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Interactions between attention and memory

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Attention and memory cannot operate without each other. In this review, we discuss two lines of recent evidence that support this interdependence. First, memory has a limited capacity, and thus attention determines what will be encoded. Division of attention during encoding prevents the formation of conscious memories, although the role of attention in formation of unconscious memories is more complex. Such memories can be encoded even when there is another concurrent task, but the stimuli that are to be encoded must be selected from among other competing stimuli. Second, memory from past experience guides what should be attended. Brain areas that are important for memory, such as the hippocampus and medial temporal lobe structures, are recruited in attention tasks, and memory directly affects frontal-parietal networks involved in spatial orienting. Thus, exploring the interactions between attention and memory can provide new insights into these fundamental topics of cognitive neuroscience.

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Introduction

Throughout the modern history of psychology and neuroscience, memory and attention have enjoyed center stage as fundamental processes of intellectual function. Yet most of this research has focused on these processes as separate topics. Memory studies have typically not explored the role of attentional selection and modulation of encoding, whereas attention studies commonly ignore the important role of perceptual experience and past knowledge. However, because memory has a limited capacity, it is crucial to understand which information is selected for encoding. Likewise, because attention operates in a world that is relatively stable over time, it is useful to rely on past experience to optimize selection. In fact, some aspects of attention and memory might even reflect the same processes. For example, memory retrieval might reflect a form of selective attention to internal representations [1,2•].

Classic psychologists such as William James stated long ago that 'we cannot deny that an object once attended to will remain in the memory, while one inattentively allowed to pass will leave no traces behind' [3]. More recently, leading neuroscientists such as Eric Kandel have stated that one of the most important problems for 21st century neuroscience is to understand how attention regulates the processes that stabilize experiential memories [4]. Here, we review studies from the past two years that reveal progress towards understanding the interactions between attention and memory in neural systems.

Attention at encoding

A major question in many people's minds is how to improve memory. It is safe to say that attention helps to improve memory encoding but the details of this modulation remain unresolved. Also, although it is uncontroversial that attending to or focusing on a fact or event will enhance the likelihood of later memory, it is less clear how attention modulates and enhances implicit, unconscious memories — those traces of experience that we cannot articulate or overtly declare. Innovations in brain imaging research have helped reveal these implicit memory traces in the mind. Similar methods have also helped characterize which brain states are more likely to lead to better memory encoding and retrieval.

But what does it mean to attend? In one sense, it means that processing resources are being allocated to a task. In another sense, attention involves selecting what deserves these resources, and preventing other things from receiving them. Think of this as an analogy to resource-demanding endeavors, such as exercising. Do I have the time and energy (resources) to exercise? If so, should I run around the neighborhood or swim laps (selection)? The distinction between resources and selection is useful for understanding how attention modulates memory. In behavioral research, for example, explicit memory is impaired when processing resources are divided between two tasks during encoding but not retrieval [5]. Many implicit memory tasks can be performed despite a demanding secondary task, although even in such cases the stimuli must be selectively attended [6,7].

In the following sections, we will discuss how resources and selection interact with memory encoding. We will focus on two neural measures of memory: first, explicit episodic memory, which typically correlates with increased activity in frontal and medial temporal regions

during encoding (subsequent memory) [8]; and second, implicit perceptual memory, which is typically revealed by decreased activity in ventral visual cortex when visual stimuli are repeated (known as repetition attenuation, repetition suppression, or functional magnetic resonance [fMR] adaptation) [9•].

Attentional resources

One popular way to study attentional effects is to require subjects to perform dual tasks. Importantly, the impact of dividing attention on memory depends on how attention is divided.

Typically, difficult versus easy auditory monitoring tasks impair memory for words presented at the same time. However, such tasks do not modulate activity in the left inferior prefrontal cortex (LIPC), which is important for the encoding of words into long-term memory [10]. In that study, a difficult monitoring task reduced encoding-related activity in dorsolateral prefrontal cortex and superior parietal regions, both of which mediate the allocation of cognitive control resources. In other words, the secondary task impaired whether episodic encoding processes were engaged or not, while leaving intact the actual encoding processes in the LIPC. Other types of secondary tasks can directly affect episodic encoding processes if they engage the same LIPC circuitry. For example, if required to switch between two incidental encoding tasks (versus repeating the same task), LIPC activity increases and memory performance decreases, presumably because task-switching engages the LIPC and interrupts episodic memory formation [11].

Although explicit episodic memory might depend on the availability of cognitive control resources in frontal and parietal regions, the same is not true for implicit perceptual memory. In one study, a highly demanding working-memory task on face stimuli at fixation had no effect on parahippocampal place area (PPA) responses to task-irrelevant background scenes [12]. When these background scenes were repeated, there was robust repetition attenuation, suggesting that the scenes were processed and at least briefly retained in perceptual memory. By contrast, repetition attenuation was eliminated in that study when the perceptual difficulty of the central task was increased. Thus, 'resources' is not a unitary concept, and the impact of dividing attention will depend on the overlap between the processing demands of the secondary task and the type of memory under investigation. This might help to explain striking demonstrations of perceptual learning for task-irrelevant subliminal stimuli [13]. Interestingly, tasks that occupy relevant resources are not always deleterious: manipulating items in working memory during encoding rather than simply rehearsing them increases dorsolateral prefrontal cortex activity and enhances subsequent episodic memory [14•].

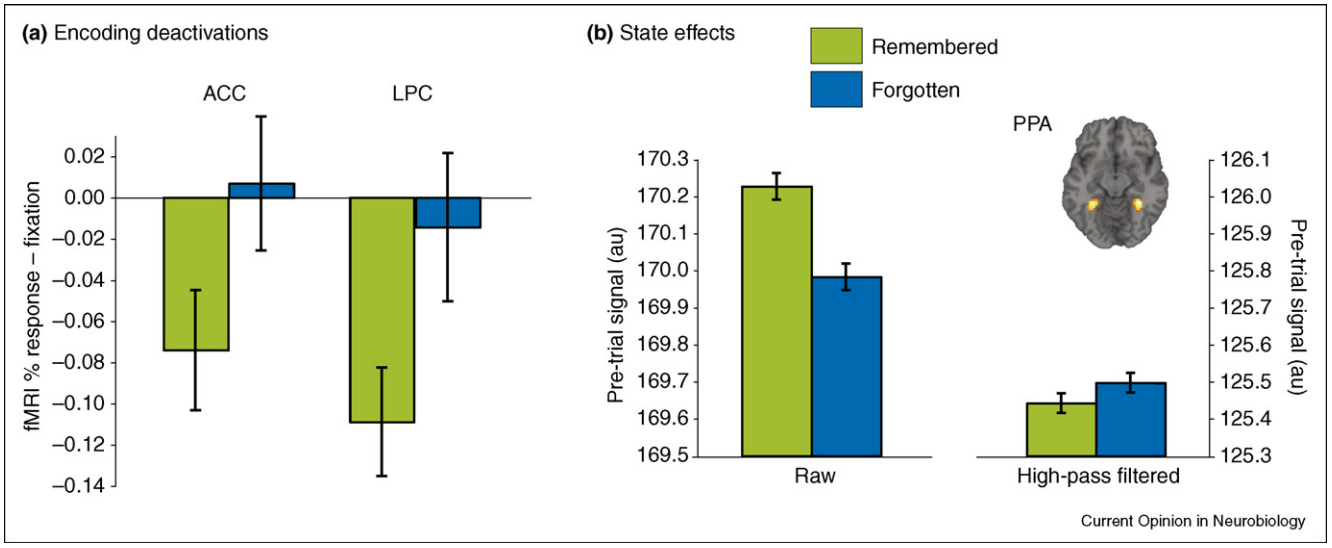
The aforementioned studies showed tradeoffs in activation between regions involved in two different attention-demanding tasks. However, such tradeoffs are not restricted to dual-task situations. Even during a single task, a 'default' network of brain regions that are otherwise active during rest become deactivated, revealing another form of tradeoff [15]. The degree of deactivation is proportional to task difficulty, and thus might reflect the availability of processing resources [16]. In fact, significant decreases in activity in posterior midline regions, including the posterior cingulate and precuneus, correlate with better episodic subsequent memory (Figure 1a) [17–19,20•]. Deactivation in the precuneus and anterior cingulate cortex is also predictive of repetition attenuation [20•]. These encoding deactivations seem to reflect the availability of general attentional resources, because they predict subsequent memory under a variety of encoding and retrieval conditions [19,21•].

Selective attention

Just because you have the resources does not mean that you can do everything at once. You still have to choose what to do. Likewise, the availability of attentional resources is not sufficient for memory encoding. For example, when faces and scenes are combined into fully overlapping composite stimuli (Figure 2), subjects can only remember what they selectively attend to. Not even implicit measures of memory such as repetition attenuation are preserved for ignored stimuli [22•], even when repeated 15 times in a 30 s block [23]. Thus, stimuli that are to be learned must be selected, whether the task is explicit or implicit [6,7,24]. (One interesting exception to this case is the demonstration of low-level perceptual learning from subthreshold stimuli [13]. However, even such cases of visual perceptual learning without perception are not fully passive, but require reinforcement from an independent, concurrent task [25,26•].)

Generally speaking, selective attention becomes crucial when there is competition between stimuli in the environment. This competition can be resolved in many ways: for example, objects are encoded in the lateral occipital complex (LOC) only if the spatial location in which they appear is selected [27], if they appear in a color that the subjects are monitoring [28], or if the experimental task requires that responses are based on features of the objects [29]. Similarly, during a detection task, faces are encoded in the fusiform face area only if they match the identity of a target face [30]. Interestingly, the necessity of attention might depend on the level of representation: repetition attenuation is observed in early visual areas even when attention is allocated to a different spatial scale or to an unoccupied spatial location [31•,32•]. Supporting this distinction, Seitz and Dinse (in this issue) review current evidence for neural plasticity and perceptual learning of low-level features in the tactile, auditory and visual modalities from passive, unattended sensory

Figure 1



Correlates of successful encoding related to attention. Subjects were presented with grayscale scenes, and were required to rapidly judge whether they depicted indoor or outdoor scenes. Scenes were then categorized based on whether they were subsequently remembered in a surprise memory test. **(a)** Encoding deactivations. The anterior cingulate cortex (ACC) and left precuneus (LPC) were deactivated relative to passive fixation during the presentation of scenes that were later remembered, but not those that were forgotten. Such deactivations might reflect the reallocation of resources to encoding processes from the default network. **(b)** Baseline activity. Greater raw fMRI signal in the parahippocampal place area (PPA) right before the appearance of a scene predicted whether that scene would be remembered. This baseline difference was eliminated by high-pass temporal filtering, and thus might have resulted from variation in low-frequency attentional states. Nevertheless, event-related responses that predicted subsequent memory, as in (a), persisted after high-pass filtering. Thus, encoding success is the result of both how stimuli are processed and the state of the brain before encoding. Adapted, with permission, from [20•].

stimulation or even direct electrical or magnetic stimulation of sensory cortices.

How does selective attention enhance repetition attenuation effects? One possibility is that attention to a particular stimulus attribute (e.g. color) modulates baseline activity in selective brain regions (e.g. V4), which in turn increases sensitivity to that attribute and magnifies subsequent stimulus-evoked responses [33]. Correspondingly, some neurophysiological models predict that the magnitude of the initial response to a stimulus might be proportional to the amount of attenuation observed upon repetition [9•]. In support of this last point, attention increases the magnitude of initial fMR imaging (fMRI) responses and the degree of attenuation that is observed upon repetition [29]. Note, however, that the lack of attenuation for unattended stimuli cannot be attributed to the fact that evoked responses to unattended stimuli are much weaker to begin with [22•,23].

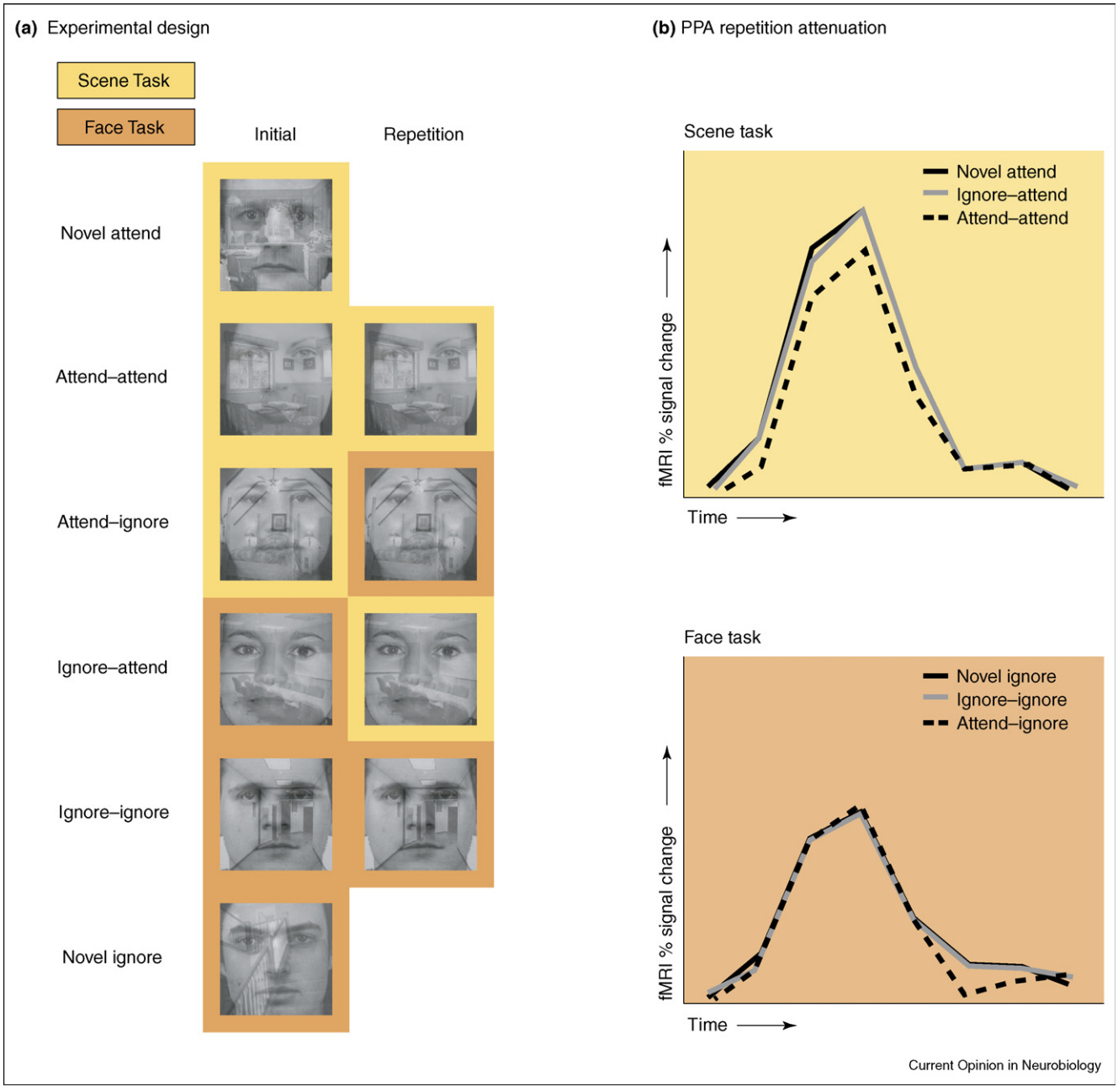
Instead of manipulating attention with behavioral tasks, researchers have begun examining a potential indirect neural correlate of attention: pre-trial activity that predicts subsequent memory. In event-related potentials, for example, negative-going activity in frontal cortex predicts that an upcoming word in the same encoding trial will be subsequently remembered [21•]. This study could not discern whether the preparatory effect was cue-related or a result of general brain states independent of the trial structure. In support of the latter, baseline activity before stimulus presentation correlates with subsequent memory in the absence of cues. Specifically, the likelihood of subsequently remembering a scene is correlated with the magnitude of the raw fMRI signal in the PPA immediately before its appearance (Figure 1b) [20•]. Such baseline effects might reflect arousal or the incidental availability of attentional resources. In this way, encoding occurs not only when stimuli are inherently memorable but also during certain favorable states of mind.

The influence of memory on attention

Although it is more common to think about how attention improves memory, there is growing appreciation for how memory optimizes attention and perception. At a basic level, memory is undoubtedly fundamental to perception. One could not recognize their mother's face or a car as a car without the ability to match perceptual input with representations stored in memory.

Memory is especially important for perception when images are degraded. In visual area V4, neuronal responses to learned stimuli are enhanced relative to responses to novel stimuli only when the target images are severely degraded, reflecting amplification of

Figure 2



The impact of attention on repetition attenuation at the time of encoding and (implicit) retrieval in the parahippocampal place area (PPA). **(a)** Schematic experimental design. Subjects were presented with composite scene–face stimuli, while monitoring either for a scene change (scene task) or for a face change (face task). These tasks required subjects to engage in object-based attention by selecting the task-relevant stimulus and inhibiting the task-irrelevant stimulus. Because responses are plotted from the PPA — a scene-selective region of the ventral visual stream — we will consider scenes presented during the scene task as attended and scenes presented during the face task as ignored. The composite images were presented in several different ways: once in the scene task (novel attend); once in the face task (novel ignore); twice in the scene task (attend–attend); twice in the face task (ignore–ignore); once in the scene task and once in the face task (attend–ignore); and once in the face task and once in the scene task (ignore-attend). Repeated stimuli were presented in separate trials. Using this factorial design, the necessity of selective attention for incidental encoding (initial) and implicit retrieval (repetition) could be evaluated. **(b)** Functional magnetic resonance imaging (fMRI) responses from the PPA for the second presentation of repeated stimuli, and the first presentation of novel stimuli. All of the scenes presented during the scene task were attended, whereas those presented during the face task were ignored. Relative to the novel conditions, repetition attenuation (difference at the peak of the responses) was observed only for stimuli that were attended during encoding and retrieval. Stimuli that were never attended, attended only during encoding or attended only during retrieval failed to elicit any repetition attenuation. Thus, even though repetition attenuation can occur in the PPA during divided attention [12], it requires selective attention at encoding and retrieval. Adapted, with permission, from [22•].

task-relevant information [34]. Ironically, the opposite pattern is more prevalent for stimuli that are not degraded. When novel and familiar images are both visually salient and clear, then there is a bias for neuronal activity to be lower for learned images [9•,35]. Such visibility-dependent reversals in response patterns for novel and familiar images were recently demonstrated in a single experiment within subjects [36]. While viewing undegraded repeated or novel scenes, fMRI responses were higher for novel images. However, when subjects viewed a different set of scene images that were degraded to be barely discriminable, then greater responses to repeated images were observed (repetition enhancement).

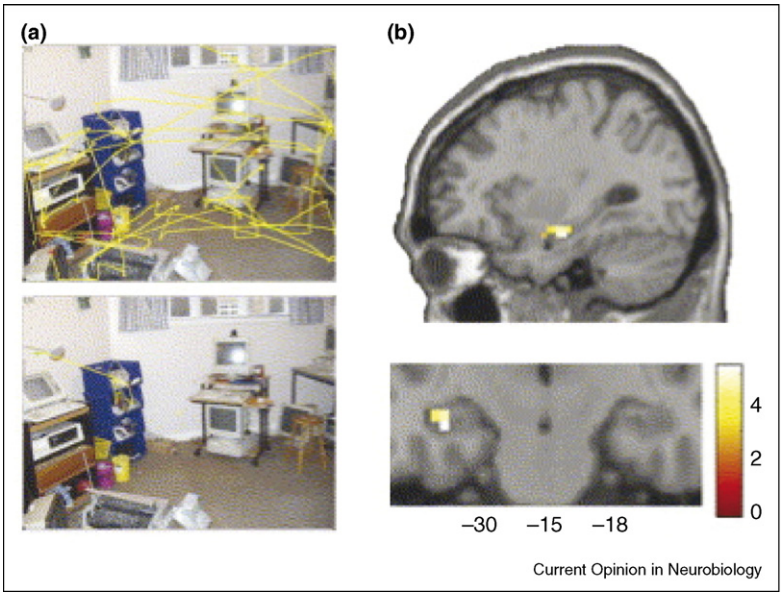
Although seemingly contradictory, both repetition attenuation and repetition enhancement enhance vision. For highly visible images, neuronal responses might be biased to orient attention to novel images that would be of adaptive value (e.g. a new source of food, a new mate or a novel threat). For degraded images, learning enhances visual selectivity, enabling the organism to recognize objects in situations where nothing would otherwise be recognizable. Together, the results show that memory mechanisms in cortical sensory circuitry serve to bias competitive interactions, influencing what is attended and selected [35].

Although learning is essential for high-level vision in these sensory cortical areas, the ability to recognize objects rapidly has been traditionally viewed as autonomous from the medial temporal lobe (MTL) memory system that is required to encode episodic information. After all, patients who have MTL damage have no trouble reading mirror-reversed letters or identifying degraded versions of pictures viewed previously [37,38], even while they are amnesic of ever having performed these tasks before.

Yet, with more complex scene-like stimuli, associative, configural learning becomes important, bringing MTL mechanisms into play. One popular task is to require visual search for targets embedded in unique, typically complex or naturalistic visual backgrounds. For example, lesions of the hippocampus, perirhinal cortex and fornix significantly impair such 'object-in-place' learning [39,40]. In another task that required association of target locations with background scenes, hippocampal neurons changed their response properties during the course of learning [41].

Functional neuroimaging studies provide converging evidence from human subjects. One elegant study showed that the hippocampus and parahippocampal regions were sensitive to the bindings of objects with their backgrounds: repetition attenuation was observed only when object–background pairings were repeated [42]. In a different task known as contextual cuing, subjects become faster at detecting targets that appear in consistent locations in repeating configurations of distractor objects, even when they are not aware of these regularities. Interestingly, extended damage of the MTL impairs contextual cuing [43,44]. Memory-based enhancement of

Figure 3



Memory-guided attention. **(a)** Examples of eye-tracking data are shown in yellow. The scene on the top contained a 'key' target stimulus within the middle compartment of the stacked blue storage boxes. There were extensive eye movements to find the key when observers first encountered the scene (top). After learning, there was a near direct eye movement to the location of the key, showing memory-based orienting that was faster than visually-driven orienting (not shown). **(b)** Hippocampal involvement during memory-guided orienting. Adapted, with permission, from [50•].

visual search performance can even be disrupted by pharmacological manipulations such as midazolam, which produces transient amnesia [45].

Learning influences how people scan images [46]. For example, eye movement recordings reveal that subjects are sensitive to subtle changes to objects in scenes from one view to the next [47]. Sensitivity to these object-in-scene changes is impaired by amnesia [48]; however, it is controversial whether subjects must be aware of these changes to detect them [49].

The aforementioned studies highlight the importance of the MTL in memory-based guidance of attention. More recent studies are investigating how such memory signals influence attentional mechanisms directly. Memory-guided search for targets that are embedded in naturalistic scenes can be compared to traditional attentional orienting, and such searching is even more rapid and effective than visually guided orienting based on peripheral cues [50•,51,52]. Moreover, fMRI has revealed that memory-guided spatial orienting recruits many of the same neural mechanisms that mediate visually guided spatial orienting (Figure 3) [50•]. These regions include the posterior parietal cortex, frontal eye fields and cingulate cortex. Brain areas that are unique to memory-guided orienting include the hippocampus — the same area involved in the previously mentioned object-in-place learning tasks.

Conclusions

The relationship between attention and memory has long been recognized. Recent neuroimaging studies have begun elucidating how attentional control mechanisms might affect episodic and perceptual encoding and how, in turn, such control and orienting might be modulated by past experience. As this research progresses, the distinction between attention and memory becomes increasingly less clear. This might help to explain difficulties in resolving where perception stops and where memory begins [53,54]: attention bridges perception and memory over delays, brief or long [55]. Much has been learned and much remains to be discovered about the rich, interactive cascade of processes that form lasting impressions of the perceptual world in our minds.

Update

A recent event-related potential study provides further evidence that attention is directly cued by contextual memory. Johnson *et al.* [56•] reported that electrophysiological measures of spatial attention reveal rapid orienting of attention to the target in contextual cuing tasks [43,44].

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