologically. They ascertained that memory-guided attention for the midazolam group was impaired. Zimmermann, Alain, and Butler (2019) found that asymptomatic carriers of the Apolipoprotein E4 (APOE4) allele (a strong marker of genetic susceptibility for late-onset Alzheimer's disease that targets the hippocampus and its connections to superior parietal attention areas) were impaired on a memory-guided attention task in comparison to healthy controls. These findings suggest that the hippocampus and parietal areas are important for memory-guided attention. In an fMRI study, Greene, Gross, Elsinger, and Rao (2007) presented participants with a spatial contextual cueing task, similar to Chun & Jiang, (1998), and found that the hippocampus was a critical structure. Further, fMRI findings by Günseli and Aly (2020), Goldfarb, Chun, and Phelps (2016), Manelis and Reder (2012), Stokes, Atherton, Patai, and Nobre (2012), and Summerfield, Lepsien, Gitelman, Mesulam, and Nobre (2006) support the account of hippocampal-dependent memory-guided attention. Together, these studies suggest that the hippocampus may be involved in the associative learning aspect of memory-guided attention.

Not all studies, however, have found hippocampal involvement in memory-guided attention. For example, Manns and Squire (2001) studied amnesic patients with extensive, but not complete, hippocampal damage. Despite damage to their hippocampus, these patients showed preserved memory-guided attention. Negash et al. (2007) tested patients with mild cognitive impairment who showed reduced hippocampal volume and found that they were still able to show effects of memory-guided attention. These results are at odds with the argument that the hippocampus is critical for memory-guided attention. Consistent with these findings, a number of functional

neuroimaging studies did not find conclusive evidence for hippocampal involvement during tasks designed to engage memory-guided attention (e.g., Pollmann & Manginelli, 2009, 2010, 2016; Rosen, Stern, Devaney, & Somers, 2018; Rosen, Stern, Michalka, Devaney, & Somers, 2015). The neural correlates underlying memory-guided attention have also been shown to differ according to the type of memory test used. Two tests of memory that can broadly be distinguished are those that test explicit memory, in which information is consciously and deliberately manipulated and retrieved, and those that test implicit memory, in which information is learned incidentally and participants may be unaware that memory is being tested (Roediger III, Weldon, & Challis, 1989; Schacter, Bowers, & Booker, 1989). When comparing the effect of memory-guided attention in implicitly instructed participants to explicitly instructed participants, Westerberg, Miller, Reber, Cohen, and Paller (2011) ascertained that the magnitude of the memory-guided attention effect was the same for both groups, and that there was considerable overlap in visual areas, the inferior parietal lobule, and the inferior frontal cortex during the task for both groups. The explicit group, however, showed additional activity in bilateral posterior hippocampal and left perirhinal cortex. This finding suggests that the hippocampus is involved in explicit recognition but not necessarily in the memory-guided attention effect. This idea would be consistent with Preston and Gabrieli's (2008) finding that the hippocampus, specifically, is correlated with explicit recognition of the repeated configurations, but that this effect is orthogonal to that of memory-guided attention. Therefore, it is possible (a) that memory-guided attention can occur regardless of whether the hippocampus is recruited or (b) that the hippocampus may be additionally recruited to support explicit recognition and behavioral expression of the effect.

A number of functional neuroimaging studies have demonstrated hippocampal involvement during the initial stage of procedural learning, but not during the subsequent stage, in which associative memory guides attention to the target (Giesbrecht, Sy, & Guerin, 2013; Greene et al., 2007; Kasper, 2013). Earlier in the article, we proposed that memory-guided attention has often been examined in two stages; (a) the learning stage and (b) the memory-guided selective attention stage. We argue, here, that while the first stage is a necessary prerequisite to the second stage, it is the second stage, in which the learned associations are actually utilized for perception, that isolates the effect of memory-guided attention. Little focus on the stage at which hippocampal involvement is implicated may contribute to the lack of clarity in the field. To date it remains unclear whether the hippocampus or surrounding MTL regions contribute individually, together, or not at all to memory-guided attention.

2.2 | Frontal and parietal contributions

Fronto-parietal activity may be especially important for interfacing long-term memory representations with attentional components (Cabeza, 2008; Chiu & Yantis, 2009; Cole & Schneider, 2007; Hutchinson et al., 2014; Leech & Sharp, 2014; Nelson et al., 2010; Sestieri, Shulman, & Corbetta, 2010; Shomstein & Yantis, 2004, 2006; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013; Vilberg & Rugg, 2009; Wagner, Shannon, Kahn, & Buckner, 2005).

The Attention to Memory (AtoM) model of episodic memory retrieval may offer insight into the processes involved in memory-guided attention (Cabeza, Ciaramelli, & Moscovitch, 2012; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008). Although this theory examines attention to internal mental representations, neuroimaging studies have revealed that AtoM and memory-guided attention share common underlying neural correlates (Gazzaley & Nobre, 2012; Nobre, Coull, & Frith, 2004). These findings suggest that parallels can be drawn between attention to internal representations and attention to external stimuli, and that extrapolating from the AtoM model may be useful for understanding memory-guided attention. Further, memory-guided attention may require attention to internal representations during retrieval to guide search effectively. Therefore, the AtoM model may help us characterize an important process involved in this effect. The AtoM model asserts that attentional guidance toward internal representations involves the recovery of the context associated with the target via hippocampal pattern completion (Eichenbaum, 2000; Norman & O'Reilly, 2003; Treves, 2004). When confidence is low and more effort is required, top-down attention is employed by the superior parietal lobe. In contrast, when confidence is high and a memory is easily accessible, bottom-up attention is employed to guide attention automatically to the memorandum (Corbetta & Shulman, 2002). Consistent with this model, two fMRI studies have shown superior and inferior parietal activation during a spatial memory-guided attention task (Giesbrecht et al., 2013; Manginelli et al., 2013). Importantly, these studies found no evidence of explicit knowledge of context repetition, suggesting (a) that the parietal cortex may be involved in nonepisodic implicit memory tasks and episodic memory tasks or (b) that both implicit and explicit memories contribute to guiding attention in these studies.

2.3 | Neural networks underlying memory-guided attention

One model of memory-guided attention contends that the effect is supported by connections between the hippocampus and the dorsal attention fronto-parietal network (Goldfarb et al., 2016; Rosen et al., 2015; Stokes et al., 2012; Summerfield et al., 2006; Zimmermann et al., 2019). The two-stage recollection process is consistent with this model and necessitates activation from both hippocampus and prefrontal areas of the brain (Moscovitch, 2008; Moscovitch, Cabeza, Winocur, & Nadel, 2016). The initial nonconscious stage involves rapid nonconscious recovery of relational memory information by the hippocampus. The second stage then involves cortical structures, such as prefrontal areas, to mediate higher-order control processes. Further, research has examined the bidirectional relationship between the hippocampus and attention (Aly & Turk-Browne, 2016a, 2016b, 2017; Córdova et al., 2019; Decker & Duncan, 2020; Günseli & Aly, 2020; Hasselmo, Bodelón, & Wyble, 2006) and suggests that the hippocampus mediates external attention and perception, while attention acts on the hippocampus to stabilize its representations. Although these findings do not speak directly to the effect of memory on attention, they highlight the interactive nature of memory and attention and could be incorporated in future work on the interaction between attention at encoding and then memory-guided attention at retrieval.

With regards to memory-guided attention, these areas may interact with parietal regions to retrieve stored information about a complex scene, and to guide attention effectively (Goldfarb et al., 2016). In fact, the selection of a target via the assistance of a stored memory template has been shown to involve a hippocampal-parietal network in conjunction with a selective attention fronto-parietal network (Bridge, Cohen, & Voss, 2017; Goldfarb et al., 2016). The fronto-parietal attention network, however, may not solely contribute to memory-guided attention. A number of studies found that this network was recruited in both memory-guided and stimulus-guided attention tasks (Rosen et al., 2015; Stokes et al., 2012; Summerfield et al., 2006). In stimulus-guided attention tasks, a long-term memory of the display/scene exists, but a long-term association between display and target does not. Therefore, involvement of the fronto-parietal attention network may be related to a more general long-term memory *retrieval* process (St Jacques, Kragel, & Rubin, 2011), rather than to a long-term memory-guided attention process that uses long-term *associations* to guide attention.

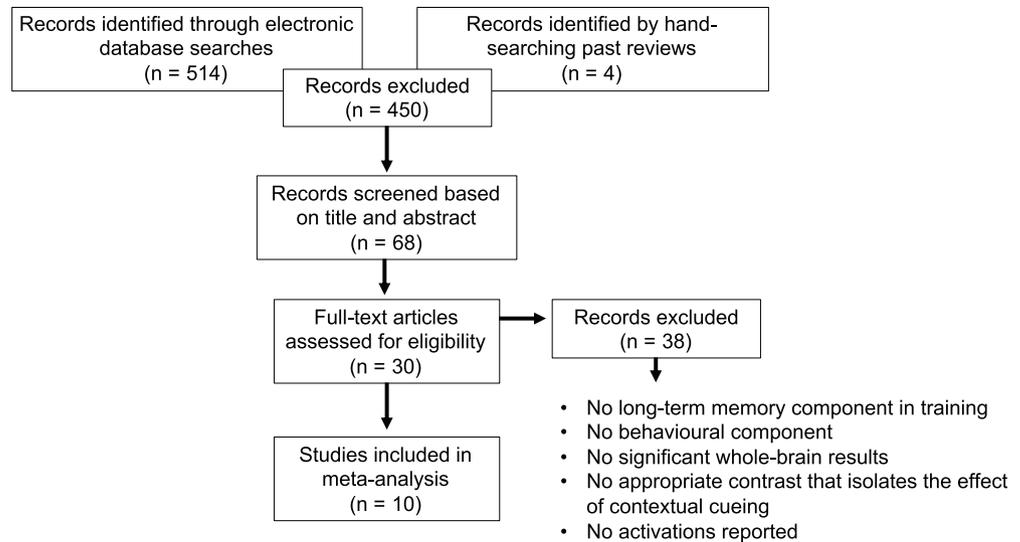
The fronto-parietal control network is another network that has been implicated in memory-guided attention (Rosen et al., 2018). This network may be especially important for interfacing long-term memory representations with external information. Furthermore, a portion of the fronto-parietal control network has been shown to be (a) connected to the fronto-parietal attention network (Dixon et al., 2018) and (b) situated in between fronto-parietal attention and hippocampal-cortical memory networks, making it an important system for integrating information (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008).

Therefore, existing models of memory-guided attention implicate fronto-parietal attention and control networks. These two networks may aid the process by interfacing memory and attentional components.

3 | CURRENT ANALYSIS

This analysis aims to identify common brain structures that are involved in the use of long-term associations between a target and its location to guide attention during search. According to current models of memory-guided attention, we expect to observe both memory and attention components of the effect in the neural response. Despite the growing interest in identifying the neural correlates of memory-guided spatial attention, there remains a lack of consensus in the field. By specifying the contrast that isolates the stage in which long-term associations are used for perception, we aim to elucidate the brain structures that support memory-guided attention. Visual and auditory memory-guided attention may be supported by a common set of areas (Corbetta & Shulman, 2002; Giesbrecht, Woldorff, Song, & Mangun, 2003; Kastner & Ungerleider, 2000; Zimmermann, Ross, Moscovitch, & Alain, 2020), but to our knowledge, functional magnetic resonance imaging (fMRI) or positron emission topography (PET) studies that examine the neural correlates of memory-guided attention in the auditory domain do not yet exist. Therefore, the current meta-analysis is restricted to the effect of memory-guided attention in the visual domain. In the discussion, however, we have considered the role of memory guided attention in other modalities, as revealed by other techniques.

FIGURE 1 Flowchart depicting screening process for studies included in the meta-analysis



4 | MATERIALS AND METHODS

4.1 | Literature search

The PsycINFO (Ovid) and PubMed databases were searched on February 6, 2020, using the following terms: Either “memory-guided,” “contextual cueing,” “contextual cues,” “configural memory” or “change detection”; with either “functional magnetic resonance imaging,” “fMRI,” “positron emission topography,” or “PET.” The search yielded 514 unique results (116 studies overlapped between the two databases). All relevant articles were then searched for potentially appropriate articles.

4.2 | Screening process and selection criteria

Each article's title and abstract were initially screened based on the eligibility criteria outlined in Figure 1. Following this step, full texts of potentially eligible articles were retrieved and screened.

We selected studies for the meta-analysis if they met the following criteria: (a) The study paradigm examined deliberate or incidental long-term associations between a visual stimulus and its spatial location. (b) The study included a behavioral component that was performed prior to, during, or after scanning. (c) The study consisted of a whole-brain analysis from fMRI or PET on 3D coordinates in either Talairach (Talairach & Tournoux, 1988) or Montreal Neurological Institute (MNI) standardized space. For example, Goldfarb et al. (2016) was excluded from the analysis because a whole-brain analysis was not reported. (d) The study conducted a contrast that isolated the effect of memory-guided attention. For example, a contrast that that we considered acceptable was one that examined greater activity for Old displays (learned context-target association) than for New ones (no context-target association) because it isolates the effect of memory-guided attention (*use* of the associations) from the effect of learning the associations themselves. A contrast that was not of interest was one that examined greater activity for New displays than for Old ones. This contrast isolates the effect of learning the association, independent of the effect of memory-guided attention and correlates with contextual-cueing behaviour (Preston & Gabrieli, 2008). (e) The study reported activations, rather than deactivations. Westerberg et al. (2011) was excluded because the contrast of interest yielded deactivation of brain areas. It is recommended that activations and deactivations be analyzed as separate meta-analyses, as the two foci represent different signal changes. As this exclusion criterion applied to one study, we only included and ran the meta-analysis on studies that reported activations. Furthermore, greater activation for Old configurations has been correlated with contextual-cueing behavior (e.g., Preston & Gabrieli, 2008). (f) The study included participants who were healthy young adults with no visual impairments or brain damage. We did not come across any studies that included patient participants or a mixture of healthy and patient participants. For a complete description of studies included in the final model see Table 1. Coordinates were included only if they

TABLE 1 Neuroimaging studies included in the analysis

References	Stimuli and contrasts revealing increasing activation	Task and behavioral findings	Number of participants (sex and age)	Field strength, foci	Coordinate space	Source in article
Giesbrecht et al. (2013), <i>Vision Research</i>	Target letter “T” embedded in letter “L” distractors. <i>Old > New displays</i> . Activity that is greater for Old displays compared to New ones. Old trials were those in which the location, orientation, and color of the distractors was fixed for a specific target location.	Search trials (old or new configurations) in which participants indicate if target is rotated to the left or right. RT Old < New driven by last epoch.	14 total (13F, $M = 22$ years, three excluded); all right-handed.	3T, 7	MNI	Table 1
Greene et al. (2007), <i>Learning & Memory</i>	Target letter “T” embedded in letter “L” distractors. <i>Interaction of array type (Old vs. New) by Reaction time</i> . Faster reaction times for Old displays correspond to greater activity compared to New ones. Old trials were those in which the location, orientation, and color of the distractors was fixed for a specific target location.	Search trials (Old or New configurations) in which participants indicate if target is rotated to the left or right. RT Old < New and shorter RT over epochs.	26 total (19F, $M = 21.4$ years); handedness not reported	1.5T, 9	Talairach	Table 1
Manginelli et al. (2013), <i>Neuroimage</i>	Target letter “T” embedded in letter “L” distractors. <i>Old > New displays</i> . Activity that is greater for Old displays compared to New ones. Old trials were those in which the location, orientation, and color of the distractors was fixed for a specific target location.	Search trials (Old or New configurations) in which participants indicate with alternative forced choice button press whether or not the target was present. RT Old < New increasingly over epochs.	23 total (13F, $M = 24.4$ years, three excluded); all right-handed	3T, 7	Talairach	Table 2
Pollmann and Manginelli (2010), <i>The Open NeuroImaging Journal</i>	Target letter “T” embedded in letter “L” distractors. <i>Configuration (Old vs. New) by Epoch (1 or 3) interaction</i> . Faster reaction times for Old displays correspond to greater activation compared to New ones at Epoch 3. 1. Old–New (Epoch 1) 2. Old–New (Epoch 3)	Search trials (Old or New configurations) in which participants indicate if target is rotated to the left or right. RT Old < New at Epoch 3.	13 total (8F, $M = 25.94$, 21–34 years, three excluded); all right-handed	3T, 3	Talairach	Table 2

TABLE 1 (Continued)

References	Stimuli and contrasts revealing increasing activation	Task and behavioral findings	Number of participants (sex and age)	Field strength, foci	Coordinate space	Source in article
Pollmann and Manginelli (2009), <i>Frontiers</i>	<p>Target letter “T” embedded in letter “L” distractors.</p> <p><i>Configuration (Old vs. New) by Change (pre/post) interaction.</i> Old displays that are pretarget change correspond to greater activity compared to New ones.</p> <p>1. Old–New (prechange) 2. Old–New (postchange) Prechange refers to Epoch 1–5 before target location is change. Postchange refers to epoch 6–10 after target location is changed.</p> <p>Old trials were those in which the location and color of the distractors was fixed for a specific target location.</p>	<p>Search trials (Old or New configurations) in which participants indicate if target is rotated to the left or right. After five blocks, target locations in Old configurations were changed to a new location.</p> <p>RT Old < New before change in target location occurs (first six blocks).</p>	13 total (12F, $M = 22.4$ years, 2 excluded); all right-handed	1.5T, 21	Talairach	Table 1
Preston and Gabrieli (2008), <i>Cerebral Cortex</i>	<p>Target letter “T” embedded in letter “L” distractors.</p> <p><i>Old > New</i> modulated by the magnitude of contextual cueing (correlated with behavior). Faster reaction times for Old displays correspond to greater activation compared to New ones.</p> <p>Old trials were those in which the location and color of the distractors was fixed for a specific target location.</p>	<p>Search trials (Old or New configurations) in which participants indicate if target is rotated to the left or right. After six blocks, target locations in Old configurations were changed to a new location.</p> <p>RT Old < New</p>	23 total (15 F, $M = 20.4$ years, 2 excluded); 12 right-handed	3T, 8	MNI	Table 1
Rosen et al. (2018), <i>Cerebral Cortex</i>	<p>Category word paired with object images.</p> <p><i>Long-term (LTM) memory-guided attention > Stimulus (STIM) guided attention.</i> Brain areas preferentially involved in LTM memory-guided attention compared to STIM memory-guided attention.</p>	<p>Participants were cued with a category word and then detected the presence/absence of a learned associate object image embedded in an array of object images. Additionally, a red arrow was placed at fixation.</p>	24 total (11F, 22–34 years— M not reported); all right-handed	3T, 19	MNI	Table 1

(Continues)

TABLE 1 (Continued)

References	Stimuli and contrasts revealing increasing activation	Task and behavioral findings	Number of participants (sex and age)	Field strength, foci	Coordinate space	Source in article
		<p><i>Stimulus-guided attention (STIM) condition:</i> A red cue arrow indicated the location in the object image array. Participants reported the presence/absence of an object image of the <i>named</i> category.</p> <p><i>Long-term-guided attention (LTM) condition:</i> Participants retrieved the location paired with the category word and reported whether or not an object image exemplar of the named category appeared at that location. Red arrows were uninformative in this condition.</p> <p>No difference in detection accuracy between LTM and STIM conditions.</p> <p>RT STIM < LTM in that the target is detected fast for the STIM condition compared to the LTM condition.</p>				
Rosen et al. (2015), <i>Cerebral Cortex</i>	<p>Outdoor Google image real-world scenes (Original vs. Altered).</p> <p><i>Long-term (LTM) memory-guided attention > Stimulus (STIM) guided attention.</i></p> <p>Brian areas preferentially involved in LTM memory-guided attention compared to STIM memory-guided attention.</p> <p>Altered scenes were those that had one change that participants learned.</p>	<p>Change detection task in which participants indicated detection of changes by clicking on location of change:</p> <p><i>Stimulus-guided attention (STIM) condition:</i> Scenes alone were studied prior to test. At test, the change was explicitly cued with a red and white nested box centered around location of potential scene change (50% chance change).</p>	23 total (10F, 23–33 years— <i>M</i> not reported); all right-handed	3T, 11	MNI	Table 1

TABLE 1 (Continued)

References	Stimuli and contrasts revealing increasing activation	Task and behavioral findings	Number of participants (sex and age)	Field strength, foci	Coordinate space	Source in article
		<p><i>Long-term-guided attention (LTM) condition:</i> Scenes and changes were studied prior to test. At test, change was not cued</p> <p>No difference in change detection (d') and RT between (LTM) memory-guided and (STIM) explicit cue conditions.</p>				
Stokes et al. (2012), <i>PNAS</i>	<p>Target (key) embedded in outdoor or indoor real-world scenes.</p> <p><i>Valid > Neutral memory cue.</i> Brain areas preferentially involved in displays that contain a memory-cue (Valid) compared to those that do not have a memory-cue (Neutral).</p>	<p>Participants cued with the scene alone and then subsequently viewed either a valid (target present and location learned during training) and neutral (target absent during training) scene and indicated if the target was present.</p> <p>RT Valid cue < Neutral cue</p>	16 total (9F, $M = 25$ years); all right-handed	3T, 16	MNI	Requested
Summerfield et al. (2006), <i>Neuron</i>	<p>Target embedded in real-world scenes.</p> <p><i>Long-term memory (LTM)-guided attention > Stimulus-guided (STIM)-guided attention.</i> Brain areas preferentially involved in LTM-guided attention)</p>	<p>Participants indicated with a left or right mouse click if the target was present (valid) or absent (neutral):</p> <p><i>LTM-guided attention condition:</i> Participants viewed Old (previously studied) scenes.</p> <p><i>Visual-orienting task STIM-guided attention condition:</i> Participants viewed New scenes with a visual cue that would flash in the location of the target).</p> <p>RT valid cue < neutral cue and RT for LTM-guided attention < STIM-guided attention for valid cues.</p>	16 total (10F; 21–41 years— M not reported); all right-handed	3T, 5	MNI	Tables 1 and 2

corresponded to activations from a direct comparison between the task of interest and a comparison task (e.g., memory-guided cue versus visually-guided cue conditions).

Ten studies met the above criteria and were included in the meta-analysis. These studies were comparable in terms of the tasks included. Six of the 10 studies adopted the paradigm used in Chun and Jiang (1998). The remaining four studies used real-world scenes as stimuli (see Table 1 for details). To our knowledge, there do not exist many studies that investigate memory-guided attention using neuroimaging. Because the research spans subfields, terminology is variable. In order to take into account the variability in terminology, we made the initial search as broad as possible. A vast number of keywords were used across subfields in Psychology to refer to the same or a similar phenomenon. For example, after conducting a preliminary search for articles on Google Scholar, memory-guided attention was found to be synonymous with the following terms: contextual cueing, memory-guided attention, contextual memory, priming and memory, searching through memory, contextual change detection, working with memory. After following a systematic selection process, our impression was confirmed that there exists scant literature regarding memory-guided attention. Sensitivity was achieved by increasing the number of keywords in the search, and this approach was complemented with careful use of AND and OR operators to increase the level of precision (Campbell, Taylor, Bates, & O'Connor-Bones, 2017). These two metrics have been identified as important tools for conducting systematic searches (Campbell et al., 2017). As the two have an inverse relationship (Best, Taylor, Manktelow, & McQuilkin, 2014, p. 351), we tried to balance them, with slightly more emphasis on sensitivity (Taylor, Killick, & McGlade, 2015).

4.3 | Activation likelihood estimate (ALE)

Using GingerALE software (v. 3.0.2) available on BrainMap (<http://brainmap.org/ale/index.html>), a coordinate-based quantitative meta-analysis of neuroimaging results was computed. Four studies were in Talairach coordinate space and six studies were in MNI space. Prior to the analysis, Talairach coordinates were converted to MNI space, using the Talairach to MNI (SPM) space transformation.

Computation of significant clusters required that the software generate a brain activation map based on the overall coordinates that were grouped by experiment, in order to determine whether the collective mean activation was statistically reliable or not. To calculate above-chance clustering maps between studies, the program modelled a three-dimensional Gaussian probability distribution centered on each focus reported in an experiment and weighted it according to the number of participants (for more information see Eickhoff et al., 2009; Turkeltaub et al., 2012). Next, it calculated combined probabilities of activation for each voxel (for more information, see Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012). Finally, voxel-wise scores were yielded, indicating convergence of activation in similar brain locations across studies.

In order to account for the possibility of false negatives introduced by the low number of studies included, we used single study p -value thresholding to detect brain regions consistently activated during memory-guided attention tasks. This method set any voxel where the p value image had a value over the threshold to zero. To counter this liberal method, we also used the recommended conservative threshold of $p < .001$. Additionally, the random effect Turkeltaub nonadditive method and a smaller more conservative mask size were used. The random effect reduces both within-group and within-experiment effects, by restricting probability values of neighboring foci from the same experiment (Turkeltaub et al., 2012). The minimum volume was set to 250 mm³.

In order to visualize the results, we used the program Mango (v.4.1), available on BrainMap (<http://brainmap.org/ale/index.html>). The ALE-statistic maps were overlaid on an MNI space template (Colin27_T1_seg_MNI.nii).

5 | RESULTS

The aim of the current analysis was to identify brain areas that are consistently recruited during memory-guided attention. Ten studies met inclusion criteria for the meta-analysis ($N = 191$) (Table 1). Given the small number of studies, we analyzed implicit and explicit studies together.

The analysis included 160 foci and yielded four significant clusters. Two clusters had peak activity in the parietal lobe, corresponding to the angular gyrus and the superior parietal lobe, one cluster corresponded to activity in the middle frontal gyrus, and one cluster corresponded to activity in the mid-cingulate cortex (Figure 2). Table 2

FIGURE 2 Activation maps generated by the ALE analysis. Cross-pointer overlaid at cluster center. The four images correspond to Cluster 1, 2, 3, and 4, respectively: (a) Right parietal lobe (BA 39). (b) Left limbic lobe (BA 23). (c) Right frontal lobe (BA 10). (d) Right parietal lobe (BA 7)

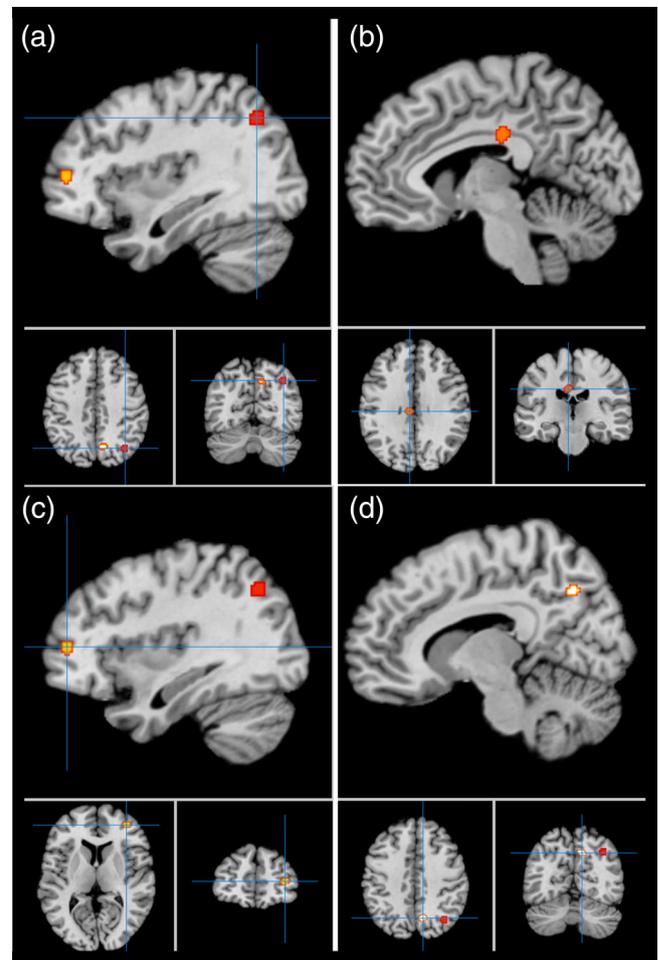


TABLE 2 A list of significant clusters generated from the meta-analysis

Cluster #	Lobe, Brodmann area	MNI coordinate of cluster center (x, y, z)	Cluster size (mm^3)	# Studies/cluster
1	Right parietal lobe, 39	35.6, -67.1, 41	352	2
2	Left limbic lobe, 23	-5.9, -22.5, 30.3	336	2
3	Right frontal lobe, 10	36.4, 47.9, 5.8	296	2
4	Right parietal lobe, 7	10, -64.7, 39.9	264	2

Note: The statistical analysis was computed on all 10 studies. The number of studies per cluster correspond to a list of studies with foci within the cluster's boundary. Foci that lie outside a cluster can still contribute to an ALE cluster, but the magnitude of the contributing effect drops as a function of distance.

displays the coordinates of the significant brain areas that were consistently activated during the memory-guided attention task.

Figure 2 shows the ALE-statistic maps for regions that were statistically significant.

6 | DISCUSSION

The objective of this analysis was to identify a common set of underlying brain areas that support memory-guided attention. The analysis yielded four significant clusters. Two of these clusters, the angular gyrus and the superior parietal lobes have been identified as part of the dorsal fronto-parietal attention network (Ptak, 2012; Ptak, Schnider, & Fellrath, 2017). This network is thought to be involved in memory-guided attention, as well as in other general long-term memory retrieval tasks (Cabeza et al., 2012; Rosen et al., 2015, 2018; Stokes et al., 2012; Summerfield et al., 2006). The remaining two clusters located in the left mid-cingulate cortex and right middle frontal gyrus may indicate

involvement of an extended fronto-parietal control network (Vincent et al., 2008; Yeo et al., 2011). This network has been shown to contribute to memory-guided attention by interfacing long-term memory representations with external incoming information during search (Leech & Sharp, 2014; Rosen et al., 2018). Together, these four areas may support the integration of memory and attentional information to guide real-time search.

As previously mentioned, the hippocampus supports relational learning and is thought to play a role in encoding context-to-target associations in memory-guided attention. While some studies have found support for the involvement of the hippocampus (Günseli & Aly, 2020; Chun & Phelps, 1999; Goldfarb et al., 2016; Manelis & Reder, 2012; Stokes et al., 2012; Summerfield et al., 2006), other studies have not (de Bourbon-Teles et al., 2014; Manginelli et al., 2013; Manns & Squire, 2001; Negash et al., 2007; Pollmann & Manginelli, 2009, 2010, 2016; Preston & Gabrieli, 2008; Rosen et al., 2015; Rosen et al., 2018; Westerberg et al., 2011). We did not find activation in the hippocampus or surrounding MTLs, suggesting that memory-guided attention can occur whether the hippocampus is recruited or not, and that the hippocampus may be additionally recruited to support explicit recognition of the effect. This finding is consistent with the conclusions drawn by Jiang, Sisk, and Toh (2019) who found no evidence in their review for the necessity of these brain regions in memory-guided attention. Further, the absence of overlap in activation in the MTLs may reflect the general lack of consensus in the field. Westerberg et al. (2011) have noted that low statistical power may also account for highly variable and inconsistent findings across studies.

6.1 | Fronto-parietal attention network

One cluster of activation was located in the right superior parietal lobe, an area that is implicated in visuospatial mnemonic processing (Zarahn, Aguirre, & D'Esposito, 2000). It is thought, also, that the superior parietal lobe is involved in the anticipatory mediation of attentional resources (Caplan, Luks, Simpson, Glaholt, & McIntosh, 2006). Another cluster of activation corresponded to the right angular gyrus within the inferior parietal lobe (BA 39). Research suggests that Brodmann area 39 is particularly important for memory and spatial attention. A number of studies have found that the inferior parietal lobe is involved in spatial processing (Petrides & Pandya, 2002), in visuospatial attention (Corbetta & Shulman, 2002), and in episodic memory (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). Specifically, the angular gyrus has been implicated in spatial attention and orienting (Chambers, Payne, Stokes, & Mattingley, 2004).

One might expect that, according to the AtoM model of reflective attention, analysis of both implicit and explicit memory-guided attention tasks together would not reveal significant overlap within parietal areas because each would activate different sub-regions of the parietal cortex. We found, however, significant activation in both the inferior parietal cortex and superior parietal cortex. This activation could be due to the fact that the inferior parietal cortex may be involved in nonepisodic implicit memory tasks, as well as in episodic memory tasks. Three out of four studies that reported explicit recognition of the displays also found evidence of activation either in the intraparietal sulcus alone (Stokes et al., 2012) or in both the inferior parietal lobe/intraparietal sulcus and the precuneus (Rosen et al., 2015; Rosen et al., 2018). The fourth study (Summerfield et al., 2006) did not report parietal activation that was specific to memory-guided attention. It is possible, therefore, that the activation that we observed in the inferior parietal cortex reflects automatic retrieval of memory templates to guide attention. This automatic component may be present during both implicit and explicit memory-guided attention tasks. As previously mentioned, two fMRI studies, in which explicit knowledge of the displays was absent, have shown activation in both superior and inferior parietal areas (Giesbrecht et al., 2013; Manginelli et al., 2013). The findings, thus, lend support for the notion that the inferior parietal cortex may be involved in both nonepisodic implicit and episodic memory-guided attention.

Together, activation in areas BA 7 and BA 39 may reflect involvement of an extended fronto-parietal attention network (Ptak, 2012; Ptak et al., 2017). It has been suggested that the fronto-parietal attention network supports the coordination of planned sequences (Duncan, 2013) and spatial attention (Mesulam, 1999; Nobre, 2001; Summerfield et al., 2006; Yantis et al., 2002) during memory-guided orienting. Our results, therefore, are consistent with previous studies that have shown that the fronto-parietal attention network is active during memory-guided attention (Goldfarb et al., 2016; Pollmann & Manginelli, 2009; Stokes et al., 2012; Summerfield et al., 2006; Zimmermann et al., 2019).

6.2 | The fronto-parietal control network in memory-guided attention

Two clusters corresponded to activation in the right middle frontal gyrus (BA 10) and left mid-cingulate cortex (BA 23). Activation of these two areas may indicate support from the fronto-parietal control network in interfacing memory and

attentional components during memory-guided attention (Leech & Sharp, 2014; Spreng, 2012; Vincent et al., 2008; Yeo et al., 2011). Importantly, the fronto-parietal control network is situated in-between the fronto-parietal attention and hippocampal-cortical memory networks, making it an important system for integrating information from these networks (Vincent et al., 2008). The mid-cingulate cortex, a structure in the network, has been shown to play a key role in regulating the focus of attention, and the posterior cingulate cortex more generally appears to be involved during the anticipation of an external event (Hayden, Nair, McCoy, & Platt, 2008; Hayden, Smith, & Platt, 2009; Leech & Sharp, 2014; Pearson, Hayden, Raghavachari, & Platt, 2009). Anticipation of an environmental change occurs when the long-term associations that are formed create expectation for perception.

The mid-cingulate cortex is, also, connected with the hippocampus and is considered part of the extended hippocampal system (Bubb, Metzler-Baddeley, & Aggleton, 2018). Our findings, therefore, complement current models that implicate sequential activation of the hippocampus and fronto-parietal networks (e.g., Bridge et al., 2017; Moscovitch, 2008; Moscovitch et al., 2016). That the fronto-parietal control network is situated between and partially overlapping with fronto-parietal attention and hippocampal-cortical memory networks (Vincent et al., 2008) suggests that it is a prime network for integrating information from both attentional and memory components to support memory-guided attention.

6.3 | Memory-guided attention: A distinct phenomenon?

What roles do the fronto-parietal attention and fronto-parietal control networks play in memory-guided attention? To address this question, we must examine first what distinguishes memory-guided attention from other forms of memory and/or attention, such as attention-to-memory and associative memory. Memory-guided attention requires the formation of an association *in order to generate expectation for perception*. In this case, attention is allocated to a specific expected stimulus feature (associate) in order to process *external* information. In attention-to-memory tasks, associations are learned and then used to guide attention toward learned *internal* representations. In associative memory tasks, an association is learned, but not used for perception. Memory-guided attention and attention-to-memory can, therefore, be distinguished from associative memory if one considers the particular function that the association serves.¹ Memory-guided attention and attention-to-memory may be distinguished further, depending on whether the associations are used for perception (external) or for cognition (internal).

Activation of the fronto-parietal attention network does not appear to be unique to memory-guided attention. Although the temporal pattern of activity differs for each memory task, the fronto-parietal attention network has been shown to play a role in all three types of memory tasks (Cabeza et al., 2008; Cabeza et al., 2012; Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010; Goldfarb et al., 2016; Law et al., 2005; Myers, Stokes, & Nobre, 2017; Stokes et al., 2012; Zimmermann et al., 2019). Therefore, the fronto-parietal attention network may not uniquely contribute to memory-guided attention (Rosen et al., 2015, 2018; Summerfield et al., 2006; Stokes et al., 2012), but may be implicated in other forms of attention tasks, as well.

Activation of the fronto-parietal control network may be especially important for controlling attentional states. Rosen et al. (2015, 2018) have found that the posterior portion of this network is uniquely involved in memory-guided attention when it is compared to stimulus-guided attention. The function of this control network in memory-guided attention may be that it facilitates the integration of memory and attention mechanisms. The mid-cingulate cortex is especially important for orchestrating this process. This network may also be active during internally-guided attention (Kam et al., 2019). Therefore, involvement of the fronto-parietal attention and control networks may help to dissociate associative memory tasks from memory-guided attention tasks (external) and attention-to-memory tasks (internal), and may not necessarily help to distinguish between externally-guided and internally-guided tasks (see discussion in Cabeza et al., 2008, 2012).

6.4 | MTL activity

What about the role of the MTLs? As previously mentioned, various models involved in recollection (Moscovitch et al., 2016), in memory-guided exploration (Bridge et al., 2017), and in memory-guided attention (Goldfarb et al., 2016; Stokes et al., 2012) implicate the hippocampus as well as fronto-parietal networks.

Earlier in the article, we outlined key arguments in the debate for and against hippocampal activity during memory-guided attention. The results of the meta-analysis did not reveal activation in the MTLs. This is not surprising as only one study included in the meta-analysis found hippocampal activation (Summerfield et al., 2006) and two other

articles found surrounding MTL activation (Greene et al., 2007; Preston & Gabrieli, 2008). One article found hippocampal activation specific to memory-guided attention, using a region of interest analysis (Stokes et al., 2012), but these foci were not included in the analysis, as region of interest coordinates may bias ALE meta-analyses (Eickhoff et al., 2009; Turkeltaub et al., 2012). Below, we outline a few possibilities as to why we did not find hippocampal activity.

The hippocampus may be involved in encoding the associations or retrieving them at the memory stage alone, given that the hippocampus has been shown to be a critical structure in relational learning (Law et al., 2005; Ryan, Althoff, Whitlow, & Cohen, 2000). The hippocampus, therefore, may not be involved in the subsequent stage in which the associations are utilized for perception. Consistent with this hypothesis, Rosen et al. (2015) observed hippocampal activation during stimulus-guided attention, but memory-guided attention. Stimulus-guided attention does not have a long-term memory component and, therefore, might involve the encoding of new information more heavily than the memory-guided attention condition in which associations are well-learned. Further, during encoding, the hippocampus has been shown to enhance attentional performance to external information (Kukulja, Thiel, & Fink, 2009). In the current analysis, two articles found greater hippocampal activation for new configurations than for old ones (Giesbrecht et al., 2013; Greene et al., 2007; Kasper, 2013). This contrast isolates *learning* or *encoding* of the target-context association from retrieval. A number of studies have found hippocampal activity for this contrast, but not for a contrast that isolates the effect of memory-guided attention. Furthermore, one article included in the analysis reported hippocampal activity that was correlated with explicit recognition of the repeated displays, but this effect was orthogonal to the memory-guided attention effect (Preston & Gabrieli, 2008). Together, these studies suggest that while the hippocampus may be important during the formation of associations or during explicit recognition, its contribution to the stage in which the associations are used for guiding attention remains unclear.

Presentation of cue and target either synchronously or asynchronously may, also, affect whether or not one observes hippocampal activity. Four studies (Rosen et al., 2015; Rosen et al., 2018; Stokes et al., 2012; Summerfield et al., 2006) presented the display (cue) prior to the target, but only Stokes et al. (2012) and Summerfield et al. (2006) were able to analyze cue and target period separately because they used an event-related design. Stokes et al. (2012) and Summerfield et al. (2006) found hippocampal activity attributable to the cue period, while Rosen et al. (2015, 2018) did not find any hippocampal activity. It is possible that by using an experimental paradigm in which the cue and the target are presented asynchronously and analyzed separately, the memory and attentional components of memory-guided attention may be teased apart. The hippocampus may be more important during retrieval of the paired associate (cue) than during attentional deployment. If the cue and the target are presented synchronously, memory and attentional components may compete with one another. Individual differences in strategy may, therefore, wash out any hippocampal effects. For example, some participants may rely more heavily on the attentional component and less on the cue to guide search.

Univariate contrasts may also be less sensitive than multi-voxel pattern analyses in capturing activity in the MTLs (Carr, Rissman, & Wagner, 2010). According to the representational-hierarchical account, univariate shortcomings may be particularly pronounced when simple stimuli (e.g., paradigms based off of Chun & Jiang, 1998) are used, as these low-dimensional memories engage neocortex and complex stimuli, such as scenes, rely on the hippocampus (Cowell, Barense, & Sadil, 2019). In the future, it would be worthwhile to examine the neural substrates of memory-guided attention at cue and at target periods, using a multivariate approach.

Finally, the lack of significant activity in the MTLs may be due to the fact that these structures are recruited additionally, depending on the task. Memory-guided attention may consistently recruit a core set of brain regions that correspond to the fronto-parietal networks and, also, recruit additional areas depending on the type of mental processing required. If this is the case, task variability may lead to nonsignificant activation in the MTLs. This possibility is consistent with Westerberg et al. (2011) who identified a common set of areas outside the MTL that was associated with implicit and explicit memory-guided attention, as well as, additional recruitment of the parahippocampus during explicit memory-guided attention tasks. Memory-guided attention, therefore, may be a distributed and nonisolatable phenomenon, and may be better characterized, for example, by a general distributed system, such as the multiple-demand system. This system contains three sub-networks in addition to other areas that are recruited, depending on the task (Camilleri et al., 2018; Müller, Langner, Cieslik, Rottschy, & Eickhoff, 2015). This flexibility allows for the multiple demand system to support a large number of complex tasks (Cabeza & Nyberg, 2000; Duncan, 2010; Müller et al., 2015), such as vigilance (Langner & Eickhoff, 2013), working memory (Rottschy et al., 2012), and inhibitory control (Cieslik, Mueller, Eickhoff, Langner, & Eickhoff, 2015). Memory-guided attention may not be a single process but may involve multiple aspects of mental functioning that cannot be reduced to a single brain network. Instead, it may recruit a core set of brain regions involved in executive control, as well as additional areas, depending on the task (Camilleri et al., 2018). This interpretation suggests that memory-guided attention may be captured more accurately

using large-scale brain networks (Bressler & Menon, 2010; Corbetta & Shulman, 2002). The MTL, and the other areas noted, may form Processing Specific Assemblies (Cabeza & Moscovitch, 2013), joining other regions that are differentially/ additionally recruited, depending on the instructions given to participants (Westerberg et al., 2011), type of stimuli used (Cowell et al., 2019), or quality (explicit/implicit) of recognition memory (Preston & Gabrieli, 2008).

6.5 | Limitations

The current meta-analysis sought to identify core brain regions that support memory-guided attention by comparing different tasks and approaches in order to examine effects that are consistent across methods and strategies (Radua & Mataix-Cols, 2012). The limited number of studies included in the analysis was due both to the size of the field and to the systematic selection criteria that aimed to balance homogeneity and quality of the studies with power. Additionally, the variability in sample size across studies may have influenced the results. Impact from this variability, however, may have been reduced, as the analysis weighted each studies' input by its sample size.

It must be noted, therefore, that the results should be interpreted with caution. When the number of studies included in a meta-analysis is low, there is a greater chance that results are driven by only a few experiments (Eickhoff et al., 2016). In the current article, most studies used variants of the Chun and Jiang (1998) classic paradigm. This homogeneity across tasks may have helped to mitigate potential statistical issues. As well, we used conservative thresholds and a smaller, more conservative, mask size in order to minimize susceptibility to false positives. We acknowledge that it is possible that activation patterns may change as additional studies are published and can be included in the analysis.

The analysis was limited to one modality and imaging technique. However, it is worth mentioning studies that examine memory-guided attention, using other techniques, such as electroencephalography (EEG), intracranial EEG, and magnetoencephalography (e.g., Chaumon, Schwartz, & Tallon-Baudry, 2009; Fischer, Moscovitch, & Alain, 2020; Johnson, Woodman, Braun, & Luck, 2007; Olson, Chun, & Allison, 2001; Patai, Doallo, & Nobre, 2012; Schankin, Hagemann, & Schubö, 2011; Schankin & Schubö, 2009, 2010; Summerfield, Rao, Garside, & Nobre, 2011; Zimmermann et al., 2020). A number of these studies have used the N2pc, a component of the ERP that is a marker of attentional focus, to reveal how memory-guided attention can facilitate perception by modulating the allocation of attention and by regulating the flow of information through sensory cortices. Additionally, during the procedural learning phase, a fronto-occipital network, synchronized with low frequency gamma oscillations, has been identified (Chaumon et al., 2009). Furthermore, Fischer et al. (2020) observed significant modulations over the fronto-central scalp region during the cue period in an auditory memory-guided attention task. These modulations may be the result of reflections from a source located in auditory cortices. Zimmermann et al. (2020) observed activity in the primary auditory cortices, parietal cortex, and MTL during the cue period. Together, activation in the auditory cortices may be consistent with the findings of Paller, Kutas, and McIsaac (1998) who found activation in primary visual cortex, indicative of the formation of visual target-to-context associations. Activation in the MTLs during the cue period may also suggest that the hippocampus is involved in the retrieval of the paired associate (cue). Together, these findings are consistent with fMRI studies investigating memory-guided attention, and they offer important information regarding the processes that contribute to it.

7 | CONCLUSION

This review and meta-analysis of fMRI studies aimed to identify a common set of brain areas underlying memory-guided attention. The findings suggest that frontal and parietal areas that have been previously identified as part of the fronto-parietal attention and control networks contribute to memory-guided attention during a visual search task. It is also possible that this activation reflects support from a more general system, such as the multiple-demand system that is implicated in general executive control (Cabeza & Nyberg, 2000; Camilleri et al., 2018; Duncan, 2010) and that memory-guided attention is a distributed phenomenon.

Memory-guided attention is a growing field. This analysis would benefit from a greater number of studies in order to help clarify the role of medial temporal structures in memory-guided attention. We have also suggested several methodological considerations that may help to advance our understanding of the neural correlates that support this phenomenon. We have proposed that memory-guided attention is a distinct phenomenon that can be defined as the biasing of attention by a familiar stimulus that contains predictive information about an associate in order to influence a perceptual decision. This effect involves the integration of both memory and attentional components. Further

elucidating the link between memory and attention will help us better understand memory as a dynamic system (Moscovitch et al., 2016; Romero & Moscovitch, 2015) that benefits from, and contributes to, attentional processes.

ACKNOWLEDGMENT

This research was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grants to Claude Alain [RGPIN-2016-05523] and to Morris Moscovitch [A8347], and an NSERC CREATE Scholarship to Manda Fischer.

CONFLICT OF INTEREST

No conflict of interest to disclose.

AUTHOR CONTRIBUTIONS

Manda Fischer: Conceptualization; data curation; formal analysis; methodology; software; visualization; writing-original draft; writing-review and editing. **Morris Moscovitch:** Conceptualization; funding acquisition; methodology; supervision; writing-review and editing. **Claude Alain:** Conceptualization; data curation; formal analysis; funding acquisition; methodology; software; supervision; writing-review and editing.

ORCID

Manda Fischer  <https://orcid.org/0000-0001-8353-9818>

ENDNOTE

¹ It is possible that the difference between memory-guided attention/attention-to-memory and associative memory is task-dependent (e.g., memory-guided attention or attention-to-memory if the task tests perceptual abilities, but associative memory if the task tests memory for an item).

RELATED WIREs ARTICLES

[Visual search](#)

[Attention and consciousness](#)

FURTHER READING

Wang, J. X., Cohen, N. J., & Voss, J. L. (2015). Covert rapid action-memory simulation (CRAMS): A hypothesis of hippocampal-prefrontal interactions for adaptive behavior. *Neurobiology of Learning and Memory*, *117*, 22–33. <https://doi.org/10.1016/j.nlm.2014.04.003>

REFERENCES

- Aly, M., & Turk-Browne, N. B. (2016a). Attention promotes episodic encoding by stabilizing hippocampal representations. *Proceedings of the National Academy of Sciences*, *113*(4), E420–E429. <https://doi.org/10.1073/pnas.1518931113>
- Aly, M., & Turk-Browne, N. B. (2016b). Attention stabilizes representations in the human hippocampus. *Cerebral Cortex*, *26*(2), 783–796. <https://doi.org/10.1093/cercor/bhv041>
- Aly, M., & Turk-Browne, N. B. (2017). How hippocampal memory shapes, and is shaped by, attention. In D. E. Hannula & M. C. Duff (Eds.), *The hippocampus from cells to systems* (pp. 369–403). Springer International Publishing AG: Switzerland.
- Best, P., Taylor, B., Manktelow, R., & McQuilkin, J. (2014). Systematically retrieving research in the digital age: Case study on the topic of social networking sites and young people's mental health. *Journal of Information Science*, *40*(3), 346–356. <https://doi.org/10.1177/0165551514521936>
- Bressler, S. L., & Menon, V. (2010). Large-scale brain networks in cognition: Emerging methods and principles. *Trends in Cognitive Science*, *14*(6), 277–290. <https://doi.org/39991125210.1016/j.tics.2010.04.004>
- Bridge, D. J., Cohen, N. J., & Voss, J. L. (2017). Distinct hippocampal versus frontoparietal network contributions to retrieval and memory-guided exploration. *Journal of Cognitive Neuroscience*, *29*(8), 1324–1338. https://doi.org/10.1162/jocn_a_01143
- Bubb, E. J., Metzler-Baddeley, C., & Aggleton, J. P. (2018). The cingulum bundle: Anatomy, function, and dysfunction. *Neuroscience and Biobehavioral Reviews*, *92*, 104–127. <https://doi.org/10.1016/j.neubiorev.2018.05.008>
- Cabeza, R. (2008). Role of parietal regions in episodic memory retrieval: The dual attentional processes hypothesis. *Neuropsychologia*, *46*, 1813–1827.
- Cabeza, R., Ciaramelli, E., & Moscovitch, M. (2012). Cognitive contributions of the ventral parietal cortex: An integrative theoretical account. *Trends in Cognitive Sciences*, *16*(6), 338–352. <https://doi.org/10.1016/j.tics.2012.04.008>
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience*, *9*(8), 613–625. <http://doi.org/10.1038/nrn2459>

- Cabeza, R., & Moscovitch, M. (2013). Memory systems, processing modes, and components: Functional neuroimaging evidence. *Perspectives on Psychological Science*, 8(1), 49–55. <https://doi.org/10.1177/1745691612469033>
- Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, 12(1), 1–47. <https://doi.org/10.1162/08989290051137585>
- Camilleri, J. A., Müller, V. I., Fox, P., Laird, A. R., Hoffstaedter, F., Kalenscher, T., & Eickhoff, S. B. (2018). Definition and characterization of an extended multiple-demand network. *NeuroImage*, 165, 138–147. <https://doi.org/10.1016/j.neuroimage.2017.10.020>
- Campbell, A., Taylor, B., Bates, J., & O'Connor-Bones, U. (2017). Developing and applying a protocol for a systematic review in the social sciences. *New Review of Academic Librarianship*, 24(1), 1–22. <https://doi.org/10.1080/13614533.2017.1281827>
- Caplan, J. B., Luks, T. L., Simpson, G. V., Glaholt, M., & McIntosh, A. R. (2006). Parallel networks operating across attentional deployment and motion processing: A multi-seed partial least squares fMRI study. *Neuroimage*, 29(4), 1192–1202. <https://doi.org/10.1016/j.neuroimage.2005.09.010>
- Carr, V. A., Rissman, J., & Wagner, A. D. (2010). Imaging the human medial temporal lobe with high-resolution fMRI. *Neuron*, 65(3), 298–308. <https://doi.org/10.1016/j.neuron.2009.12.022>
- Chambers, C. D., Payne, J. M., Stokes, M. G., & Mattingley, J. B. (2004). Fast and slow parietal pathways mediate spatial attention. *Nature Neuroscience*, 7, 217–218. <http://doi.org/10.1038/nn1203>
- Chaumon, M., Schwartz, D., & Tallon-Baudry, C. (2009). Unconscious learning versus visual perception: Dissociable roles for gamma oscillations revealed in MEG. *Journal of Cognitive Neuroscience*, 21(12), 2287–2299. <https://doi.org/10.1162/jocn.2008.21155>
- Chiu, Y. C., & Yantis, S. (2009). A domain-independent source of cognitive control for task sets: Shifting spatial attention and switching categorization rules. *Journal of Neuroscience*, 29, 3930–3938. <https://doi.org/10.1523/JNEUROSCI.5737-08.2009>
- Chun, M. M., & Jiang, Y. (1998). Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive Psychology*, 36, 28–71. <https://doi.org/10.1006/cogp.1998.0681>
- Chun, M. M., & Phelps, E. A. (1999). Memory deficits for implicit contextual information in amnesic participants with hippocampal damage. *Nature Neuroscience*, 2(9), 844–847. <http://doi.org/10.1038/12222>
- Ciaramelli, E., Grady, C., Levine, B., Ween, J., & Moscovitch, M. (2010). Top-down and bottom-up attention to memory are dissociated in posterior parietal cortex: Neuroimaging and neuropsychological evidence. *Journal of Neuroscience*, 30(14), 4943–4956. <https://doi.org/10.1523/JNEUROSCI.1209-09.2010>
- Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, 46(7), 1828–1851. <http://doi.org/10.1016/j.neuropsychologia.2008.03.022>
- Cieslik, E. C., Mueller, V. I., Eickhoff, C. R., Langner, R., & Eickhoff, S. B. (2015). Three key regions for supervisory attentional control: Evidence from neuroimaging meta-analyses. *Neuroscience & Biobehavioral Reviews*, 48, 22–34. <https://doi.org/10.1016/j.neubiorev.2014.11.003>
- Cole, M. W., & Schneider, W. (2007). The cognitive control network: Integrated cortical regions with dissociable functions. *NeuroImage*, 37(1), 343–360. <https://doi.org/10.1016/j.neuroimage.2007.03.071>
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, 3(3), 201–215. <http://doi.org/10.1038/nrn755>
- Córdoba, N. I., Turk-Browne, N. B., & Aly, M. (2019). Focusing on what matters: Modulation of the human hippocampus by relational attention. *Hippocampus*, 29(11), 1025–1037. <https://doi.org/10.1002/hipo.23082>
- Cowell, R. A., Barense, M. D., & Sadiq, P. S. (2019). A roadmap for understanding memory: Decomposing cognitive processes into operations and representations. *eNeuro*, 6(4), 1–19. <https://doi.org/10.1523/ENEURO.0122-19.2019>
- de Bourbon-Teles, J., Bentley, P., Koshino, S., Shah, K., Dutta, A., Malhotra, P., ... Soto, D. (2014). Thalamic control of human attention driven by memory and learning. *Current Biology*, 24(9), 993–999. <https://doi.org/10.1016/j.cub.2014.03.024>
- Decker, A. L., & Duncan, K. (2020). Acetylcholine and the complex interdependence of memory and attention. *Current Opinion in Behavioral Sciences*, 32, 21–28. <https://doi.org/10.1016/j.cobeha.2020.01.013>
- Dixon, M. L., De La Vega, A., Mills, C., Andrews-Hanna, J., Spreng, R. N., Cole, M. W., & Christoff, K. (2018). Heterogeneity with the frontoparietal network. *Proceedings of the National Academy of Sciences*, 115(7), E1598–E1607. <https://doi.org/10.1073/pnas.1715766115>
- Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: Mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, 14(4), 172–179. <https://doi.org/10.1016/j.tics.2010.01.004>
- Duncan, J. (2013). The structure of cognition: Attentional episodes in mind and brain. *Neuron*, 80(1), 35–50. <https://doi.org/10.1016/j.neuron.2013.09.015>
- Eichenbaum, H. (2000). A cortical-hippocampal system for declarative memory. *Nature Reviews Neuroscience*, 1(1), 41–50. <http://doi.org/10.1038/35036213>
- Eickhoff, S. B., Bzdok, D., Laird, A. R., Kurth, F., & Fox, P. T. (2012). Activation likelihood estimation meta-analysis revisited. *NeuroImage*, 59(3), 2349–2361. <http://doi.org/10.1016/j.neuroimage.2011.09.017>
- Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging data: A random-effects approach based on empirical estimates of spatial uncertainty. *Human Brain Mapping*, 30, 2907–2926. <https://doi.org/10.1002/hbm.20718>
- Eickhoff, S. B., Nichols, T. E., Laird, A. R., Hoffstaedter, F., Amunts, K., Fox, P. T., ... Eickhoff, C. R. (2016). Behavior, sensitivity, and power of activation likelihood estimation characterized by massive empirical simulation. *NeuroImage*, 137(15), 70–85. <https://doi.org/10.1016/j.neuroimage.2016.04.072>
- Fischer, M., Moscovitch, M., & Alain, C. (2020). Incidental auditory learning and memory-guided attention: Examining the role of attention at the behavioural and neural level using EEG. *Neuropsychologia*, 147, 187506. <https://doi.org/10.1016/j.neuropsychologia.2020.107586>

- Gazzaley, A., & Nobre, A. C. (2012). Top-down modulation: Bridging selective attention and working memory. *Trends in Cognitive Sciences*, 16(2), 129–135. <https://doi.org/10.1016/j.tics.2011.11.014>
- Giesbrecht, B., Sy, J. L., & Guerin, S. A. (2013). Both memory and attention systems contribute to visual search for targets cued by implicitly learned context. *Vision Research*, 85, 80–89. <https://doi.org/10.1016/j.visres.2012.10.006>
- Giesbrecht, B., Woldorff, M. G., Song, A. W., & Mangun, G. R. (2003). Neural mechanisms of top-down control during spatial and feature attention. *NeuroImage*, 19, 496–512. [https://doi.org/10.1016/s1053-8119\(03\)00162-9](https://doi.org/10.1016/s1053-8119(03)00162-9)
- Goh, J. O., Siong, S. C., Park, D., Gutchess, A., Hebrank, A., & Chee, M. W. (2004). Cortical areas involved in object, background, and object-background processing revealed with functional magnetic resonance adaptation. *Journal of Neuroscience*, 24(45), 10223–10228. <https://doi.org/10.1523/JNEUROSCI.3373-04.2004>
- Goldfarb, E. V., Chun, M. M., & Phelps, E. A. (2016). Memory-guided attention: Independent contributions of the hippocampus and striatum. *Neuron*, 89(2), 317–324. <https://doi.org/10.1016/j.neuron.2015.12.014>
- Greene, A. J., Gross, W. L., Elsinger, C. L., & Rao, S. M. (2007). Hippocampal differentiation without recognition: An fMRI analysis of the contextual cueing task. *Learning and Memory*, 14(8), 548–553. <http://doi.org/10.1101/lm.609807>
- Günseli, E., & Aly, M. (2020). Preparation for upcoming attentional states in the hippocampus and medial prefrontal cortex. *eLife*, 9, e53191. <https://doi.org/10.7554/eLife53191>
- Hannula, D. E., & Ranganath, C. (2009). The eyes have it: Hippocampal activity predicts expression of memory in eye movements. *Neuron*, 63(5), 592–599. <https://doi.org/10.1016/j.neuron.2009.08.025>
- Hasselmo, M. E., Bodelón, C., & Wyble, B. P. (2006). A proposed function for hippocampal theta rhythm: Separate phases of encoding and retrieval enhance reversal of prior learning. *Neural Computation*, 14(4), 793–817. <https://doi.org/10.1162/089976602317318965>
- Hayden, B. Y., Nair, A. C., McCoy, A. N., & Platt, M. L. (2008). Posterior cingulate cortex mediates outcome-contingent allocation of behavior. *Neuron*, 60, 19–25. <https://doi.org/10.1016/j.neuron.2008.09.012>
- Hayden, B. Y., Smith, D. V., & Platt, M. L. (2009). Electrophysiological correlates of default-mode processing in macaque posterior cingulate cortex. *Proceedings of the National Academy of Science USA*, 106, 5948–5953. <https://doi.org/10.1073/pnas.0812035106>
- Henke, K. (2010). A model for memory systems based on processing modes rather than consciousness. *Nature Review Neuroscience*, 11(7), 523–532. <http://doi.org/10.1038/nrn2850>
- Hirsh, R. (1974). The hippocampus and contextual retrieval of information from memory: A theory. *Behavioral Biology*, 12(4), 421–444. [https://doi.org/10.1016/S0091-6773\(74\)92231-7](https://doi.org/10.1016/S0091-6773(74)92231-7)
- Hutchinson, J. B., Uncapher, M. R., Weiner, K. S., Bressler, D. W., Silver, M. A., Preston, A. R., & Wagner, A. D. (2014). Functional heterogeneity in posterior parietal cortex across attention and episodic memory retrieval. *Cerebral Cortex*, 24, 49–66. <https://doi.org/10.1093/cercor/bhs278>
- Jiang, Y. V., Sisk, C. A., & Toh, Y. N. (2019). Implicit guidance of attention in contextual cueing: Neuropsychological and developmental evidence. *Neuroscience & Biobehavioral Reviews*, 105, 115–125. <https://doi.org/10.1016/j.neubiorev.2019.07.002>
- Johnson, J. S., Woodman, G. F., Braun, E., & Luck, S. J. (2007). Implicit memory influences the allocation of attention in visual cortex. *Psychonomic Bulletin and Review*, 14(5), 834–839.
- Kam, J. W. Y., Lin, J. J., Solbakk, A., Endestad, T., Larsson, P. G., & Knight, R. T. (2019). Default network and frontoparietal control network theta connectivity supports internal attention. *Nature Human Behaviour*, 3, 1263–1270. <https://doi.org/10.1038/s41562-019-0717-0>
- Kasper, R.W. (2013). *Knowing where to look: The role of memory, attention, and response processes when implicitly learned context facilitates visual search*. (Unpublished doctoral dissertation). University of California, Santa Barbara.
- Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23, 315–341. <https://doi.org/10.1146/annurev.neuro.23.1.315>
- Konkel, A., & Cohen, N. J. (2009). Relational memory and the hippocampus: Representations and methods. *Frontiers in Neuroscience*, 3, 166–174. <https://doi.org/10.3389/neuro.01.023.2009>
- Kukolja, J., Thiel, C. M., & Fink, G. R. (2009). Cholinergic stimulation enhances neural activity associated with encoding but reduces neural activity associated with retrieval in humans. *Journal of Neuroscience*, 29(25), 8119–8128. <https://doi.org/10.1523/JNEUROSCI.0203-09.2009>
- Langner, R., & Eickhoff, S. (2013). Sustaining attention to simple tasks: A meta-analytic review of the neural mechanisms of vigilant attention. *Psychological Bulletin*, 139(4), 870–900. <http://doi.org/10.1037/a0030694>
- Law, J. R., Flanery, M. A., Wirth, S., Yanike, M., Smith, A. C., Frank, L. M., ... Stark, C. E. (2005). Functional magnetic resonance imaging activity during the gradual acquisition and expression of paired-associate memory. *Journal of Neuroscience*, 25, 5720–5729. <https://doi.org/10.1523/JNEUROSCI.4935-04.2005>
- Leech, R., & Sharp, D. J. (2014). The role of the posterior cingulate cortex in cognition and disease. *Brain*, 137, 12–32. <https://doi.org/10.1093/brain/awt162>
- Manelis, A., & Reder, L. M. (2012). Procedural learning and associative memory mechanisms contribute to contextual cueing: Evidence from fMRI and eye-tracking. *Learning and Memory*, 19, 527–534. <http://doi.org/10.1101/lm.025973.112>
- Manginelli, A. A., Baumgartner, F. B., & Pollmann, S. (2013). Dorsal and ventral working memory-related brain areas support distinct processes in contextual cueing. *NeuroImage*, 67, 363–374. <https://doi.org/10.1016/j.neuroimage.2012.11.025>
- Manns, J. R., & Squire, L. R. (2001). Perceptual learning, awareness and the hippocampus. *Hippocampus*, 11(6), 776–782. <https://doi.org/10.1002/hipo.1093>

- Mesulam, M. M. (1999). Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 354, 1325–1346. <https://doi.org/10.1098/rstb.1999.0482>
- Moscovitch, M. (2008). The hippocampus as a stupid, domain-specific module: Implications for theories of recent and remote memory, and of imagination. *Canadian Journal of Experimental Psychology*, 62(1), 62–79. <http://doi.org/10.1037/1196-1961.62.1.62>
- Moscovitch, M., Cabeza, R., Winocur, G., & Nadel, L. (2016). Episodic memory and beyond: The hippocampus and neocortex in transformation. *Annual Review of Psychology*, 67, 105–134. <http://doi.org/10.1146/annurev-psych-113011-143733>
- Müller, V. I., Langner, R., Cieslik, E. C., Rottschy, C., & Eickhoff, S. B. (2015). Interindividual differences in cognitive flexibility: Influence of gray matter volume, functional connectivity and trait impulsivity. *Brain Structure and Function*, 220(4), 2401–2414. <http://doi.org/10.1007/s00429-014-0797-6>
- Myers, N. E., Stokes, M. G., & Nobre, A. C. (2017). Prioritizing information during working memory: Beyond sustained internal attention. *Trends in Cognitive Science*, 21(6), 449–461. <https://doi.org/10.1016/j.tics.2017.03.010>
- Negash, S., Petersen, L. E., Geda, Y. E., Knopman, D. S., Boeve, B. E., Smith, G. E., ... Petersen, R. C. (2007). Effects of ApoE genotype and mild cognitive impairment on implicit learning. *Neurobiology of Aging*, 28(6), 885–893. <http://doi.org/10.1016/j.neurobiolaging.2006.04.004>
- Nelson, S. M., Cohen, A. L., Power, J. D., Wig, G. S., Miezin, F. M., Wheeler, M. E., ... Petersen, S. E. (2010). A parcellation scheme for human left lateral parietal cortex. *Neuron*, 67, 156–170. <https://doi.org/10.1016/j.neuron.2010.05.025>
- Nobre, A. C. (2001). The attentive homunculus: Now you see it, now you don't. *Neuroscience and Biobehavioral Reviews*, 25(6), 477–496. [https://doi.org/10.1016/S0149-7634\(01\)00028-8](https://doi.org/10.1016/S0149-7634(01)00028-8)
- Nobre, A. C., Coull, J. T., & Frith, C. D. (2004). Orienting attention to locations in perceptual versus mental representations. *Journal of Cognitive Neuroscience*, 16(3), 363–373. <http://doi.org/10.1162/089892904322926700>
- Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review*, 110(4), 611–646. <http://doi.org/10.1037/0033-295x.110.4.611>
- Olsen, R. K., Moses, S. N., Riggs, L., & Ryan, J. D. (2012). The hippocampus supports multiple cognitive processes through relational binding and comparison. *Frontiers in Human Neuroscience*, 6, 146. <https://doi.org/10.3389/fnhum.2012.00146>
- Olson, I. R., Chun, M. M., & Allison, T. (2001). Contextual guidance of attention: Human intracranial event-related potential evidence for feedback modulation in anatomically early temporally late stages of visual processing. *Brain*, 124(7), 1417–1425. <https://doi.org/10.1093/brain/124.7.1417>
- Paller, K. A., Kutas, M., & McIsaac, H. K. (1998). An electrophysiological measure of priming of visual word-form. *Consciousness and Cognition*, 7, 54–66. <https://doi.org/10.1006/ccog.1998.0329>
- Park, H., Quinlan, J., Thornton, E., & Reder, L. M. (2004). The effect of midazolam on visual search: Implications for understanding amnesia. *Proceedings of the National Academy of Sciences of the United States of America*, 101(51), 17879–17883. <http://doi.org/10.1073/pnas.0408075101>
- Patai, E. Z., Doallo, S., & Nobre, A. C. (2012). Long-term memories bias sensitivity and target selection in complex scenes. *Journal of Cognitive Neuroscience*, 24(12), 2281–2291. http://doi.org/10.1162/jocn_a_00294
- Pearson, J. M., Hayden, B. Y., Raghavachari, S., & Platt, M. L. (2009). Neurons in posterior cingulate cortex signal exploratory decisions in a dynamic multi-option choice task. *Current Biology*, 19(18), 1532–1537. <https://doi.org/10.1016/j.cub.2009.07.048>
- Petrides, M., & Pandya, D. N. (2002). Association pathways of the prefrontal cortex and functional observations. In D. T. Stuss & R. T. Knight (Eds.), *Principles of frontal lobe function* (pp. 31–50). New York, NY: Oxford University Press. <http://doi.org/10.1093/acprof:oso/9780195134971.001.0001>
- Pollmann, S., & Manginelli, A. A. (2009). Anterior prefrontal involvement in implicit contextual change detection. *Frontiers in Human Neuroscience*, 3(28), 1–13. <http://doi.org/10.3389/neuro.09.028.200>
- Pollmann, S., & Manginelli, A. A. (2010). Repeated contextual search cues lead to reduced BOLD-onset times in early visual and left inferior frontal cortex. *The Open Neuroimaging Journal*, 4, 9–15. <https://doi.org/10.2174/1874440001004010009>
- Pollmann, S., & Manginelli, A. A. (2016). Neural structures involved in visual search guidance by reward-enhanced contextual cueing of the target location. *NeuroImage*, 124, 887–897. <https://doi.org/10.1016/j.neuroimage.2015.09.040>
- Preston, A. R., & Gabrieli, J. D. E. (2008). Dissociation between explicit memory and configural memory in the human medial temporal lobe. *Cerebral Cortex*, 18(9), 2192–2207. <https://doi.org/10.1093/cercor/bhm245>
- Ptak, R. (2012). The frontoparietal attention network of the human brain: Action, saliency, and a priority map of the environment. *The Neuroscientist*, 18(5), 502–515. <http://doi.org/10.1177/1073858411409051>
- Ptak, R., Schnider, A., & Fellrath, J. (2017). The dorsal frontoparietal network: A core system for emulated action. *Trends in Cognitive Sciences*, 21(8), 589–599. <https://doi.org/10.1016/j.tics.2017.05.002>
- Radua, J., & Mataix-Cols, D. (2012). Meta-analytic methods for neuroimaging data explained. *Biology of Mood & Anxiety Disorders*, 2, 6. <https://doi.org/10.1186/2045-5380-2-6>
- Roediger, H. L., III, Weldon, M. S., & Challis, B. H. (1989). Explaining dissociations between implicit and explicit measures of retention: A processing account. In H. L. Roediger, III & F. I. M. Craik (Eds.), *Varieties of memory and consciousness: Essays in honour of Endel Tulving* (pp. 3–41). Hillsdale, NJ: Erlbaum.
- Romero, K., & Moscovitch, M. (2015). Amnesia: General. In *International encyclopedia of the social and behavioral sciences* (2nd ed.). UK: Elsevier Ltd.

- Rosen, M., Stern, C., Michalka, S., Devaney, K., & Somers, D. (2015). Cognitive control network contributions to memory-guided visual attention. *Cerebral Cortex*, *26*(5), 2059–2073. <http://doi.org/10.1093/cercor/bhv028>
- Rosen, M. L., Stern, C. E., Devaney, K. J., & Somers, D. C. (2018). Cortical and subcortical contributions to long-term memory-guided visuo-spatial attention. *Cerebral Cortex*, *28*, 2935–2947. <https://doi.org/10.1093/cercor/bhx172>
- Rottschy, C., Langner, R., Dogan, I., Reetz, K., Laird, A. R., Schulz, J. B., ... Eickhoff, S. B. (2012). Modelling neural correlates of working memory: A coordinate-based meta-analysis. *NeuroImage*, *60*, 830–846. <https://doi.org/10.1016/j.neuroimage.2011.11.050>
- Ryan, J. D., Althoff, R. A., Whitlow, S., & Cohen, N. J. (2000). Amnesia is a deficit in relational memory. *Psychological Science*, *11*(6), 454–461. <https://doi.org/10.1111/1467-9280.00288>
- Schacter, D. L., Bowers, J., & Booker, J. (1989). Intention, awareness, and implicit memory: The retrieval intentionality criterion. In S. Lewandowsky, J. C. Dunn, & K. Kirsner (Eds.), *Implicit memory: Theoretical issues* (pp. 47–65). Hillsdale, NJ: Erlbaum.
- Schacter, D. L., Dobbins, I. G., & Schnyer, D. M. (2004). Specificity of priming: A cognitive neuroscience perspective. *Nature Reviews Neuroscience*, *5*, 853–862. <http://doi.org/10.1038/nrn1534>
- Schankin, A., Hagemann, D., & Schubö, A. (2011). Is contextual cueing more than the guidance of visual-spatial attention? *Biological Psychology*, *87*(1), 58–65. <https://doi.org/10.1016/j.biopsycho.2011.02.003>
- Schankin, A., & Schubö, A. (2009). Cognitive processes facilitated by contextual cueing: Evidence from event-related brain potentials. *Psychophysiology*, *46*(3), 668–679. <https://doi.org/10.1111/j.1469-8986.2009.00807.x>
- Schankin, A., & Schubö, A. (2010). Contextual cueing effects despite spatially cued target locations. *Psychophysiology*, *47*(4), 717–727. <https://doi.org/10.1111/j.1469-8986.2010.00979.x>
- Sestieri, C., Shulman, G. L., & Corbetta, M. (2010). Attention to memory and the environment: Functional specialization and dynamic competition in human posterior parietal cortex. *Journal of Neuroscience*, *30*, 8445–8456. <https://doi.org/10.1523/JNEUROSCI.4719-09.2010>
- Shomstein, S., & Yantis, S. (2004). Control of attention shifts between vision and audition in human cortex. *Journal of Neuroscience*, *24*, 10702–10706. <https://doi.org/10.1523/JNEUROSCI.2939-04.2004>
- Shomstein, S., & Yantis, S. (2006). Parietal cortex mediates voluntary control of spatial and nonspatial auditory attention. *Journal of Neuroscience*, *26*, 435–439. <https://doi.org/10.1523/jneurosci.4408-05.2006>
- Spreng, R. N. (2012). The fallacy of a “task-negative” network. *Frontiers in Psychology*, *3*, 145. <https://doi.org/10.3389/fpsyg.2012.00145>
- Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. *Journal of Cognitive Neuroscience*, *25*, 74–86. https://doi.org/10.1162/jocn_a_00281
- St Jacques, P. L., Kragel, P. A., & Rubin, D. C. (2011). Dynamic neural networks supporting memory retrieval. *NeuroImage*, *57*(2), 608–616. <https://doi.org/10.1016/j.neuroimage.2011.04.039>
- Stokes, M. G., Atherton, K., Patai, E. Z., & Nobre, A. C. (2012). Long-term memory prepares neural activity for perception. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(6), E360–E367. <https://doi.org/10.1073/pnas.1108555108>
- Summerfield, J. J., Lepsienski, J., Gitelman, D. R., Mesulam, M. M., & Nobre, A. C. (2006). Orienting attention based on long-term memory experience. *Neuron*, *49*(6), 905–916. <http://doi.org/10.1016/j.neuron.2006.01.021>
- Summerfield, J. J., Rao, A., Garside, N., & Nobre, A. C. (2011). Biasing perception by spatial long-term memory. *The Journal of Neuroscience*, *31*(42), 14952–14960. <https://doi.org/10.1523/JNEUROSCI.5541-10.2011>
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: An approach to cerebral imaging*. New York: Thieme Medical Publishers, Inc. <https://doi.org/10.1017/S0022215100111879>
- Taylor, B. J., Killick, C., & McGlade, A. (2015). *Understanding and using research in social work*. Los Angeles, CA: Learning Matters.
- Treves, A. (2004). Computational constraints between retrieving the past and predicting the future, and the CA3–CA1 differentiation. *Hippocampus*, *14*(5), 539–556. <https://doi.org/10.1002/hipo.10187>
- Turkeltaub, P. E., Eickhoff, S. B., Laird, A. R., Fox, M., Wiener, M., & Fox, P. (2012). Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. *Human Brain Mapping*, *33*(1), 1–13. <http://doi.org/10.1002/hbm.21186>
- Vilberg, K. L., & Rugg, M. D. (2009). Left parietal cortex is modulated by amount of recollected verbal information. *Neuroreport*, *20*(14), 1295–1299. <https://doi.org/10.1097/WNR.0b013e3283306798>
- Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, *100*(6), 3328–3342. <https://doi.org/10.1152/jn.90355.2008>
- Voss, J. L., Galvan, A., & Gonsalves, B. D. (2011). Cortical regions recruited for complex active-learning strategies and action planning exhibit rapid reactivation during memory retrieval. *Neuropsychologia*, *49*, 3956–3966. <http://doi.org/10.1016/j.neuropsychologia.2011.10.012>
- Voss, J. L., Gonsalves, B. D., Federmeier, K. D., Tranel, D., & Cohen, N. J. (2011). Hippocampal brain-network coordination during volitional exploratory behavior enhances learning. *Nature Neuroscience*, *14*, 115–120. <http://doi.org/10.1038/nn.2693>
- Voss, J. L., Warren, D. E., Gonsalves, B. D., Federmeier, K. D., Tranel, D., & Cohen, N. J. (2011). Spontaneous revisitation during visual exploration as a link among strategic behavior, learning, and the hippocampus. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(31), E402–E409. <http://doi.org/10.1073/pnas.1100225108>
- Wagner, A. D., Shannon, B. J., Kahn, I., & Buckner, R. L. (2005). Parietal lobe contributions to episodic memory retrieval. *Trends in Cognitive Sciences*, *9*, 445–453. <https://doi.org/10.1016/j.tics.2005.07.001>
- Wang, J. X., & Voss, J. L. (2014). Brain networks for exploration decisions utilizing distinct modeled information types during contextual learning. *Neuron*, *82*(5), 1171–1182. <https://doi.org/10.1016/j.neuron.2014.04.028>

- Westerberg, C., Miller, B. B., Reber, P. J., Cohen, N. J., & Paller, K. A. (2011). Neural correlates of contextual cueing are modulated by explicit learning. *Neuropsychologia*, *49*(12), 3439–3447. <http://doi.org/10.1016/j.neuropsychologia.2011.08.019>
- Yantis, S., Schwarzbach, J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., & Courtney, S. M. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature Neuroscience*, *5*, 995–1002. <https://doi.org/10.1038/nn921>
- Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., ... Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*(3), 1125–1165. <https://doi.org/10.1152/jn.00338.2011>
- Zarahn, E., Aguirre, G., & D'Esposito, M. (2000). Replication and further studies of neural mechanisms of spatial mnemonic processing in humans. *Cognitive Brain Research*, *9*(1), 1–17. [https://doi.org/10.1016/s0926-6410\(99\)00033-6](https://doi.org/10.1016/s0926-6410(99)00033-6)
- Zimmermann, J., Ross, B., Moscovitch, M., & Alain, C. (2020). Neural dynamics supporting auditory long-term memory effects on target detection. *NeuroImage*, *218*, 116979. <https://doi.org/10.1016/j.neuroimage.2020.116979>
- Zimmermann, J. F., Alain, C., & Butler, C. (2019). Impaired memory-guided attention in asymptomatic APOE4 carriers. *Scientific Reports*, *9* (8138), 1–14. <https://doi.org/10.1038/s41598-019-44471-1>

How to cite this article: Fischer M, Moscovitch M, Alain C. A systematic review and meta-analysis of memory-guided attention: Frontal and parietal activation suggests involvement of fronto-parietal networks. *WIREs Cogn Sci*. 2020;e1546. <https://doi.org/10.1002/wcs.1546>

APPENDIX

TABLE A1 Coordinates in MNI space

Giesbrecht et al. (2013)		
X	Y	Z
–15	–69	–15
36	–66	39
24	–33	45
33	–54	63
63	18	27
–57	21	12
–15	54	27
Greene et al. (2007)		
X	Y	Z
–34.28	–17.42	16.37
–7.64	–2.66	51.01
–40.92	–29.65	17.62
–36.02	–15.19	51.41
6.38	–15.83	50.54
–15.62	18.2	43.75
–29.07	–17.5	43.03
–23.07	–37.58	–4.81
–9.75	–42.87	–5.99
Manginelli et al. (2013)		
X	Y	Z
27.15	–87.87	–8.68
–29.27	–73.46	–23.71

(Continues)

TABLE A1 (Continued)

38.86	-66.22	-18.87
38.71	-60.77	-29.49
-38.33	-47.79	33.29
53.17	-47.72	5.95
-40.39	-4.34	50.32
Pollmann and Manginelli (2010)		
<i>X</i>	<i>Y</i>	<i>Z</i>
-61.27	2.77	24.2
7.63	-79.74	-12.51
-3.1	-82.55	-7.57
Pollmann and Manginelli (2009)		
<i>X</i>	<i>Y</i>	<i>Z</i>
-21.64	57.28	8.04
37.47	43.09	-20.69
-1.88	47.62	29.95
-26.83	46.81	22.62
-10.46	36	32.37
8.11	34.33	47.91
-12.1	27.48	-12.7
-12.15	8.47	-20.9
7.33	6.62	-18.81
34.95	3.63	28.08
1.57	4.34	37.54
-11.45	-0.48	32.64
8.09	-1.91	39.17
-47.16	-4.31	28.02
38.33	-10.63	36.15
-51.34	-10.94	37.71
28.7	-22.05	40.81
15.61	-38.34	28.08
23.82	-49.18	-7.97
-51.53	-52.89	13.85
-7.43	-83.74	-8.5
Preston and Gabrieli (2008)		
<i>X</i>	<i>Y</i>	<i>Z</i>
56	-64	50
-60	-46	42
-54	-64	38
60	-58	40
54	-78	28
14	-96	22
-14	-10	-30
-20	-4	-42

TABLE A1 (Continued)

Rosen et al. (2016)		
X	Y	Z
-5.8	-64.5	30.7
12.7	-64.2	38.6
-4	-22.3	31
5.3	-25.7	29.5
-22.3	43.9	27.7
-39.7	19.8	39.7
33.7	48.1	5
-48.6	-58.9	38.2
45.5	-56.9	43.2
12.7	36.4	21.8
7.2	-74.8	30
Rosen et al. (2018)		
-13.6	-67.4	39.6
6.9	-65.2	40.9
-7.9	-22.4	29.3
8.4	-36.1	27.9
-38.5	44.5	1.4
38.8	47.6	6.5
-40.8	19.5	31.5
44.6	27	27.8
-30.3	11.1	49.3
22.7	13.6	41.9
-53.7	-40.6	43
35.5	-68.1	42.4
-26.6	23.5	-8.2
32.6	16.9	1.1
-55.1	-42.7	-9.9
55	-46	-3.7
-8.9	11.8	42.8
7.7	23.5	39.3
12.2	20.5	26.9
Stokes et al. (2012)		
12	-54	-45
-48	-63	-6
0	-75	-33
-9	-57	-33
30	15	9
-15	-39	-18
54	-60	-6
-24	-6	-9
27	0	48

(Continues)

TABLE A1 (Continued)

-24	-63	0
-21	-63	48
-45	39	24
9	21	21
63	-36	36
42	6	24
30	36	36
Summerfield et al. (2006)		
X	Y	Z
3	21	48
9	21	39
6	9	54
-3	6	51
6	-27	30
33	6	51
45	3	57
-27	-3	51
-30	-3	60
-39	-6	54
-42	-3	51
42	9	27
51	12	33
-42	3	30
-57	15	33
39	21	-3
54	15	0
-36	18	3
27	-66	45
-27	-63	51
33	-75	27
-27	-72	36
54	-45	18
12	-51	9
21	-57	18
-18	-60	12
21	-33	0
-21	-33	-3
36	-39	-21
-30	-33	-24
45	-72	15
39	-81	12
-33	-81	21
-42	-81	12
33	-90	12

TABLE A1 (Continued)

-30	-90	9
9	-93	-6
-12	-99	0
36	-87	3
27	-72	-12
27	-84	-12
45	-69	-15
42	-78	-12
-42	-75	-12
-30	-81	-15
-36	-84	-12
24	-42	-15
42	-57	-15
33	-54	-15
30	-60	-12
30	-51	-9
-30	-48	-21
-27	-54	-9
-36	-66	-12
-39	-60	-9
15	9	3
15	-3	12
-12	0	6
-15	-3	12
12	-18	9
9	-12	3
-12	-18	9
-30	-15	-18
-36	39	0
-24	-30	6
-18	-39	-33
18	-42	-33