What Is Memory-Guided Attention? How Past Experiences Shape Selective Visuospatial Attention in the Present

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Contents

Abstract What controls our attention? It is historically thought that there are two primary factors that determine selective attention: the perceptual salience of the stimuli and the goals based on the task at hand. However, this distinction doesn't neatly capture the varied ways our past experience can influence our ongoing mental processing. In this chapter, we aim to describe how past experience can be systematically characterized by different types of memory, and we outline experimental evidence suggesting how attention can then be guided by each of these different memory types. We highlight findings from human behavioral, neuroimaging, and neuropsychological work from the perspective of two related frameworks of human memory: the multiple memory systems (MMS) framework and the neural processing (NP) framework. The MMS framework underscores how memory can be separated based on consciousness (declarative and non-declarative memory), while the NP framework emphasizes different forms of memory as reflective of different brain processing modes (rapid encoding of flexible associations, slow encoding of rigid associations, and rapid encoding of single or unitized items). We describe how

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memory defined by these frameworks can guide our attention, even when they do not directly relate to perceptual salience or the goals concerning the current task. We close by briefly discussing theoretical implications as well as some interesting avenues for future research.

Keywords Basal ganglia · Covert attention · Hippocampus · Long-term memory · Overt attention

1 Introduction

A core principle of selective visuospatial attention is that, at any given moment, our sensory receptors receive vastly more information than our brain can ultimately process. Past work has consistently suggested that which information ultimately gets attended to can be determined by factors both external to the observer, such as the perceptual salience of the information (exogenous or stimulus-driven attention), and those internal to the observer, such as the relevance of the information to an ongoing task (endogenous or goal-directed attention) (Carrasco 2011; Chun et al. 2011; Corbetta and Shulman 2002; Knudsen 2007). However, recent critiques of this dichotomy have highlighted instances where attention can be influenced by factors that are not quite captured by either the perceptual salience of the stimuli or the ongoing goals of the observer (Awh et al. 2012; Theeuwes 2018; Sisk et al. 2018). Here, we focus on one class of such influences in particular: memory (for related reviews, see Chun and Turk-Browne 2007; Dudukovic and Wagner 2006; Hutchinson and Turk-Browne 2012; Logan 2002; Võ and Wolfe 2015; Woodman and Chun 2006).

As will be reviewed below, there are many ways in which our past experience can shape our ongoing information processing. Indeed, even in our daily lives, there are countless examples of how our memory can guide attention and subsequently modify our behavior. For example, when you are at a noisy party where it is hard to hear what your friend next to you is talking about, your attention might be drawn to a background conversation that mentions your favorite childhood TV show. On the other hand, the repeated occurrence of the loud sound from the leaf blower made by your neighbor at the same time every morning will attract your attention less and less as you get used to it.

Generally, memory is critical for behavior as it can orient our attention toward information which has acquired relevance through experience (e.g., the so-called cocktail party effect (Moray 1959)). Just as importantly, memory can help us notice new things in our environment, allowing us to selectively process novel information in order to learn about the world (Fantz 1964; Tulving et al. 1996; Ranganath and Rainer 2003). Theoretically, the role of memory is important to consider in order to fully understand attention as it does not fit cleanly into the existing dichotomy of stimulus-driven and goal-directed attention. That is, memory is not fully stimulus-driven, since stimuli might exert attentional influence only as a result of prior

experience, nor is it necessarily goal-directed, since we are able to encode (put into memory) and retrieve information about the world even if it is not directly relevant to the task at hand (e.g., Fan and Turk-Browne 2016; Hall et al. 2008; Kuhl et al. 2013; Neill et al. 1990; Turk-Browne et al. 2010).

Despite the potentially profound importance of memory for selective attention, there have been relatively few attempts to catalog how and when memory might influence attention. Here, we aim to provide context to the work described elsewhere in this book by giving an overview of how forms of memory beyond working memory might relate to visuospatial attention. Specifically, we will briefly summarize a representative cross-section of empirical findings concerning how memory shapes our attention. We consider these findings from the perspective of two related, non-mutually exclusive frameworks of human memory: a traditional multiple memory systems (MMS) framework and a more recently proposed neural processing (NP) framework. First, we introduce and present evidence for how memory defined in terms of the traditional MMS framework offers insight into how visuospatial attention can be modulated by past experience, highlighting the impact from both declarative and non-declarative forms of memory. Second, we discuss how recent neuroscientific definitions of memory might inform how the neural operations underlying visuospatial attention could be intertwined with those of memory. Finally, we conclude by highlighting theoretical implications and open questions awaiting future research.

2   Multiple Memory Systems and Their Role in Attention

2.1   *Introduction to the Multiple Memory Systems (MMS) Framework*

Over the past decades, memory research has deeply been shaped by the idea that memory is not a unitary or homogeneous entity but rather involves a confluence of multiple brain systems that mediate different yet interacting types of memory (Gabrieli 1998; Poldrack and Packard 2003; Squire et al. 1993). Scientists have sought to delineate these systems from one another and experimentally isolate their defining features using a wide range of behavioral, neuropsychological, neuroimaging, and computational modeling techniques.

The MMS framework took shape in the 1950s with the case study of patient H. M., who underwent a bilateral medial temporal lobectomy in an effort to cure his epilepsy. After his surgery, he was unable to form new memories about the events in his life (episodic memory) and also had trouble retrieving some memories of events which occurred before the surgery happened (Scoville and Milner 1957). Strikingly, other aspects of his memory, general intelligence, and other cognitive functions remained intact (Scoville and Milner 1957; Squire and Wixted 2011). For example, patient H.M. was able to perform a hand-eye coordination task that required motor
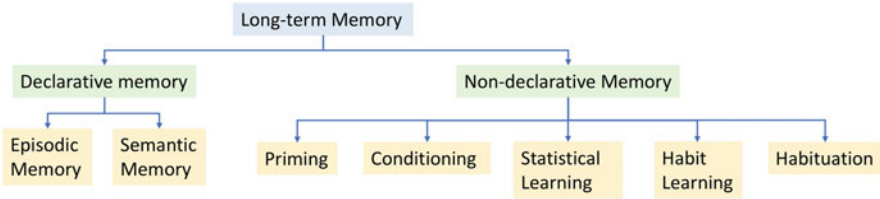
Fig. 1 Taxonomy of memory based on multiple memory systems. In the MMS framework, long-term memory generally can be divided into declarative and non-declarative types. Declarative memory consists of episodic memory and semantic memory, whereas non-declarative memory includes phenomena such as priming, conditioning, statistical learning, habit learning, and habituation

skill learning despite having no memory of actually performing the task (Milner 1962). These and related findings (Cohen and Squire 1980) strongly suggested that memory could not be considered a unitary entity and was instead composed of multiple memory systems. The work with patient H.M. laid the groundwork for MMS, and, based on these findings as well as many other neuropsychological studies, it was proposed that long-term memory could be broadly separated into at least two systems: declarative (sometimes referred to as explicit) and non-declarative (sometimes referred to as implicit) memory (Squire 1992) (Fig. 1).

Declarative Memory Declarative memory refers to knowledge based on past experience that is consciously available and can be further divided into two forms of long-term memory: semantic and episodic. Semantic memory refers to one's general factual knowledge about the world. For example, knowing who was the first president of the United States, how many degrees Fahrenheit is one degree Celsius, and what color combined with blue creates purple are all examples of semantic knowledge. Episodic memory, on the other hand, refers to one's specific memory about an event that most likely occurred only once. For example, remembering what you said to your friend this morning, which restaurant you went with your parents last week, and what type of cake you had on your last birthday are all likely to be episodic memories.

Non-declarative Memory In contrast, non-declarative memory refers to the knowledge that is not consciously accessible and yet can often automatically influence one's behavior. Non-declarative memory[1] includes, but is not limited to, priming, conditioning, statistical learning, habit learning, and habituation. Priming refers to how exposure to a stimulus can later facilitate a response to the same, or related, stimulus. For example, in a case of semantic priming, a flash of the word

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[1]Note that we do not exhaustively cover the subcategories of non-declarative memories but rather focus on those that are most relevant to attentional guidance. Some studies further distinguish associative and nonassociative forms of memory within non-declarative memory. Here we do not stress this distinction as to provide more specific distinctions in terms of the relationship to attention literature.

"nurse" can help a person recognize the word "doctor" faster, when compared with the word "manager." Conditioning is a type of associative learning where responses can be elicited from the systematic pairing of stimuli with rewards or punishments. The most famous example, articulated by Ivan Pavlov, is that after pairing the presence of food with the sound of a metronome, his dog eventually began to salivate in response to the metronome without the food being present (Pavlov 1927). Statistical learning can broadly refer to the ability to learn the regularities present in the environment over time. For example, when we are young, we learn to group phonemes with higher statistical co-occurrence to effectively parse discrete words from what is in fact continuous auditory input (speech; Saffran et al. 1996). Habit learning can be acquired through repeated responding to certain stimuli so as to form context-response associations in memory. If, after you dropped your phone in the water several times, you spontaneously check your phone every time you hear the sound of running water, you have learned a habit. Lastly, habituation is an adaptive, nonassociative learning process, where a response to something decreases after repetition and is not driven by sensory adaptation or motor fatigue. For example, when there is the constant loud banging noise of construction right outside your office, you might initially find it distracting, but as you get accustomed to the noise over time, your attention is less likely to be captured by it.

Memory research has long benefited from this taxonomy of separable but interacting memory systems, and here we aim to highlight how such a viewpoint might help to better understand the manner in which memory can influence attention. We consider several key memory systems in turn.

2.2 Studies of Attention and the Multiple Memory Systems Framework

2.2.1 Episodic Memory

Just one or a few events, or episodes, in the past might be sufficient for guiding attention in the present. For example, you probably will not need to search for your desk effortfully on your second day at a new job, because your attention can be directed to the spot that you worked on your first day. Interactions between episodic memory and attention are important, as they might be critical in order to incorporate rapidly learned information into ongoing processing when that information is behaviorally relevant or useful for supporting further learning. Here, we briefly highlight a few lines of work which demonstrate the impact of episodic memory on attention.[2]

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[2]Note that some of the studies discussed here contain more than a single encoding event, thus not meeting strict definitions of episodic memory which emphasize single exposure acquisition but do align with definitions which include multiple exposures (e.g., so-called "repisodic" memory (Neisser 1981)).

Selective visuospatial attention is intimately related to the location of our gaze (Corbetta and Shulman 2002; Hayhoe and Ballard 2005). It has been known for some time that eye movements can be influenced by a range of factors, including the current task or experimental context (e.g., Rothkopf et al. 2007; Yarbus 1967). Recent work has highlighted that episodic memory might also influence eye movements. For example, Ryan et al. (2007) showed that viewing behavior of previously studied or novel faces was different as early as the first fixation in the context of both the experiment and real-world exposure. The results further suggested that attention and representations stored in memory can be drawn, retrieved, and compared in an obligatory manner. Similarly, previewing of specific objects facilitates later search of that object embedded in a scene, such that studied objects were fixated sooner than unstudied ones (Chanon and Hopfinger 2008).

Additionally, numerous studies employing variants of common attention paradigms, such as visual search or change detection, have found evidence that past experience can facilitate subsequent performance. For example, Summerfield et al. (2006) had participants search for the location of targets embedded in scene images (e.g., an image of a key within an outdoor scene) repeatedly to learn the locations of the targets and then perform a visual search task for the target 1 or 2 days later. They found that the reaction time for finding targets was lower when they were in the same location as the prior session. Stokes et al. (2012), similarly, found facilitation of target search, when the target location within a specific scene was encoded 1 day earlier (Fig. 5a–c). Beyond visual search tasks, Rosen et al. (2014) found in a change blindness paradigm that participants were able to detect multiple changes after one or two exposures to a changing image. More broadly, there is evidence that a single, prior exposure to visual information, whether single objects/locations or entire scenes, can facilitate performance in tasks of attention (Castelhano and Henderson 2007; Hollingworth 2009). Taken together, the above findings highlight how only one or few experiences might be able to provide detailed information that can then be exploited in a manner which facilitates selective attention.

2.2.2 Semantic Memory

Our knowledge about the world, ranging from abstract concepts to everyday objects, contributes to the deployment of attention. Although attention is often studied in controlled laboratory conditions, it is not possible to truly remove the presence of this knowledge base. Thus, even in situations where the meaning of a word or image has no direct relevance for the task at hand, there still might be an impact on attention from semantic memory.

A hallmark of our semantic knowledge is that it specifies how different things are related to each other, and this general knowledge about associative relationships can help or hinder performance on attention tasks depending on the context (Becker and Rasmussen 2008; Davenport and Potter 2004; Neider and Zelinsky 2008; Torralba et al. 2006). For example, participants were able to identify a foreground object more
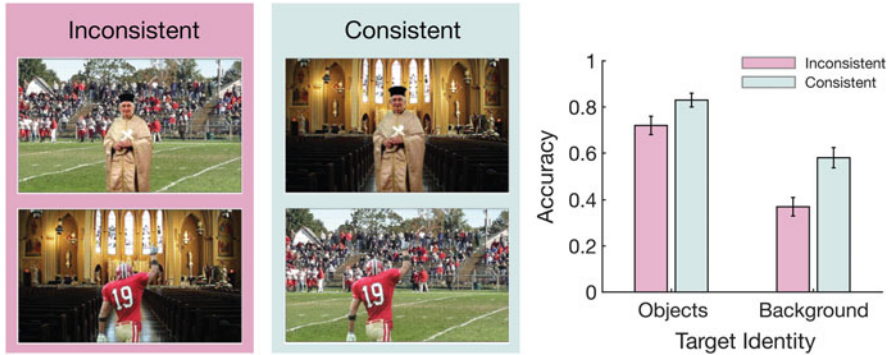
Fig. 2 Influence of semantic information on attentional guidance. In Davenport and Potter (2004), both foreground objects and the backgrounds were more likely to be reported accurately when they were consistent than when they were inconsistent

accurately when it was displayed in a semantically consistent setting (e.g., a football player in a football field) than when it was displayed in an inconsistent setting (e.g., a pope in a football field) with fewer eye movements (Davenport and Potter 2004; see Fig. 2). It has also been found that people direct their attention to the object that is semantically related to a key word held in working memory, such as attending to a motorbike helmet while maintaining the word motorbike (Moores et al. 2003; also see Seidl-Rathkopf et al. 2015). In one experiment which used a more natural viewing environment, participants searched through everyday objects on a table for a given target object adjacent to either a related object (e.g., a wallet when the credit card is the target) or an unrelated object (e.g., a marker when a pair of headphones are the target) (Mack and Eckstein 2011). Using data recorded from mobile eye-trackers, it was found that search time decreased in the condition where the target was located near a related object and participants were more likely to fixate at the related object than the rest of the nontarget objects available on the table.

Interestingly, semantic association is not inherently facilitative for attention in service of the task at hand. For example, visual search (e.g., for a bird) can be impaired in terms of accuracy and search time by the presence of a semantically related competitors (e.g., a feather) compared with when there was no such associate present in the condition when the target was absent (Belke et al. 2008; Moores et al. 2003). In another study, when participants were asked to search for a target traffic sign among several black-and-white signs and one colorful distractor sign, they were more likely to be distracted by a sign with related color of the target traffic sign (e.g., when the distractor was a red speed limit sign when the target was a red stop sign), compared to in the condition where the distractor was in an unrelated color (Olivers 2011). One study even found that saccade trajectories tended to deviate away from irrelevant, peripheral taboo words compared to neutral words (Weaver et al. 2011). Taken together, these results suggest that semantic knowledge permeates processing of visual information when everyday/real-world stimuli are being attended to.

2.2.3 Priming

Non-declarative forms of memory are also thought to be able to meaningfully guide attention. One such form of non-declarative memory, priming, generally refers to the observation that repetition of information leads to decreased processing time (e.g., as measured by decreased reaction times upon second presentation of a stimulus compared to the initial presentation). This consequence of repetition has subtle but potentially important effects on attention.

One major effect that priming might have on attention is that the fluency conferred on repeated information can influence the dynamics of attention in visual search. For example, Krueger (1970) found that people were able to find a single letter faster when embedded in real words compared to non-words and for common words compared to rare words, suggesting that repeated exposure might facilitate perceptual processing and influence the deployment of attention. Indeed this relationship is supported by the novelty bias effect (Reicher et al. 1976; Wolfe 2001) wherein participants are faster to find an unfamiliar target (e.g., inverted letter) among familiar distractors (e.g., non-inverted letters) than they are to find a familiar target among unfamiliar distractors (also compare to Flowers et al. 1981). Notably, as underscored by this particular set of examples, whether repeated information effectively attracts attention or effectively promotes attention to less fluently processed information varies depending on the exact experimental context.

Another aspect of priming that has been explored in numerous studies of visuospatial attention is the so-called "priming of pop-out" effect. Priming of pop-out refers to the phenomenon that during visual search involving a conspicuous pop-out object (e.g., a color singleton), intertrial repetition of the properties of the target and the distractor improves performance in both humans (Kristjnsson 2010; Maljkovic and Nakayama 1994, 1996) and monkeys (Bichot and Schall 1999) in an implicit manner (Maljkovic and Nakayama 2000). For example, when searching for a red singleton among green distractors, participants showed improved performance when the features of the target and distractors were repeated (Maljkovic and Nakayama 1994). This improvement is not observed when the target and distractor features are switched in-between trials; that is, switching the features between trials causes more erroneous selection (Becker and Rasmussen 2008; Leber et al. 2009; McPeek et al. 1999). Further work has suggested that this phenomenon cannot be accounted for by episodic memory retrieval (Becker 2008) and spans a range of perceptual features and experimental settings (e.g., Hillstrom 2000; Maljkovic and Nakayama 1994, 1996). Notably, the effect is observed even when the features of the target are irrelevant to the task at hand (Huang et al. 2004; Lee et al. 2009; Kristjnsson 2010) (also compare to Fecteau 2007). Priming of pop-out is an important consideration in tasks of attention and has figured into debates on, e.g., the limits of top-down influences on attentional capture (Folk and Remington 1998; Theeuwes and Burg 2011).

2.2.4 Conditioning

Conditioning, specifically classical conditioning, is another mnemonic phenomenon that might influence attention. Classical conditioning emphasizes the aspect of reinforcement in which a particular response known to be elicited from a given stimulus (unconditioned stimulus) can be associated with another arbitrary stimulus (conditioned stimulus) by, e.g., presenting the stimuli together in time. In the example of Pavlov's dog, salivation was ultimately elicited by the sound of a metronome (conditioned stimulus) because it had been consistently paired with the saliva-inducing presence of food (unconditioned stimulus) (Pavlov 1927). Although there is not much work in the attention literature which uses classical conditioning, here, we briefly highlight one study that assessed attention and novelty preference using a classical conditioning paradigm.

In this study, Snyder et al. (2008) instructed participants to view a series of polygon-shaped, solid color objects presented one at a time. Each polygon was immediately followed by either a positive image (e.g., a kitten), a negative image (e.g., a snake), or simply a grey square. Then each polygon was presented alongside another novel polygon, while participants' gaze location was recorded. For unconditioned neutral trials, looking times revealed a familiarity preference in the early time window followed by a shift of gaze toward the novel item. However, this lagged novelty preference was not found in the conditioned trials. Thus, although only a single study, the results are suggestive that learned or conditioned information can influence attentional dynamics (e.g., override a tendency to shift attention to novelty).

2.2.5 Statistical Learning

Statistical learning broadly refers to our ability to extract regularities from our environment based on the co-occurrence of multiple events, items, or features. Such a mechanism is thought to be critical for driving learning early in life (e.g., language acquisition; Saffran et al. 1996) as well as enabling specific predictions about future events (Chun and Turk-Browne 2008; Schapiro and Turk-Browne 2015).

Although very much an active area of research, there is evidence that statistical regularities of a series of events in and of itself might receive attentional priority over noisier, more randomly sequenced information (Yu and Zhao 2015; Zhao et al. 2013) and often in an implicit manner (e.g., Turk-Browne et al. 2005, 2008, 2010). For example, in one study (Zhao et al. 2013), participants were asked to view four streams of simultaneously changing symbols (Fig. 3). Critically, one stream contained repeated triplets of symbols, while other streams did not have any reliable sequential consistency. Periodically, a search array was presented with items at the locations of the streams, and participants had to perform a target discrimination task. Even though the statistical structure of the streams was not related to the target discrimination task, it was found that participants were faster to respond when the
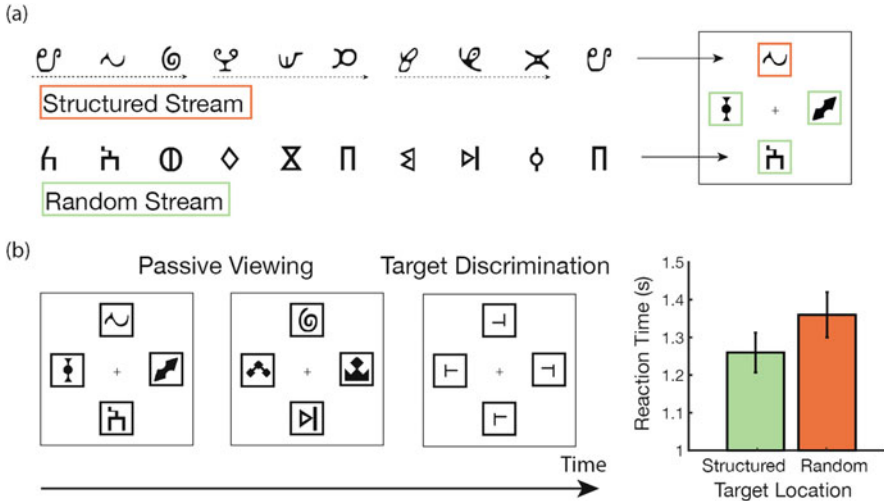
Fig. 3 Attentional guidance by statistical regularities. (**a**) In Zhao et al. (2013), four streams of symbols were shown at four fixed locations. One of the streams contained temporal regularities (the structured stream) in which triplets of symbols always appeared in the same order. The other three streams contained symbols without temporal regularities (each symbol was randomly chosen to be presented). (**b**) The four parallel streams of shapes were occasionally interrupted by a target discrimination task. Targets were discriminated faster when at the location of the structured stream than the random streams, despite participants reporting no explicit knowledge of the structure. Figure adapted with permission from Zhao et al. (2013)

target appeared at the location of the structured stream relative to the unstructured stream. Interestingly, this attentional bias toward statistical regularities was also found to extend to cases where regularities existed in other feature domains (e.g., color) or along entire feature dimensions (Zhao et al. 2013). It has also been found that this acquired bias is persistent and attention to the location can remain even when statistical regularities change location (Yu and Zhao 2015).

2.2.6 Habit Learning

Although they might take some time to acquire, habits are extremely powerful drivers of behavior. They can be instilled voluntarily such as when parents teach their children to wash their hands before eating but can also arise purely through repetition and persist beyond conscious initiation, such as how you might reach for your cell phone, even if you don't have it on you. Habit learning can be generally defined as the acquisition of the associated relationship between stimuli and responses across many repetitions.

In terms of visuospatial attention, habits can be experimentally induced by, e.g., increasing the probability of a target appearing at the same location (sometimes called "probability cuing"; Jiang 2018). For example, Shaw and Shaw (1977) asked participants to search for a target letter in one of the eight possible locations and found that recognition accuracy was higher at locations that were more likely than others to contain a target (also see, e.g., Miller 1988; Hoffmann and Kunde 1999). Interestingly, spatial probabilities governing target location can be considered an implicit attentional cue that differs from both typical explicit endogenous cues and exogenous cues (Geng and Behrmann 2005; Salovich et al. 2018). Much like the everyday habits described above, such search habits can persist even when no longer suitable for the task at hand. For example, even when the viewpoint changes and the target becomes equally likely to appear at any location, search habits based on initial probability cues can persist for hundreds of trials (Jiang and Swallow 2013). Notably, such search habits might also extend to not just learning target locations but learning about the properties of distractor items as well (also see, e.g., Goschy et al. 2014; Kelley and Yantis 2009).

2.2.7 Habituation

Habituation is a form of nonassociative implicit memory that allows people to tune out information after frequent exposure in order to attend to, e.g., more behaviorally relevant stimuli. There are many everyday examples of habituation such as when you learn to "tune out" distracting noises like the murmur of background chatter at the office.

Habituation of distraction can occur in the context of an attention paradigm and is subtly different from the case where locations frequently containing a target are prioritized (see last section). Habituation has been studied heavily in infants (e.g., Aslin 2007; Bornstein 1985), and, more generally, habituation of the orienting response in particular has been long known about (Sokolov 1963). Although there is comparatively less work in adults in studying visuospatial attention (e.g., in audition, Elliott and Cowan 2001), at least one recent line of work has explored the potential properties of habituation to distraction in the context of visuospatial attention (Turatto and Pascucci 2016; Turatto et al. 2018). Turatto et al. (2018) had participants perform a cued target discrimination task. On half of the trials, the onset of the target was immediately preceded by the sudden visual onset of a task-irrelevant distractor. Consistent with habituation, attentional capture by the distractor as measured by reaction time was diminished across the course of the session. Critically, participants were then divided into two groups. Half of the participants came back for a second session to perform the same task but without the distractors, serving as an extinction condition (i.e., the habituated orienting response to the distractor would be extinguished). The other half did not perform this second session. Then, in a final session, all of the participants performed the task with

distractor. It was found that participants assigned to the extinction condition showed a spontaneous recovery of capture to the distractor (i.e., there was no habituation of the response any longer), while the non-extinction group did not show any sign of attentional capture, suggesting the habituated response remained. Interestingly, they found that the habituation effect persisted for many days, even after only roughly 45 min of training.

3 Neural Processing of Memory and Its Role in Attention

3.1 Introduction to the Neural Processing Framework

Although the above MMS framework has been extremely fruitful for guiding systematic research on human memory, there has been an emerging trend to consider memory not as a set of discrete systems defined by phenomenology but rather as a product of one or several basic neural operations or processing modes (Henke 2010). Here, we provide an overview of this related neural processing (NP) framework and highlight some neuroscientific findings suggesting how these basic neural characteristics might be involved in the dynamics of visuospatial attention.

Although the NP and MMS frameworks are far from mutually exclusive, they do differ in terms of how to think about what particular regions of the brain do in the service of memory. For example, there is notable divergence between how the two frameworks characterize the role of the key memory structure of the hippocampus. The MMS framework was heavily informed by the finding that damage to the medial temporal lobe, and the hippocampus in particular, led to the specific loss of the ability to form episodic memories. This causal relationship was effectively extended to equating the functionality of the hippocampus to declarative, long-term (episodic) memory. However, there is growing evidence suggesting the structure's involvement in rapid associative learning with or without conscious awareness and in both long- or short-term memory.

In terms of the role of the hippocampus in non-declarative memory, there is evidence that both declarative and non-declarative learning can be impaired by hippocampal damage. Numerous studies have suggested that healthy participants (Graf and Schacter 1985; Moscovitch et al. 1986) and patients without extensive hippocampal damage (Gabrieli et al. 1997; Goshen-Gottstein et al. 2000) display intact non-declarative memory for forming arbitrary associations (e.g., priming for semantically unrelated, studied word pairs). However, this ability is impaired in patients with hippocampal damage. Shimamura and Squire (1989) found that hippocampal amnesic patients, after they were presented with two unrelated words in the same sentences (e.g., A BELL was hanging over the baby's CRADLE), showed no evidence for associative priming from those two words, such that they did not

complete the word displayed in the same context (e.g., BELL-CRA___) more than those in different context (e.g., APPLE-CRA___), while healthy participants who performed the same task did. Further, Hannula et al. (2007) found that after viewing a scene image, healthy participants showed disproportionately greater looking time toward face images associated with the scenes, despite not being able to explicitly identify the correct associated face. However, this implicit measure of associative memory was not seen in amnesic patients with hippocampal damage (also see Degonda et al. 2005; Hannula and Ranganath 2009; Henke et al. 2003a, b).

In terms of the role of the hippocampus in non-long-term memory, there is evidence for hippocampal involvement in short-term and working memory tasks and even some perceptual tasks (Ranganath and Blumenfeld 2005). For example, several studies have observed activity in the hippocampus and its neighboring medial temporal structures during performance of short-term memory tasks in both primate (Davachi and Goldman-Rakic 2001) and humans (Hannula and Ranganath 2008; Ranganath et al. 2005; Ranganath and D'Esposito 2001). Lesion studies have also found that patients with hippocampal damage display impaired visual working memory in particular settings (Olson et al. 2006a, b). Even in a perceptual discrimination task, there is evidence of hippocampal involvement under certain conditions. Aly et al. (2013) found that patients with hippocampal damage had difficulty detecting changes between similar pairs of images which differed slightly in terms of how their components related to each other (e.g., by contracting or "pinching" together one image compared to the other) (c.f., e.g., Urgolites et al. 2018) (Fig. 4).

Together, the above evidence is suggestive that the hippocampus is not exclusively linked to long-term, declarative memories but rather supports rapid encoding of flexible associations with or without conscious awareness. Indeed, when considering other brain regions, the NP framework suggests that instead of linking
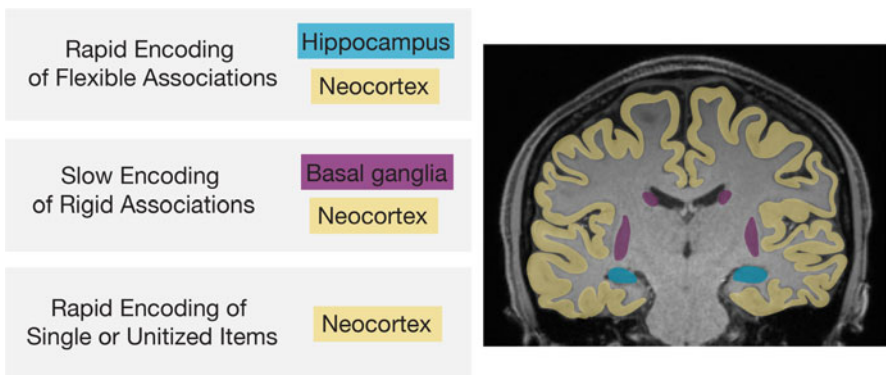

Fig. 4 A simplified depiction of the neural-based processing framework for memory. This framework does not distinguish memory based on consciousness per se but rather on different modes that can generate qualitatively distinct memories. Here we focus on three such modes: rapid encoding of flexible associations, slow encoding of rigid associations, and rapid encoding of single or unitized items. Figure adapted with permission from Henke (2010)

particular brain regions with particular memory systems per se, it instead might be preferable to consider the brain's contribution to memory in terms of its supported component operations or processing modes. Specifically, Henke (2010) distinguishes several dimensions along which memory differs and highlights the various neural regions thought to support such differences. That is, memories can be rapidly created (what type of cake was at your last birthday party) or slowly formed (what goes on at birthday parties in general). They can contain associations of a number of arbitrary items or features (remembering the name that goes with a particular person) or instead be focused on a single item (recognizing that person when you pass them in the hallway). They can be flexible and compositional (recalling either the setting of a play or the actors in it depending on your goal) or rigid and unitized (recognizing the exact costume of one character). Here, following the emphasis of the NP framework, we briefly cover three key types of memory in terms of these underlying dimensions:

Rapid Encoding of Flexible Associations The rapid encoding of flexible associations refers to remembering based on a single trial that involves many different features of an event. This processing mode depends on *the hippocampus* and the neocortex. In general, this processing mode supports the encoding of rich, multisensory events and complex spatial information after only one or few exposures. It is thought that memory might first be enabled by synaptic changes in the hippocampus and then eventually "consolidated" into the cortex through thalamically mediated communication between the hippocampus and neocortex.

Slow Encoding of Rigid Associations The slow encoding of rigid associations requires learning from a large number of trials and is thought to engage *the basal ganglia*, cerebellum, and cortex. The formation of semantic memory, habit learning, categorical learning, and procedural learning can be included in this category of memory (Foerde and Shohamy 2011). For example, stimulus-response association learning is thought to depend on the striatum, the largest component of the basal ganglia. Knowlton et al. (1996) reported that Parkinson patients with damage in the striatum were impaired at learning which stimuli consistently were followed by which outcomes without any explicit feedback.

Rapid Encoding of Single or Unitized Items The rapid encoding of single or unitized items often complements the encoding of flexible associations by the hippocampus but critically is not dependent on it and can be supported by *the cortex* alone. This mode of processing is potentially related to the behavioral priming phenomena we described in the last section as well as the subjective sense of faint familiarity in certain situations (e.g., when you run into someone that you know that you've met before, but you cannot recall where or any other details about them).

Below, we summarize a collection of empirical findings which highlight how these modes and key neural structures are involved in various manipulations of attention.

3.2 Studies of Attention and the Neural Processing Framework

3.2.1 The Hippocampus and the Rapid Encoding of Flexible Associations in Attention

As perhaps the most studied brain structure in memory, the hippocampus is thought to support associative relationships and thus plays an important role in, but not restricted to, the formation and retrieval of episodic memories where multiple aspects of an event need to be associated together (e.g., Eichenbaum et al. 2007; Moscovitch et al. 2016; Scoville and Milner 1957). In the context of memory-guided attention, for example, Summerfield et al. (2006) reported hippocampal involvement when visual search could be facilitated by remembering how a particular object was associated with a particular scene (i.e., its location) in the past. Specifically, on day one, participants were presented with scene images, some of which contained a target object at a fixed location. The next day, participants performed a visual search task where they were instructed to locate target objects embedded in scene images. Critically, the scene images were the same from the day before, and the location of the target was sometimes cued perceptually (by a white dotted frame) or via memory (the scene had contained a target object in the last session). Both perception and memory cues were always valid: they predicted the subsequent target location. As indicated by comparing reaction times to a neutral (non-cued) condition, the participants were able to orient their attention efficiently to the target when validly cued by either memory or perception. And, interestingly, performance benefited more from memory cues than perception cues. Consistent with the behavioral results, the authors also found hippocampal activation in valid vs neutral trials in memory-cued trials relative to those in perception-cued trials. Moreover, the magnitude of hippocampal activation was positively correlated with the magnitude of reaction time difference produced by the validity effect more so in memory-cued trials than in perception-cued trials, suggesting a role for hippocampally mediated memory in guiding attention in a similar manner as a perceptual cue might. Stokes et al. (2012) (Fig. 5) further found that hippocampal activity is specifically triggered by the presentation of the memory cue instead of the target (but see, e.g., Rosen et al. 2016), suggesting the important role of the hippocampus during memory-guided attention (Aly and Turk-Browne 2017).

Similar to how memory for a target object embedded in a particular scene might serve to cue attention through hippocampal involvement, it is possible that memory for targets embedded in basic visual search arrays, such as in contextual cueing paradigms, might also rely on the hippocampus. The contextual cueing effect refers to instances where visual search is facilitated when entire search arrays are repeated (see Fig. 6a, b for details) (Chun and Jiang 1998). Critically, this effect is typically not accompanied by explicit awareness of the repetition (Chun and Jiang 1999, 2003; Chun and Turk-Browne 2008; Chun 2000). Contextual cueing effects can be retained in memory immediately (e.g., Chun and Jiang 1998) and persist up to a
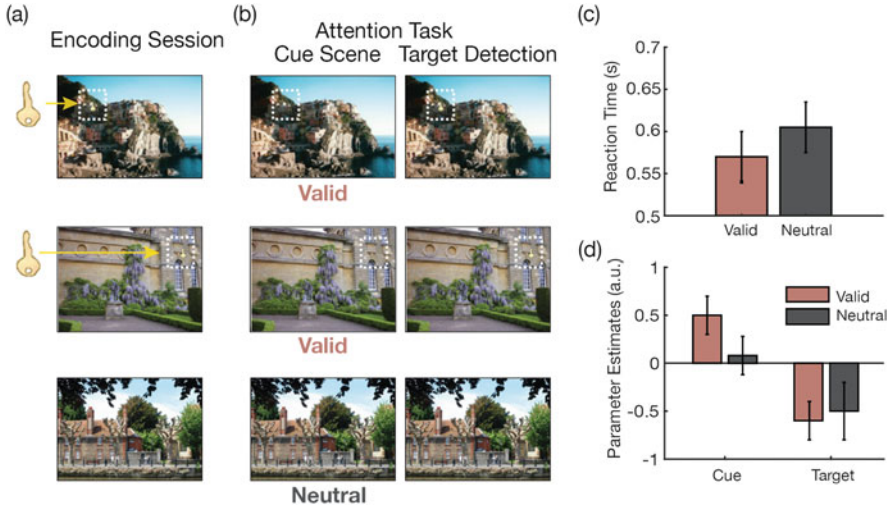
Fig. 5 Visual search and the hippocampus. (**a**) Participants were asked to search for an object (e.g., key) embedded in scenes on some trials (valid) and not others (neutral). (**b**) The following day, the same scenes were first presented as cues without targets, and then the participants searched for the target which would appear, on 50% of the trials, at the learned location. (**c**) Detection of the target was faster after valid memory-based cues than after neutral cues. (**d**) The hippocampus showed higher activation for memory-cued trials than for neutral trials during the cue period and not the target period suggesting hippocampal involvement in guiding subsequent search and not the appearance of the familiar target. Figure adapted with permission from Stokes et al. (2012)

week after acquisition (Chun and Jiang 2003). In terms of hippocampal involvement in contextual cueing, it was first reported by Chun and Phelps (1999) that patients with medial temporal lobe damage showed impaired contextual cueing, despite having intact perceptual learning. Using fMRI, Greene et al. (2007) reported that healthy adults show a relationship between hippocampal activity and repeated versus novel arrays without explicit recognition for the repeated arrays. The involvement of the hippocampus in contextual cueing has been noted in different experimental paradigms (e.g., as measured by eye movements (Neider and Zelinsky 2008) and using real-world scenes (Brockmole and Henderson 2006)).

3.2.2 Basal Ganglia and the Slow Encoding of Rigid Associations in Attention

The basal ganglia, and in particular the striatum, is crucial for creating rigid associations between, e.g., stimulus and response in memory (Packard et al. 1989), and its function is largely separable from that of the hippocampus (McDonald and White 1994). In contrast with the sizable literature regarding hippocampal involvement in attention, less is known on how striatal learning mechanisms might interact with attention. One interesting comparison between these two systems, however,

was provided by Goldfarb et al. (2016) who found dissociable contributions of hippocampal and striatal memory using fMRI during a visual search task. In a modification of the classic contextual cueing task, participants were asked to locate a rotated T-shaped target among L-shaped distractors. Unbeknownst to the participants, some trials were designed to recruit the striatum by containing probabilistic stimulus-response (SR) associations such that the color of the presented items probabilistically (80% of the time) predicted both the quadrant of the target location and the correct response (the direction of the target). Other trials were designed to recruit the hippocampus through a more traditional contextual cueing (CC) approach (arrays were repeated even though the correct responses varied). SR and CC trials were randomly interleaved with trials that did not provide mnemonic cues, allowing a comparison of different forms of memory-guided attention in the same task. The behavioral results showed general learning as reflected by decreased reaction times with greater improvement of performance on CC and SR trials versus those with no mnemonic component (Fig. 6c). CC and SR cued trials did not differ in reaction times, suggesting a similar enhancement of attention, and participants did not demonstrate any explicit awareness of either manipulation. Also, participants were not faster at locating the target when the color of the items did not match the learned SR color cue, indicating the rigid association between the target and the SR cue. The authors found that hippocampal activity predicted subsequent attention benefits indexed by reaction times on CC trials (interestingly, lower hippocampal activation related to faster subsequent RTs), while striatal activity did not, and the striatal activity predicted attention on subsequent SR trials, while the hippocampus did not (with more striatal activity related to faster subsequent RTs; Fig. 6d). Also, reflective of the difference in the putative learning time courses of the hippocampus (rapid) and basal ganglia (slow), CC-guided attention correlated more with hippocampal activity early on, while SR-guided attention correlated more with striatal activity later in the task, suggesting the slow speed of the striatal encoding relative to the hippocampus. Although awaiting replication, these results indicate the separable involvement of the hippocampus and the striatum during in a single attention task.

Another common setting for rigid stimulus-response associations is in studies of reinforcement learning and reward. Reward and the reward history of stimuli are closely linked to basal ganglia function (Schultz 2016) and are thought to have an impact on attention. Indeed, Awh et al. (2012) have argued that the top-down and bottom-up dichotomy of attention is inadequate, in part, because it does not capture the influence of selection history, including reward, on visual selection. The sub-regions of the basal ganglia, including the substantia nigra (Sato and Hikosaka 2002), caudate nucleus (Lauwereyns et al. 2002; Watanabe et al. 2003), and striatum (Hollerman et al. 1998), have been found crucial in terms of expecting rewards, even in the context of a visual attention task. For example, Leong et al. (2017) had participants perform a task in which three multi-dimensional stimuli in each trial were probabilistically associated with different reward outcomes. Only one dimension was relevant for predicting reward in a given experimental round. Within that dimension, one feature was associated with a high probability of a reward, while other features in that dimension were associated with a low probability of reward.
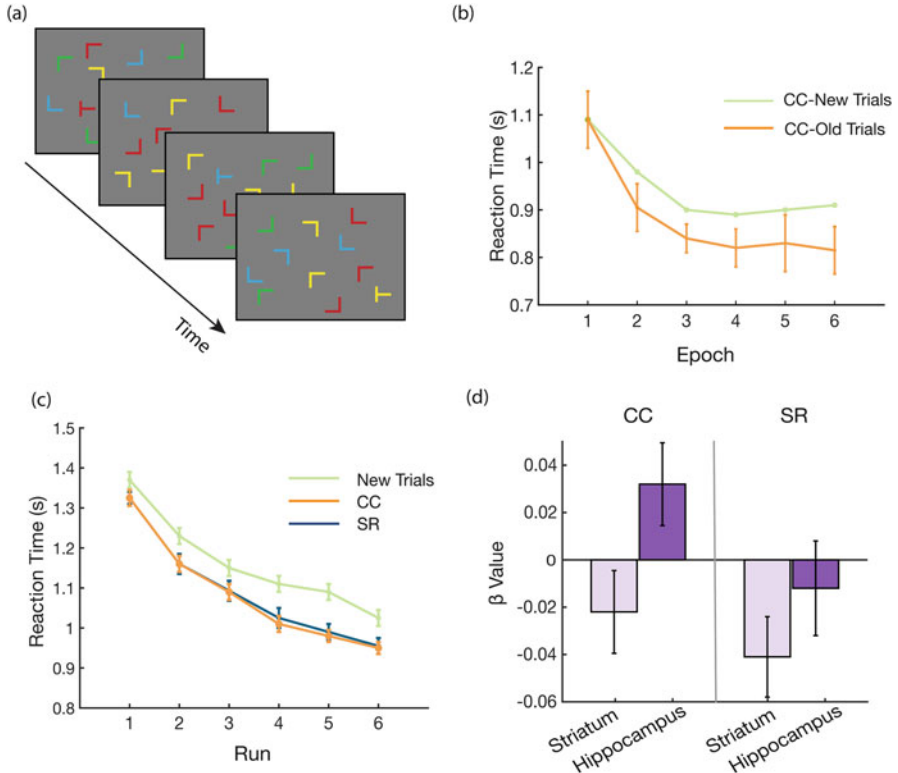
Fig. 6 Hippocampal and striatal involvement in attention. (**a**) A typical contextual cueing paradigm from Chun and Jiang (1998). Participants were asked to search for a rotated T-shaped target among L-shaped distractors. Critically, some of the trials contained configurations that were repeated multiple times throughout the experiment, while other trials contained new configurations. In the repeated trials, the targets appeared at consistent locations relative the distractors. (**b**) Search time of the target was faster in repeated configurations (CC – old trials) than in new configurations (CC – new trials), suggesting facilitated visual search. (**c**) Goldfarb et al. (2016) used a similar paradigm and found that repeated arrays using the standard contextual cueing (CC) manipulation or more specific stimulus-response (SR) repetition (see text for details) both led to reduced reaction times relative to novel configurations. (**d**) Model estimates of the relationship between trial-evoked BOLD responses and subsequent reaction times (indicative of facilitated attention). Specifically, only the hippocampus could significantly predict subsequent CC trial RTs, while only the striatum predicted subsequent SR trial RTs. Panel (**b**) adapted with permission from Chun and Jiang (1998) (also see Chun (2000)). Panels (**c**) and (**d**) adapted with permission from Goldfarb et al. (2016)

Without explicit cues, participants learned to choose the stimulus with the rewarding feature over time. Using a combination of computational modeling of learning, eye-tracking, and fMRI, it was found that allocation of attention on a trial-by-trial basis could be influenced by ongoing learning. In turn, the neural signals guiding learning ("prediction error") in the striatum were found to be influenced by attention, suggesting a bidirectional relationship between the allocation of attention and learning during decisionmaking. Further, given the tight relationship between the

oculomotor system and selective attention (Corbetta and Shulman 2002), it is worth noting that several studies of nonhuman primates have shown that particular eye movements can be linked with neuronal activity in the basal ganglia when, e.g., saccades are associated with reward (Watanabe et al. 2003; Kawagoe et al. 1998). These results, in general, provide evidence that the basal ganglia might play an important role in reward-related attentional guidance, particularly in situations where the relationship between reward and attention is relatively fixed (e.g., to a particular location or feature dimension) and slowly acquired.

3.2.3 Cortical Dynamics and the Rapid Encoding of Single or Unitized Items in Attention

The cerebral cortex encompasses a vast and functionally diverse region of the brain. The cortex is closely linked to virtually all aspects of human psychology including executive function, decisionmaking, language, motor planning, and sensory perception. As noted above, the cortex plays at least some role in all three types of processing modes. Although we will not attempt to catalog all ways in which the cortex might facilitate interactions of memory and attention, a shortlist of key dynamics has been already noted within the context of the biased competition model of selective attention. This model suggests that, at any given time, objects in the visual field compete for processing capacity (Desimone and Duncan 1995; Desimone 1996) and that the competition can be biased by, e.g., what information is most relevant for the task at hand. Notably, Desimone (1996) outlined several ways in which past experience alters cortical activity in ways which might influence attention: decreased response after repetition (attenuation), increased response after repetition (enhancement), persistent response after stimulus offset (delay activity), tuning (as in perceptual learning), and association (e.g., potentially as mediated by the hippocampus). Rather than assess all the ways in which the cortex might be involved in supporting the relationship between memory and attention, here, we highlight recent work on the first of these memory-related dynamics, repetition attenuation or a decreased response upon repetition of the same stimulus (Grill-Spector et al. 2006), and highlight how it might fit into competitive dynamics underlying attention.

One study has looked at such repetition attenuation and its potential role in guiding attention. In two fMRI experiments by Hutchinson et al. (2015), participants viewed a series of images which were organized in a triplet trial structure. That is, in each trial, the first two events contained the same image repeated twice in a row, but then the third event contained either that same image presented at the same time as a novel image or instead two novel images appearing at the same time (see examples in Fig. 7a). In line with the predictions of the biased competition framework, it was hypothesized that when old and new information was presented concurrently in the third event, an attenuated response to the repeated image should promote processing of the novel image which did not have an attenuated response. Consistent with this hypothesis, it was found that subsequent memory, a measure tightly related to
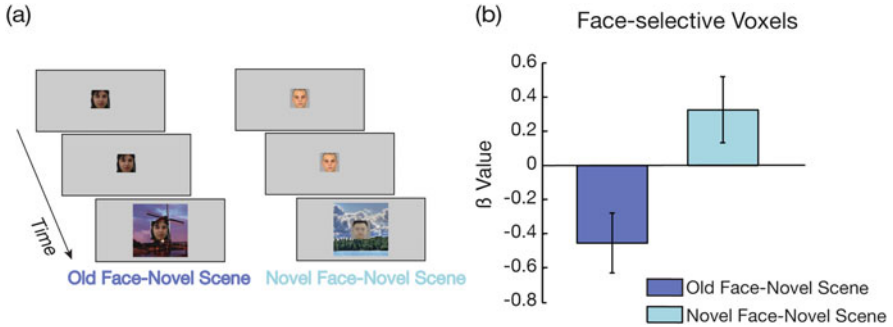
Fig. 7 Repetition attenuation and competitive processing. (**a**) Two example trials from Hutchinson et al. (2015). In the critical Old Face-Novel Scene condition, a face image was repeated twice in a row and followed by the same face embedded in a novel scene. In the control condition (Novel Face-Novel Scene), the third event contained two novel images. (**b**) Using logistic regression, it was found that there was a significant negative relationship between BOLD activity in face-selective voxels and subsequent scene memory. That is, the more the response for the repeated face was attenuated, the more likely the novel, competing scene would be processed (encoded into memory). Figure adapted with permission from Hutchinson et al. (2015)

selective attention, was greater for novel images presented with the repeated images than with other novel images, suggestive of attenuation influencing processing. Critically, a neural measure of repetition could be calculated in regions of the brain which responded preferentially to the repeated stimuli. Relating this neural measurement of activity to the repeated item to the processing of the concurrently presented novel item (as indexed by subsequent memory) was then done across trials for each participant (Fig. 7b). Across experiments, it was found that there was a reliable relationship wherein the greater the amount of attenuation for the repeated item, the more likely it was that the concurrently presented novel item would be later remembered. Although a single study, these results reflect how cortical dynamics might influence attentional processing in situations where both old and new information is present.

4 Conclusion

In this chapter, we have attempted to provide a concise overview of the ways in which different forms of memory might systematically influence selective visuo-spatial attention. Attention has been historically studied in the context of sensory systems: how attentional deployment is influenced by the current perceptual environment and how attention, in turn, impacts the sensory processing of the perceptual input. Here, we highlighted work which instead speaks to the influence of our internal mnemonic environment on attention. We have provided some evidence suggesting memory can meaningfully guide attention and, at the same time, does not fit cleanly into the prevailing dichotomy of stimulus-driven or goal-

directed attention. Memory often acts on perceptual information independent of the attentional task at hand and is defined by prior experience, not purely perceptual attributes. We highlighted two related taxonomies of human memory, the multiple memory systems framework and the neural processing framework, in an attempt to provide a broader context of the work to date on memory-guided attention, as well as provide potential guiding principles for research moving forward. The classic view of memory systems, MMS, has influenced the field of memory research and serves as useful way to catalog different empirical, particularly behavioral, findings in the attention literature. Although MMS has been extremely fruitful for exploring the different manner in which memory interacts with other cognitive domains including attention, the neural processing framework offers insight into how particular neural mechanisms of memory might be integrated with what we know about how attention is enabled by the brain.

Beyond the departure from the traditional stimulus-goal dichotomy described above, considering the role of memory has other consequences for theories of attention. For example, historic debates over early versus late attentional selection (Broadbent 1958; Pashler 1998) might be revisited by recasting various experimental factors (e.g., learned importance (Moray 1959)) in terms of their putative memory system, when possible. Also, as noted in Sect. 3, the biased competition model offers specific insight as to how various neural signatures of memory might influence competitive processing (Desimone 1996). Other neural consequences of remembering, such as cortical reinstatement (e.g., elevated activity in the visual cortex when you vividly recollect visual details; Wheeler et al. 2000), might be evaluated through the lens of competitive processing. Also of potential interest will be understanding how neural representations in structures such as the hippocampus might themselves be influenced by attention (Aly and Turk-Browne 2016a, b). More broadly, a major open theoretical question at the heart of memory-guided attention is the degree to which past experience is compartmentalized from ongoing processing (Waugh and Norman 1965; Glanzer and Cunitz 1966; Cowan 1988) versus fundamentally intertwined (e.g., Rao and Ballard 1999; Barrett and Simmons 2015; Clark 2013; Panichello et al. 2013).

Future empirical work on attention might also benefit from incorporating, or accounting for, specific elements from the field of memory research. For example, decisions concerning optimal trial sequence, condition frequencies, stimuli choice, and trial-to-trial featural overlap can be informed by many of the studies described above. Also, studies which seek to understand how past experience might influence a particular measure of attention can vary item history in a manner that is explicitly related to a specific form of memory as outlined by either the MMS or NP frameworks. Critically, as the understanding of how memory guides attention is still maturing, research of patient groups with specific damage to key memory structures or systems is vital. Patient studies contribute greatly in informing us of the necessity of a given brain region for various mnemonic and attentional processes (e.g., Chun and Phelps 1999; Hannula et al. 2007; Schapiro et al. 2014; Shimamura and Squire 1989). And new, targeted studies exploring how such groups perform on tasks of

selective attention involving memory will provide key insight as to the range and specific attributes of memory-guided attention.

In conclusion, we highlight how memory can and does meaningfully guide attention and suggest that different types of memory, whether indexed by the MMS or NP framework, can be systematically explored in experimental settings. It is not hard to find in our daily lives instances where previous experience can direct our attention and a single episode in the present might alter your attention for years in the future. Although studied in isolation for decades, the interactions between memory and attention guide much of our conscious experience, determine what we learn about our world, and, compared to either faculty alone, largely await future research.

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