somewhat surprising in the task used by Nicolle et al., because the respective variables they represent are, at least superficially, irrelevant to the choice at hand. One possibility is that the representation of the valuations according to the alternative preference set in dmPFC corresponds to their storage in a temporary buffer. In the event of a change of decision context, those signals can be immediately transferred into vmPFC, permitting rapid deployment of the now behaviorally relevant preference set. Another possibility is that (although not applicable in the specific task used by Nicolle et al., 2012), the representation of the alternative valuations in dmPFC may allow for the ongoing updating of those model-based value signals on the basis of new information about the sensory environment as it is received.

The study by Nicolle et al. invites several important directions for further research going forward. First of all, if "other" versus "self" is not the relevant dimension for differentiating ventromedial versus anterior dorsomedial prefrontal function, but instead the distinction is between the choice relevance of alternative state-space models, one might expect a similar pattern of results in a task involving switching between two state-space models, even in a completely nonsocial context. Second, if it is the case that the dmPFC is acting as a buffer to store alternative models of the decision problem at hand to enable rapid transferring of choice-relevant models into vmPFC, what happens in the dmPFC if more than two such frameworks are to be used for a given task, such as, for example, if participants had to make choices on behalf of two other people as well as themselves? Regardless of the outcome of such future research, the study by Nicolle et al. illustrates how, through the use of quantitative computational approaches married to dynamic measurements of brain function, it is possible to gain insight into the specific computational functions of brain regions involved in even the most complex social-cognitive processes.

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Attending to the Present When Remembering the Past

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In this issue of *Neuron*, Guerin et al. (2012) provide novel evidence that distinct parietal mechanisms for attention and memory compete when past experiences are compared to current perceptual input. While dorsal parietal cortex supports attention to perceptual stimuli, high attentional demands suppress ventral parietal regions important for veridical remembering.

When walking down a street, sitting in a restaurant, or boarding a plane, we often find our attention captured by a person that looks like someone we know. We find ourselves wondering: *do I know this person?* In these situations, we focus on perceptual features of this candidate acquaintance and compare these perceived features to our internal representation (memory) of the neighbor, colleague, or relation that they resemble. Through this process we may determine that this person *is not* a person we know (in which case we would likely opt to not wave or say hello) or that this person *is* someone we know (in which case we may still find ourselves debating whether the situation permits a wave or hello).
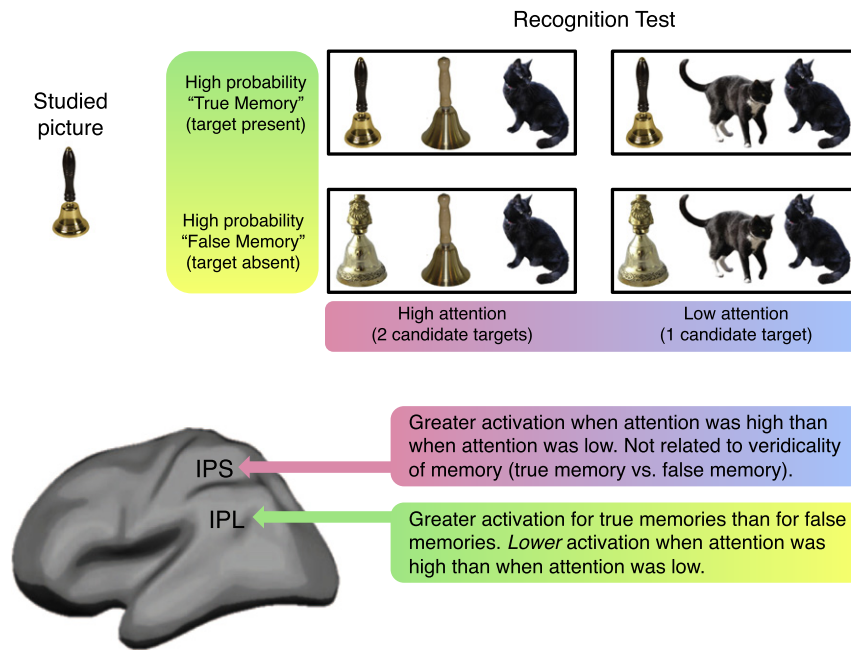
Figure 1. Experimental Paradigm and Results from **Guerin et al., 2012**

This common experience illustrates two important ways in which memory and attention interact: (1) our memories of the past can powerfully direct how attention is allocated in the present and (2) comparing our perceptions to the contents of memory is often an attentionally demanding process. It is commonly acknowledged that memory and attention interact (Chun and Johnson, 2011), but they have historically been studied in isolation.

A particularly interesting facet of the interaction between attention and memory is that the product of these interactions may ultimately be a memory error. The most common cases are when we are inattentive during the encoding of an event (e.g., absentmindedly setting down our keys and failing to recall their location later). However, attention and memory interactions may also explain errors during retrieval. Returning to the initial example: when seeing a familiar-looking person, we may erroneously deem this person an acquaintance because we fail to bring to mind a high-fidelity memory of the known person and/or we fail to properly compare that memory to our current perception. When errors of this type occur—saying hello to a stranger that resembles a colleague—

are they caused by lapses of memory, attention, or a failed interaction between the two?

Understanding the interaction between memory and attention should involve consideration of the common versus distinct neural systems that contribute to each. While *episodic memory* (our explicit memories of past events or episodes) critically depends on structures in the medial temporal lobes, including the hippocampus (Eichenbaum, 2004), there is now abundant evidence from human neuroimaging indicating that activity in lateral parietal cortex tracks successful retrieval of episodic memories (Wagner et al., 2005). This observation is particularly intriguing because of the known role of lateral parietal cortex in visuospatial attention (Corbetta and Shulman, 2002; Kastner and Ungerleider, 2000), which has led researchers to propose that orienting to external perceptual stimuli and internally generated memories may involve a common form of attention (Cabeza et al., 2008).

In this issue of *Neuron*, Guerin et al. (2012) consider how memory and attention interact during attention-demanding acts of memory retrieval. Using an elegant experimental paradigm, the authors separately manipulated the propensity

for false memories to occur and the attentional demands of memory retrieval. This unique approach allowed for direct comparison of the neural systems that tracked the veridicality of memory and those that supported the *top-down* allocation of attention. Does top-down allocation of attention to perceptual input positively relate to memory veridicality? Are there tradeoffs between attention and memory?

In the experiment, human subjects first studied a series of pictures of objects (e.g., a bell; see Figure 1). Subjects then completed a recognition test that occurred during fMRI scanning. In the recognition test, subjects were presented with three pictures on each trial and were instructed to choose which of the pictures was previously studied or whether none had been previously studied (see Figure 1). Each picture fell into one of three types: (1) a previously studied picture—*target*, (2) a new picture, unrelated to previously studied pictures—*novel*, or (3) a new picture from the same semantic category as a previously studied picture—*related* (e.g., another picture of a bell). Critically, all trials in the recognition test contained two pictures from a common semantic category (e.g., two bells) along with a third picture from a distinct category (e.g., cat). What varied across trials was whether a target was present or absent (a memory manipulation) and whether there were one or two pictures that were reasonable target candidates (an attention manipulation). Specifically, on some trials, the two pictures from the same semantic category were novel (e.g., two novel cats) and the third picture (from a distinct category) was a target (e.g., the previously studied bell). This situation required low attention because two of the pictures (the cats) could easily be rejected. On other trials, however, the two pictures from the same category included one target and one related picture (e.g., the previously studied bell and a new bell). This situation required greater attention because two of the pictures (the bells) were reasonable candidates. Additionally, there were also cases when the target was absent, with attention varied for these trials, as well. Namely, in some cases there were two novel items from a common category (e.g., two cats) and one related item (e.g., a new

bell)—a situation requiring low attention because two pictures (the cats) could be easily rejected. In other cases, one novel picture (e.g., a cat) was presented along with two related items from a common category (e.g., two new bells), which required high attention because two pictures were reasonable candidates. Thus, target presence/absence was crossed with the attentional demands.

Behavioral analysis of subjects' performance confirmed that the memory manipulation was effective, with subjects generally successful at recognizing targets but also prone to memory errors in certain situations. Specifically, subjects were highly successful (76% accuracy) at identifying the target picture when it was paired with two novel items from a category distinct from the target. When the target was paired with a related item, subjects were still usually able to identify the target (65%) and rarely selected the related item (10%), indicating that subjects retained enough perceptual information about the target in memory to discriminate it from a very similar picture. Interestingly, however, when two related items (from a common category) were presented (target absent), subjects falsely "recognized" one of these pictures very frequently (47%), even though they were explicitly warned about the presence of highly similar, but new pictures. Even when a single related item was presented (alongside two novel items), it was also falsely recognized quite often (38%). Thus, when the target was not perceptually available, subjects frequently falsely remembered pictures based on a *gist memory*. When the target was perceptually available, however, these gist-based false memories were suppressed in favor of true memories of the target. It is the comparison of true memories in the target present conditions versus false memories in the target absent conditions that is of central interest.

The manipulation of attention was strongly validated by eye tracking data that were simultaneously collected during fMRI scanning. These data revealed that subjects initiated more saccades between the two pictures from the same category (e.g., the two bells) in the high attention conditions than the low attention conditions—that is, when these pictures consisted of a target and a related picture

or two related pictures. It should be emphasized that this attention manipulation was based purely on memory. All trial types were perceptually equivalent, containing two semantically similar items and one unique item, meaning that attention was not always allocated to the pictures from a common category. Rather, attention was preferentially allocated to the pictures from a common category *when they overlapped with information stored in memory*.

Turning to the fMRI data, Guerin and colleagues found striking and largely dissociable effects of attention and memory. The effect of attention was evident in dorsal frontoparietal cortex, including the intraparietal sulcus (IPS), with this network exhibiting greater activation when attention demands were high. This finding is consistent with more traditional studies of top-down visuospatial attention (Corbetta and Shulman, 2002). Notably, by simultaneously recording eye movements, the authors were able to confirm that these dorsal parietal responses were not simply attributable to eye movements. Rather, even when eye movements were controlled for, the effect of attention in IPS was robust. In contrast to the effect of attention, the effect of memory was evident in more ventral aspects of parietal cortex, mostly in the inferior parietal lobule (IPL), with greater activation for true memories than false memories. It is worth emphasizing that the contrast of true versus false memories involved a comparison of trials on which subjects made identical behavioral responses—claiming to recognize an item as having been previously studied. Thus, this comparison isolates differences in memory veridicality, not behavioral responding. Follow-up analyses indicated that not only was a positive effect of attention absent in IPL, it was in fact reversed, with IPL exhibiting *lower* activation when attention demands were high than when attention demands were low.

The findings of Guerin et al. (2012) build on prior evidence that memory can powerfully bias attention (Summerfield et al., 2006; Chun, 2000), indicating that the dorsal attention network is more heavily recruited when multiple stimuli in the environment are under consideration as potential matches with items stored in

memory. It seems likely that this top down attention was allocated to the external perceptual stimuli, but another possibility is that the dorsal attention network can be oriented toward internal representations such as memories (Cabeza et al., 2008). While the study by Guerin and colleagues could not directly test this idea, recent studies suggest that distinct aspects of dorsal parietal cortex are modulated by visuospatial attention and episodic memory (Hutchinson et al., 2009, Sestieri et al., 2010). Thus, while it remains to be seen whether there is an analogous dorsal/ventral organization in lateral parietal cortex across memory and visuospatial attention, there does not appear to be perfect overlap in the specific parietal regions that govern each.

While visuospatial attention is expected to play a role in a memory task that involves fine-grained perceptual discriminations, it is surprising that this recruitment of top down attention was dissociable from memory outcomes. Namely, activity in IPS did not differ as a function of whether subjects correctly recognized targets or falsely recognized related items. Of course, this result does not indicate that IPS played no role in memory success—top-down attention to candidate pictures was presumably a prerequisite for successful decisions—rather, it suggests that top down attention may have been effectively deployed both when memory succeeded (true memories) and when it failed (false memories). What, then, determined whether a true memory or false memory would be produced? In large part, it was the presence or absence of the target that determined the outcome: when the target was present subjects exhibited sufficiently detailed memory to reliably select the target over the related picture. But when the target was absent, false memories were common. Critically, these different outcomes were robustly related to activity in IPL—not IPS—indicating that IPL tracked the veridicality of memory. One interesting question not addressed by Guerin et al. (2012) is whether IPL activity would predict memory outcomes when only considering situations where the target was absent. In other words, while false memories were more likely to occur when the target was absent, there were also cases where subjects successfully

rejected two related items to (correctly) indicate that the target was absent. Was this because the target was retrieved from memory with sufficient perceptual detail to suppress a false memory? If so, would this situation also be characterized by greater IPL activation as compared to when a false memory occurred?

Together, the findings of Guerin et al. (2012) suggest that top-down attention and memory retrieval do not always go hand in hand. Indeed, their findings suggest that these processes may compete: when attention demands were high, IPL activity actually decreased. To the extent that IPL activity reflected processes related to memory or internal thoughts, the reduction in IPL activity during situations of high attention may reflect an antagonistic relationship between memory and attention. It remains to be seen whether this reflects a tradeoff between orienting to the external environment versus internal representations (Chun et al., 2011) or a more generalizable dissociation between attention and memory.

In summary, the findings of Guerin and colleagues provide a compelling characterization of how distinct aspects of lateral parietal cortex contribute to situations in which we must carefully compare the present with the past. These findings are relevant to a very active debate concerning the role of lateral parietal cortex in memory (for reviews, see Cabeza et al.,

2008; Shimamura, 2011; Wagner et al., 2005). Additionally, the study makes an important contribution to our understanding of memory failures (Johnson, 1997; Schacter, 1999), highlighting both the situations in which false memories are likely to occur and the neural responses that are associated with these lapses. An interesting question for future work is how necessary the contributions of lateral parietal cortex are to successful episodic remembering. While damage to lateral parietal cortex has not been associated with robust memory deficits—clearly not to the degree that occurs with damage to the medial temporal lobe system—it is possible that lateral parietal regions make subtle but meaningful contributions to memory. This could be addressed by carefully probing memory functioning in neglect patients with parietal damage. For example, in the paradigm employed by Guerin et al. (2012), perhaps damage to IPS would impair the initial step of allocating attention to candidate pictures. Damage to IPL, on the other hand, may result in a diminished ability to make subtle discriminations between targets and related (but new) items. Both neuroimaging and patient work can further characterize the competitive interactions between IPL and IPS in tasks that carefully and cleverly separate attentional demands and memory success as Gueirin and colleagues have done.

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