

Working memory and active sampling of the environment: Medial temporal contributions

STEFAN POLLMANN^{1*} AND WERNER X. SCHNEIDER²

¹*Department of Psychology and Center for Behavioral Brain Sciences, Otto-von-Guericke-University, Magdeburg, Germany*

²*Department of Psychology and Center for Cognitive Interaction Technology, Bielefeld University, Bielefeld, Germany*

Abstract

Working memory (WM) refers to the ability to maintain and actively process information—either derived from perception or long-term memory (LTM)—for intelligent thought and action. This chapter focuses on the contributions of the temporal lobe, particularly medial temporal lobe (MTL) to WM. First, neuropsychological evidence for the involvement of MTL in WM maintenance is reviewed, arguing for a crucial role in the case of retaining complex relational bindings between memorized features. Next, MTL contributions at the level of neural mechanisms are covered—with a focus on WM encoding and maintenance, including interactions with ventral temporal cortex. Among WM use processes, we focus on active sampling of environmental information, a key input source to capacity-limited WM. MTL contributions to the bidirectional relationship between active sampling and memory are highlighted—WM control of active sampling and sampling as a way of selecting input to WM. Memory-based sampling studies relying on scene and object inspection, visual-based exploration behavior (e.g., vicarious behavior), and memory-guided visual search are reviewed. The conclusion is that MTL serves an important function in the selection of information from perception and transfer from LTM to capacity-limited WM.

LONG-TERM MEMORY, SHORT-TERM MEMORY, AND WORKING MEMORY¹

Since the beginning of psychology as an empirical science, memory has been divided into long-term and short-term memory (e.g., James, 1890). Next to the different time course, capacity limitations pose a crucial difference for both types of memories. Unlike (or contrary to) long-term memory (LTM), short-term memory (STM) is highly capacity-limited (often 3–4 chunks of information; e.g., Luck and Vogel, 1997; Cowan, 2001, see, also, Bays and Husain, 2008) and only spans brief periods of time. During recent decades, the distinction between LTM and STM has been replaced by the

distinction between LTM and working memory. In a highly influential paper, Baddeley and Hitch (1974) postulated that the abilities of short-term retention of information as well as of “manipulation” (e.g., creating a visual image) by one common system called working memory (WM). Later Baddeley (1986) defined WM as “the temporary storage of information that is being processed in any of a range of cognitive tasks” (p. 34). Viewed this way, WM is a necessary component of intelligent actions beyond automatized behavior (e.g., D’Esposito and Postle, 2015; Badre, 2020; Schneider et al., 2020). Crucially, Baddeley and Hitch (1974) offered a mechanistic decomposition of WM, based on numerous experimental studies

¹Long-Term Memory, Short-Term Memory, and Working Memory Abbreviations used in the chapter are listed at the end of the chapter before References section.

*Correspondence to: Prof. Dr. Stefan Pollmann, Department of Psychology, Otto-von-Guericke Universität, Universitätsplatz 2, Magdeburg 39106, Germany. Tel: +49-391-675-8474, Fax: +49-391-6711947. E-mail: stefan.pollmann@ovgu.de

(mostly behavioral), into different types of short-term stores (e.g., phonological loop, visuospatial sketchpad), that—together with central executive processes—build the core of WM. This basic structure of WM consisting of different stores (components) has been retained by Baddeley and his associates but revisions have been made in terms of the number of stores (e.g., adding an episodic buffer), their relationships among each other, and their relationship with LTM (e.g., [Baddeley, 2012](#); [Baddeley et al., 2020](#)). An alternative to the multicomponent model of Baddeley is offered by the “levels of accessibility” model of WM that views working memory as consisting of an activated part of LTM (e.g., [Cowan, 1995](#); [Oberauer, 2002, 2020](#)). Within this activated LTM, a severely limited set of chunks (e.g., a few objects) defines WM in the narrow sense, consisting of information that can be used for short-term retention and further cognitive processing, also including conscious accessibility. This capacity-limited part of activated LTM is called either the “focus of attention” ([Cowan, 1995](#)) or “region of direct access” ([Oberauer, 2002](#)).

WORKING MEMORY AND THE MEDIAL TEMPORAL LOBE: NEUROPSYCHOLOGICAL EVIDENCE

This chapter shows how the medial temporal lobe (MTL) might be related to WM. In contrast to its importance for LTM, the role of MTL for WM has been debated. Empirical research from more than six decades demonstrated the crucial role of MTL structures in various LTM abilities. Most well-known is the case of patient H.M., who suffered from anterograde amnesia and gradual retrograde amnesia after bilateral resection of large parts of his MTLs ([Scoville and Milner, 1957](#); [Corkin et al., 1997](#)). In contrast to his severe LTM deficits, short-term retention was normal, as long as no distracting events occurred ([Scoville and Milner, 1957](#)). Further studies of patients with MTL lesions initially reported no deficits in short-term retention of single items such as digits, words, fractals, or spatial locations ([Scoville and Milner, 1957](#); [Drachman and Ommaya, 1964](#); [Warrington, 1974](#); [Holdstock et al., 2000](#); [Warrington, 2009](#)). Thus, these studies argued for intact STM abilities. Subsequent studies, however, indicated that this conclusion was premature. For certain STM tasks—especially retaining novel and complex material or multiple items and retention over longer delays—reliable memory performance deficits emerged after MTL lesions.

WM maintenance: Amount and duration

WM deficits following MTL lesions were mostly observed for larger sets of objects. This led to a debate about whether these deficits in the retention of complex

material should be considered as a WM or rather as an LTM deficit. The concept of subspan vs supraspan memory claims that MTL is not necessary for subspan memory—e.g., in the bounds of 3–4 items of visual WM capacity ([Luck and Vogel, 1997](#))—but that it becomes necessary when the amount of information to be retained exceeds working memory storage capacity (“supraspan”) requiring storage in LTM ([Jeneson and Squire, 2011](#)). Subsequently, however, deficits in delayed matching tasks were observed even for single items that changed in one feature (color, orientation, or location; [Goodrich et al., 2019](#)). The difference from previous studies that had observed intact STM for low set sizes was that subtle differences of hue, orientation, and location and their combination had to be retained, whereas the previous studies had used clearly distinct colors or shapes as stimuli.

Patients with MTL lesions also showed deficits in retention when delay duration increased. For instance, retention of object-location pairs was normal, even for large sets (up to 6) at a delay of 1 s, replicating and extending the previous studies. Already at delays of 3–8 s, however, performance was reduced at set sizes of three or more object location pairs ([Olson et al., 2006](#); [Jeneson et al., 2012](#)). Moreover, in some tasks, visual working memory storage capacity may have been viewed too optimistically because visual working memory could be bypassed by verbal rehearsal strategies. When verbal rehearsal was made difficult, MTL was necessary even for brief retention of faces, colors, and spatial locations ([Olson et al., 2006](#)).

Whereas early studies investigated the capacity of STM in MTL patients in terms of discrete numbers of items or chunks of information—the “slot models” of WM—more recent studies also looked at the precision of the retained information using a continuous response procedure (e.g., [Bays and Husain, 2008](#)). That is, instead of asking patients for dichotomous (correct/incorrect) responses, they were asked to indicate certain features of a stimulus to be remembered within a scale of a visual dimension (e.g., orientation), allowing for the assessment of the precision of WM information. In this way, subtle deficits were already observed at very short delays. For instance, when the precision of spatial working memory for object locations was tested, patients with damage restricted to the hippocampus showed substantial displacement errors already after a 1 s memory delay for sets of 4–5 objects ([Jeneson et al., 2010](#); [Manohar et al., 2017](#)). If more WM resources are needed to represent an item with high precision—e.g., to indicate subtle feature values (e.g., precise color) after a delay—there will be fewer resources for maintaining further items. These apparent discrepancies between slot (e.g., [Luck and Vogel, 1997](#)) and resource models (e.g., [Bays and](#)

Husain, 2008) can be resolved if WM-storage capacity is assumed to be shaped by several types of capacity limitations (such as the number of object slots and number of resources consumed by features, e.g., van den Berg et al., 2014).

The key role of complex relational bindings in the case of MTL involvement in WM

Beyond short-term maintenance of simple memory contents, it is often necessary to bind features into objects or larger configurations. Current reviews on MTL contributions to these WM functions (e.g., Eichenbaum, 2011; Yonelinas, 2013; Aly and Turk-Browne, 2017; Manohar et al., 2017; Voss et al., 2017; Ryan et al., 2020) emphasize that relational binding among memory elements is a key variable, especially if binding refers to complex structures beyond simple associations.

A closer look at the errors committed in binding tasks supports the importance of the MTL for relational binding. Amnesic patients committed swap errors on small sets of objects that could be retained individually. They falsely bound objects and locations or colors and orientations, or they misplaced objects in an object-location matching task. For instance, when asked to briefly memorize a set of three objects and subsequently select an object and drag it to its location, the patients did not randomly misplace the object, but they selected the location of other objects in the sample set much more often (Pertzov et al., 2013; Zokaei et al., 2019). Likewise, when they had to remember three oriented color bars, they matched the target color with a distractor orientation more often than controls (Pertzov et al., 2013). Thus, they memorized stimulus features and locations, but not their correct binding.

Memory deficits are not only observed after focal MTL lesions, but also in dementia of the Alzheimer type (DAT) where the MTLs are affected early on (Braak et al., 1993). Consistent with a role of the MTL in feature binding, short-term retention of feature bindings was selectively impaired in patients with DAT, but not in patients with other dementia etiologies (Parra et al., 2009; Della Sala et al., 2012; Liang et al., 2016). In single case studies of a patient with selective bilateral hippocampal damage, however, intact binding of individual shapes and colors, even if presented simultaneously at separate locations, was reported (Baddeley et al., 2010), as well as intact performance for three-item sets in a location-color binding task (Allen et al., 2014). Importantly, visual features in these experiments were clearly discriminable avoiding advanced fine-grain feature representations.

The observation that MTL lesions lead to deficits in working memory for complex or demanding but not

for simple relational working-memory tasks led to the view that MTL structures contribute to working memory if high-resolution relational information is needed (Yonelinas, 2013; Manohar et al., 2017). This type of relational binding seems to be carried by MTL structures (e.g., hippocampus (HC), Ryan et al., 2020) as well as by prefrontal structures (e.g., Manohar et al., 2019).

NEURAL MECHANISMS OF WM: MTL CONTRIBUTIONS

Given the evidence on MTL contributions to certain WM tasks, the next question is which type of neural mechanisms might be involved in the key functions of short-term encoding, retention, and manipulation of WM information. How might individual neurons as well as networks of neurons realize the representation and processing of WM information? Primarily, we focus on electrophysiological studies of nonhuman and human primates as well as functional imaging studies have been used to address these questions.

MTL involvement in WM encoding

It is not trivial to distinguish between encoding and maintenance-related neural activity in working-memory tasks. A straightforward way to distinguish the two processes is to look for activation that occurs during presentation of the to-be-remembered stimulus that does not continue into the subsequent memory delay period. In this way, encoding-related MTL activity has been observed in a number of studies (e.g., Hannula and Ranganath, 2008; Libby et al., 2014; Schon et al., 2016). However, there is a debate as to whether encoding into WM is the same as or different from encoding into LTM (see Forsberg et al., 2021). Furthermore, it has been noted that the activation lasting from initial stimulus presentation to the delay period could be caused by extended encoding processes into LTM (Jonides et al., 2008; Shrager et al., 2008).

However, behavioral data suggest that encoding into WM usually occurs during a short time frame. When a mask is presented early on during the memory delay, it can disrupt visual WM consolidation. By varying the onset of the mask, the time needed to consolidate the fleeting perceptual input into visual WM can be measured. In this way, Vogel et al. (2006) showed that visual WM encoding typically completes within a few hundred milliseconds. Interestingly, encoding into visual WM can be accelerated if an LTM representation of the visual input to be consolidated already exists, i.e., if the same or a similar input has already been perceived in the past and remembered (Blalock, 2015; Xie and Zhang, 2017a). Similarly, more items could be held in visual STM if highly familiar items had to be retained,

compared with low familiar items (Xie and Zhang, 2017b). The speed of visual STM consolidation is reflected by the latency of the contralateral delay activity, an event-related potential that reflects the amount of information encoded into STM over time (Zhang and Luck, 2008). The influence of existing LTM representations on WM consolidation nicely demonstrates that WM immediately interacts with LTM, and LTM representations modulate WM representations, enabling more efficient WM maintenance. The MTL may very well play a central role in this interaction between WM and LTM. Medial temporal activation was increased for novel relative to familiar items held in working memory, whereas the reverse pattern was observed in prefrontal and posterior parietal cortices, which may suggest that the MTLs are specifically involved in the encoding and maintenance of novel stimuli in working memory, whereas prefrontal cortex may support the updating and monitoring of existing representations (Stern et al., 2001). Furthermore, functional magnetic resonance imaging (fMRI) activation strength in left HC and dorsolateral prefrontal cortex during the early part of memory delays in a delayed matching to sample (DMS) task was correlated with subsequent memory performance in a postscan memory test, indicating LTM encoding, whereas such a correlation was not observed for the late part of the delay activity (Ranganath et al., 2005). The time frame (seconds) of these delay parts was too coarse to be a direct support of the behavioral data, indicating encoding is restricted to the first few hundred milliseconds. Nevertheless, these data support the view that encoding-related activity does not span the whole delay duration.

MTL involvement in WM maintenance

In terms of the neural basis of WM maintenance, early concepts such as those of Hebb (1949) suggested that the neural substrate of LTM retention should be structural changes (e.g., synaptic changes), while STM retention should correspond to persistent neural activity for sensory stimuli that are not present anymore, an STM period that has also been called delay period (e.g., Fuster and Alexander, 1971). Therefore, this memory-based neural activity is also called persistent delay activity. This equation of short-term maintenance with persistent activation of neurons dominated neuroscience research on WM for many decades (e.g., Fuster and Alexander, 1971; Goldman-Rakic, 1995; Eichenbaum, 2011). Recently, this fundamental distinction has been questioned by claiming that even short-term retention might rely on “activity silent” neural codes (e.g., Stokes, 2015), and short-term synaptic changes might be one form of realizing WM maintenance at the neural level (e.g., Stokes et al., 2020). Furthermore, synchronous neuronal

oscillations have been observed in the MTL and may support the maintenance of WM contents (Axmacher et al., 2010; Roux and Uhlhaas, 2014) as well as executive processes (e.g., manipulation), supported by frontal and temporal structures (Lara and Wallis, 2014; Sreenivasan et al., 2014). Synchronizing the neural activity in fronto-temporal networks has even been reported to improve WM performance in elderly participants (Reinhart and Nguyen, 2019).

A detailed treatment of these different neural codes is beyond the scope of this chapter. For recent reviews, see Stokes (2015), Stokes et al. (2020), and Kamiński and Rutishauser (2020). However, even if WM contents may be preserved in an activity-silent manner, processing information within WM (e.g., for manipulating information) requires firing neurons (Trübtschek et al., 2019).

PERSISTENT DELAY ACTIVITY IN THE MTL

Persistent delay activity during DMS tasks in structures of the MTL has been reported in numerous studies in human and nonhuman primates (e.g., Eichenbaum, 2011). Intracranial recordings in humans (Axmacher et al., 2007) and monkeys (Lehky and Tanaka, 2007) revealed delay activity in perirhinal cortex. In monkeys, delay activity was reported in entorhinal, perirhinal, and parahippocampal cortices (Baylis and Rolls, 1987; Meunier et al., 1993, 1996; Suzuki et al., 1993).

In fMRI studies of the human brain, delay activity is often more prominently revealed in frontal and parietal cortices (Sreenivasan and D’Esposito, 2019). Nevertheless, fMRI studies specifically designed to investigate WM processes demonstrated delay activity in the MTL. Differential delay activity in the right hippocampus and parahippocampal gyrus was observed for correct vs incorrect matches (Pessoa et al., 2002). Hippocampal, parahippocampal, and mid-fusiform delay activity in DMS tasks with trial-unique stimuli correlated positively with successful performance in a subsequent recognition memory task (Schon et al., 2004; Nichols et al., 2006). Likewise, during a two-back WM task, hippocampal activity was observed for trial-unique stimuli, but not for familiar stimuli (Stern et al., 2001).

Another study demonstrated that novelty rather than the unique presentation was the decisive quality that led to hippocampal and parahippocampal delay activation (Schon et al., 2013). In line with this finding, brief maintenance of repeatedly presented stimuli led to delay period activity in anterior hippocampus, entorhinal cortex, and perirhinal cortex with higher magnitude of activity on correctly remembered than incorrectly remembered trials. In contrast, posterior hippocampus, parahippocampal cortex, and fusiform gyrus activity linearly increased across a 30-s

delay period, suggesting an anticipatory response (Olsen et al., 2009). In the same study, greater study-period activity in perirhinal vs entorhinal cortex contrasted with greater delay-period activity in entorhinal vs perirhinal cortex.

The human neuroimaging findings of delay activity in the MTL have been complemented by electrophysiological recordings from human MTL cells. Among the visually responsive neurons, the proportion of cells with delay activity was high in perirhinal (38%), particularly entorhinal cortex (71%) (Nakamura and Kubota, 1995). Furthermore, recording of “concept cells” in human hippocampus and amygdala was obtained in epilepsy patients with electrodes implanted for medical diagnostic purposes. Concept cells are highly selective cells that respond to images of, e.g., a specific person or a building (Quiroga et al., 2005). These cells showed persistent maintenance activity that was predictive of memory performance. While persistent activity was also recorded in the presupplementary eye field and dorsal anterior cingulate cortex, memory content could be decoded from MTL regions, but not from the medial frontal regions. Decoding in MTL was stable across encoding and maintenance phases (Kamiński et al., 2017). A related study recorded from several MTL structures found the highest number of concept cells in parahippocampal gyrus compared with entorhinal cortex, hippocampus, and amygdala (Kornblith et al., 2017) in a modified Sternberg task. Some of these cells showed the same stimulus preferences during the inter-item delays and the maintenance period between the presentation of the last item of the set and the probe, suggesting a role in the maintenance of the WM content across distracting stimulation. The strength of this stimulus-selective activation was stronger when the patients correctly remembered the probe stimulus than when they did not.

WM functions of the temporal lobe beyond MTL: Ventral temporal cortex

The MTL can be seen as the top of a visual processing hierarchy (Felleman and Van Essen, 1991). It is linked to high-level visual areas in inferior temporal cortex (IT) in the monkey brain. IT neurons display persistent activity during brief memory delays (Miyashita and Chang, 1988; Miller et al., 1993; Nakamura and Kubota, 1995). Inactivation (Fuster et al., 1981; Horel and Pytko, 1982; Horel et al., 1987) or lesions (Petrides, 2000) can impair short-term retention of visual stimuli.

Analogous to IT in monkeys, high-level visual areas involved in object processing have been characterized in human ventral temporal cortex. Among them, probably the most well-known areas are the fusiform face area

(FFA) and the parahippocampal place area, the two areas that are well known to respond to the perception of faces and scenes (Kanwisher et al., 1997; Epstein and Kanwisher, 1998). With regard to WM, maintaining faces or scenes led to persistent delay activity in the FFA and parahippocampal place area (Ranganath et al., 2004). Load-dependent delay activation in a scene WM task was observed in entorhinal, perirhinal, and parahippocampal cortices, but not in HC (Schon et al., 2016). Moreover, delay activity in the FFA for face stimuli increased with the number of faces that had to be retained (Druzgal and D’Esposito, 2003). Multivariate activation patterns of FFA delay activity correlated with hippocampal activation during memory delays, indicating functional connectivity (Gazzaley et al., 2004). Furthermore, functional connectivity between FFA and HC increased with memory load in a face WM task (Rissman et al., 2008), in agreement with the contribution of the HC to high WM demands observed in patient studies (Section “WM maintenance: Amount and duration”).

The absence of mass-univariate delay activation in a brain structure does not necessarily indicate lacking maintenance-related processes. For example, in one study no enhanced univariate delay activation was observed in a task asking for mental rotation of a spatial stimulus configuration during a brief delay (Hannula and Ranganath, 2008). However, when the same data were reanalyzed with representational similarity analysis (Kriegeskorte et al., 2008), the multivariate pattern of voxel activations in the parahippocampal cortex and posterior hippocampus turned out to be more similar between trials when the configurations to be rotated shared identical object locations (independent of object type) than when they differed. Likewise, activation patterns in perirhinal cortex were more similar when the configurations had more objects (independent of their locations) in common (Libby et al., 2014). Thus, while no overall activation differences were observed in these areas, the activation patterns within them conveyed information about the retained configurations.

These data show that the MTL communicates with object-specific visual areas in ventral temporal cortex in the maintenance of perceptual representations during brief memory delays.

WM, LTM, AND ACTIVE SAMPLING OF ENVIRONMENTAL INFORMATION: CONTRIBUTIONS FROM MTL AND BEYOND

Earlier in this chapter, we emphasized that WM is a necessary component of intelligent actions beyond automatized behavior (e.g., Oberauer, 2009; D’Esposito and Postle, 2015; Schneider et al., 2020). Without the ability

to briefly retain relevant information and manipulate it in the service of the current task, only habitual forms of actions would be possible. Given that the consciously accessible part of WM refers to a highly capacity-limited space that can retain and process only a few chunks of information simultaneously, it is a crucial question how input selection to WM works.

Active sampling for WM access by covert attention and eye movements

Where does information within capacity-limited WM come from? Given the strong capacity limitations of WM (e.g., 3–4 chunks), this is a key question. Two main lines of selected inputs have been named, namely information from activated LTM (e.g., Cowan, 1995; Oberauer, 2009) and information from the senses, e.g., from visual perception (e.g., Luck and Vogel, 1997; Schneider, 2013). At any time, the environment and LTM offer much more information than capacity-limited WM can hold. Therefore, the question of input selection to WM is central for understanding intelligent behavior (e.g., Chun et al., 2011; Schneider et al., 2020; Fig. 20.1).

Here, we focus on the selection of visual input to WM. Since the start of experimental psychology, it has been

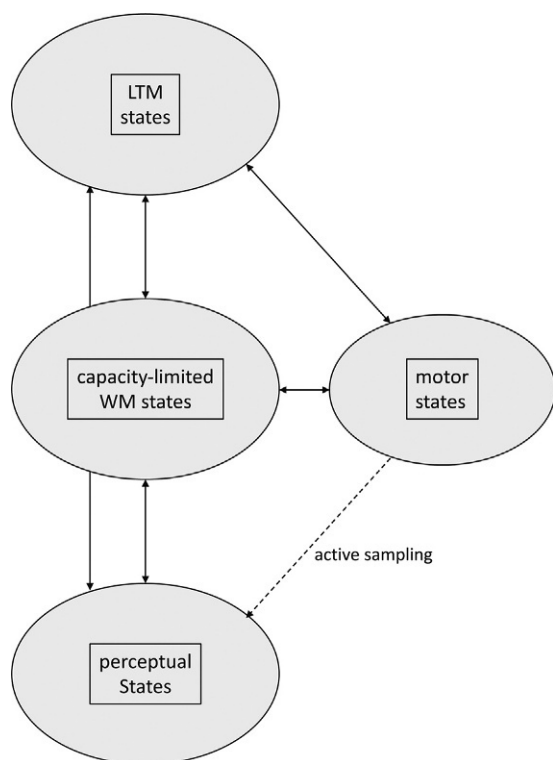


Fig. 20.1. Relationships between perceptual, WM, LTM, and motor states (for eye movement control). Note that active sampling is influenced by perceptual, WM, and LTM states as well as responsible for selecting perceptual states (dashed line).

emphasized that vision offers much more input during one eye fixation (e.g., a natural scene with multiple objects, agents, and activities) than the highly capacity-limited WM can hold. This input selection process to WM is usually identified with covert visual attention (e.g., Von Helmholtz, 1894; Sperling, 1967; Bundesen, 1990). It refers to the ability to process relevant parts of visual information within a single eye fixation with priority. Information with high priority should have a much better chance to access capacity-limited WM than low-priority information (e.g., Bundesen, 1990; Desimone and Duncan, 1995). In this chapter, we define covert attention as the ability to prioritize processing of visual information within a single eye fixation (e.g., Schneider, 2013), without committing us to a specific theory or framework (e.g., Wolfe, 1994; Desimone and Duncan, 1995; Bundesen et al., 2005).

Besides covert visual attention within an eye fixation, there is a second evident class of selection processes that determines the environmental input to WM, namely orienting of the body, the head, and the eyes in space. The eyes fixate at a given moment in the environment determines the retinal input to the brain. The primate eyes rapidly jump in a nonrandom manner from one location to the next in the form of saccadic movements (usually 3–4 saccades per second) and fixations (relatively stable eye position), forming saccade sequences (e.g., Land and Tatler, 2009). So, where we fixate at a certain moment in time with our eyes determines crucially what enters WM from vision.

Since the early days of experimental psychology, it has been known that covert attention (processing priority) can be allocated away from the fovea to relevant information sources in the periphery of the retina (e.g., Von Helmholtz, 1894; Posner, 1980). Specifically, during the preparation of an eye movement to a location in space—the saccade target selection process—perceptual processing priority by covert attention within the eye’s fixation is highest at the target location of the upcoming peripheral saccade (e.g., Kowler et al., 1995; Deubel and Schneider, 1996). In other words, selection of where to look next binds selection-for-perception within an eye fixation, that is, covert visual attention (e.g., Rizzolatti et al., 1987; Schneider, 1995; Schneider and Deubel, 2002; Deubel, 2014). A crucial implication of this coupling is that the current eye position can be considered as a “proxy” for the preceding covert spatial attention allocation. If we know by eye tracking where humans or monkeys looked within a scene, we can conclude that these fixation locations must also have been covertly attended before, namely prior to making the eye movement to this location.

The term “active sampling” indicates that covert attention and eye movements for selective processing

of the environment are not only driven by salient features of the environment (e.g., a moving object) but also massively guided by intentions (e.g., based on the current task) and expectations about the environment (e.g., Posner, 1980; Land and Tatler, 2009; Awh et al., 2012; Gottlieb and Oudeyer, 2018). Although studies of active sampling have largely focused on the attention and decision networks of the brain, it is quite likely that the MTL as a comparator of sensory input and LTM contents may have an important role in active sampling. Below we review evidence for this claim.

To summarize, active sampling of environmental information via the visual sense implies saccadic eye movements to informative locations in space (allocation of the fovea) as well as covert attentional priority of processing within an eye fixation. The joint result of sampling processes (saccades and selective covert processing within a fixation) determines which visual information from the environment might enter WM and therefore build the basis of intelligent thought and action. It is still an open question whether selection by these two types of sampling processes is sufficient for access and encoding into WM/STM (e.g., Bundesen, 1990; Hollingworth, 2004) or whether an additional selection process beyond eye and attentional selection is necessary for true WM encoding that may involve processes such as short-term consolidation (e.g., Schneider, 2013).

LTM, working memory, and active sampling: Evidence for MTL contributions from scene and object inspection studies

Information in capacity-limited WM has to come either from memory or from the senses. The amount of potential information in the current environment usually exceeds the amount of information that we can perceive and encode in memory from a single glance (e.g., eye fixation). As reviewed, covert attention and eye movements as means of active sampling are crucial for this selection function. On the other hand, memory contents are also involved in shaping the selective sampling of the environment (e.g., Kuhl and Chun, 2014; Voss et al., 2017). Note that we talk about the interaction of sampling and memory in general. The role of WM in relation to active sampling will be discussed later. Based on eye-movement studies in patients with MTL lesions, it has been proposed that visual exploration—in our terms, active sampling—is a memory-formation process linked to medial temporal function in a bidirectional way, so that, in an iterative fashion, sampling behavior determines the content available for memory formation and memories may in turn optimize sampling (Voss et al., 2017; Ryan et al., 2020).

The importance of sampling processes increases with the complexity of tasks and the complexity of the environment. As we have seen in Section “Neural mechanisms of WM: MTL contributions,” encoding and retaining complex stimulus arrangements lead to hippocampal involvement. This may be a first hint that the hippocampus is involved in active sampling (Voss et al., 2017). Relatedly, subsequent memory effects, i.e., the prediction of retrieval success by neural activity during encoding, in the HC increase with the complexity of the memorized material (Kim, 2011). This is typically explained by the associative complexity of the stimuli, but it may also be caused by more complex visual exploration during encoding (Voss et al., 2017).

Active sampling of the environment with eye movements supports memory formation, as has been demonstrated in a number of paradigms (Loftus, 1972; Henderson et al., 2005; Johansson and Johansson, 2014; Olsen et al., 2014). Effects of sampling on memory and vice versa can be seen both during learning of a new image and during inspection of a previously learned image. During learning, higher fixation counts for objects later remembered than for forgotten objects that were observed in normal controls, but not in a patient with developmental amnesia associated with hippocampal volume loss (Olsen et al., 2016).

In healthy observers, fixation patterns for successfully remembered scenes are often more similar to the patterns at encoding than for forgotten scenes (Damiano and Walther, 2019). Moreover, when a previously learned image is looked at frequently, a repetition effect is seen, in that fewer fixations suffice to explore repeatedly presented faces or scenes (Ryan et al., 2000; Damiano and Walther, 2019). These differences between remembered and forgotten images are often seen early in the active sampling, suggesting that successful encoding leads to fast and efficient eye movements during the second viewing of the same scene (Damiano and Walther, 2019).

Beyond quantitative differences in the number of fixations, hippocampal lesions also lead to more random fixation patterns during encoding. An arrangement of arbitrary “nonsense” shapes was presented for 16s in one study, to be remembered briefly in order to reconstruct its spatial arrangement after a delay of 4s (Lucas et al., 2019). Control participants showed a relation between the entropy (nonrandomness) of gaze paths during learning and later reconstruction errors. The less random the gaze tracks were during learning, the fewer errors were committed during reconstruction. In patients with hippocampal lesions, gaze paths were more random than in controls, and patients made more errors during pattern reconstruction, particularly swap errors, where the overall pattern was retained, but the locations of individual shapes were swapped. Thus, the hippocampus

contributes to the effectiveness of active sampling during encoding of novel visual information, thereby improving visuospatial relational memory.

The influence of memory on sampling has further been probed by studying eye movements in scenes that have been changed after repeated presentations. These scene-specific changes led to increased visual exploration of the altered scene regions (e.g., longer gaze durations)—regardless of conscious awareness—in healthy observers. This pattern was also observed in patients with hippocampal lesions when a delay of about 2 s separated the original and the altered scenes (Ryan and Cohen, 2004). In contrast, the increased exploration of the altered scenes was no longer observed when they were presented 1–3 min after the original scenes (Ryan et al., 2000). This lack of a relational manipulation effect in the patients occurred in spite of a normal repetition effect, i.e., fewer fixations for repeated images.

What can we learn from the neural activation patterns accompanying active sampling? In a face judgment task, the number of face fixations was correlated with the bilateral activation of the hippocampi as well as of the FFA (Liu et al., 2017). However, while this correlation was observed for novel and repeated faces alike in the FFA, it was observed only for novel faces in the hippocampus. In fact, when more fixations were made during the first presentation of a face, repeated presentation of the same face was accompanied by stronger repetition suppression of hippocampal activity. This repetition suppression was not observed in the FFA. Thus, while the FFA activation appeared to mirror perceptual processes, the hippocampus seemed to represent memory processes, most likely the encoding of novel views, possibly including the on-the-fly set of bindings between features of the novel stimulus. The correlation of fixation numbers and activation strength was replicated in a study with scene stimuli, where regions in posterior HC and the PPA showed bilaterally stronger activation for free viewing than fixed viewing (Liu et al., 2020). In addition, functional connectivity between both regions was higher under free viewing. Thus, the communication between high-level visual cortices and the MTLs is modulated by eye movements.

LTM, working memory, and active sampling: Evidence for MTL contributions from scene and object studies with strong cognitive control requirements

The studies on inspections of scenes and objects reviewed in the last section demonstrate clear interaction between memory on the one hand and attention and eye movements on the other hand. Now, we move on with active sampling studies that involve strong executive control processes, sometimes also called cognitive

control (e.g., Badre, 2020) in relation to MTL. In these studies, scenes and objects are inspected, recognized, and compared for changes, in addition an active model of scenes and objects (sometimes called a situation model, e.g., Schneider et al., 2020, or a cognitive map, e.g., Behrens et al., 2018) is constructed ad hoc and used for guiding sampling via eye movements. These cognitive control operations likely involve the capacity-limited space of working memory (e.g., Schneider et al., 2020). Therefore, this section will concentrate more closely on MTL contributions to the relationship of working memory, cognitive control, and active sampling.

Active exploration behavior in rodents is often studied in tasks in which memory contents have to be combined with cognitive control operations such as scene or object image construction and use. When the animals have to make a choice, e.g., which direction to take in a labyrinth, they often make back-and-forth eye movements into the alternative directions (Muenzinger, 1938; Tolman, 1938; Redish, 2016). This “vicarious” behavior was much reduced after hippocampal lesions (Hu and Amsel, 1995). It was further found that the activity of location-sensitive hippocampal neurons was most predictive of future visited locations during these episodes of vicarious trial and error. An analogous behavior to vicarious trial and error in humans may be the spontaneous revisitation phenomenon, which has been described in an object-memory paradigm. In this paradigm, objects were arranged in a regular grid. The display was covered by a semitransparent mask, which had only a small window through which the objects could be viewed clearly. Object memory was improved when participants could actively move this window to look at the objects compared to when the same path of the window was presented to the next participant who could just passively watch the contents of the window. Importantly, the advantage for active sampling was not observed after hippocampal damage (Voss et al., 2011b).

The exploration sequences frequently contained spontaneous revisitations of previously looked-at objects, which might be analogous to the vicarious trial and error behavior in rodents. Spontaneous revisitations were defined as moving the window back to a previously watched object after at least one other object had been looked at in between. Amnesic patients with MTL lesions including the hippocampus showed less of these revisitations. If revisitations occurred, they included not more than the last three objects, compared to longer path lengths in controls—an indication of a WM storage limitation. Whereas revisited objects were memorized better in controls, no such improvement was observed in amnesics (Voss et al., 2011a). Functional neuroimaging in young healthy controls using the same paradigm showed increased activation in left anterior hippocampus, left

medial prefrontal cortex, and right cerebellum during active revisitations. These studies show quite clearly that the MTL is involved in the active processing of perceived and memorized events in the short time frame of working memory, thereby improving the quality of encoding.

In the above studies, it is quite likely that item revisitations were used to compare perceptual input to LTM content—a function that posits WM on the interface between perception and LTM (e.g., [Schneider et al., 2020](#)). In a related study, revisitations of already fixated objects occurred even when LTM demands were virtually absent ([Voss and Cohen, 2017](#)), but WM demands were quite likely. In this task, odd-one-out targets had to be found among perceptually very similar objects, so that perceptual features had to be kept in memory from one fixation to the next. In other words, referring to LTM contents was not helpful in this task, because the correct response depends on spotting minute featural differences of items just perceived. Even in this working-memory task—fixation contents just sampled had to be retained in a range of seconds—hippocampal activation accompanied revisitations, along with dorsal medial frontal and cerebellar activations. Interestingly, the medial frontal activation overlapped with the locations of two eye movement control regions, the supplementary and pre-supplementary eye fields. The authors suggested that medial prefrontal cortex and hippocampus cooperate for decisions on ongoing behavior in that the medial prefrontal cortex rapidly generates multiple possible action plans—cognitive control operations—that cue hippocampal memory retrieval to simulate potential action outcomes ([Wang et al., 2015](#)).

In a model-based fMRI study, involvement of the hippocampus in exploratory decisions was further investigated ([Wang and Voss, 2014](#)). It was again found that hippocampal activation was associated with active exploratory decisions rather than passive information intake. Furthermore, hippocampal activation occurred when the current trial offered new task-related information. In contrast, striatal activation was associated with cumulative information across the experiment. It is noteworthy that the decision-related activation of the hippocampus was closely linked to eye movement patterns preceding exploratory decisions. Along with the hippocampal activation, exploratory decisions were accompanied by activations in superior and inferior frontopolar cortex. Frontopolar cortex has been implicated in exploratory behavior in a number of different paradigms, both in humans and in nonhuman primates ([Daw et al., 2006](#); [Boschin et al., 2015](#); [Mansouri et al., 2015](#); [Pollmann, 2016](#)). It appears to be essential for self-initiated learning and exploration ([Boschin et al., 2015](#); [Pollmann, 2016](#); [Ort et al., 2019](#)). In the context of visual search, a prime form of active sampling, joint frontopolar cortex, and

hippocampal activation was observed during self-initiated exploratory changes of attention between visual dimensions ([Pollmann et al., 2000](#)). In contrast to self-initiated exploratory changes of attention, rule-based changes typically do not lead to frontopolar activation ([Dove et al., 2000](#); [Ort et al., 2019](#); [Worringer et al., 2019](#)), nor are they impaired by frontopolar lesions ([Boschin et al., 2015](#); [Mansouri et al., 2015](#)). The contribution of MTL structures to exploratory behavior fits well with the well-known role of the MTL in novelty processing.

Relationships of MTL with inferior temporal cortex in active sampling

In Section “[WM functions of the temporal lobe beyond MTL: Ventral temporal cortex](#),” we have reviewed the commonalities and differences of MTL and ventral temporal structures such as the FFA and PPA in terms of WM-related delay activity. Both MTL and ventral temporal cortex are also intimately linked to active sampling via eye movements. For instance, looking at a face or a house leads to category-specific gaze paths. Retracing such face- or house-specific gaze paths by following a sequence of dots on a uniform background led to fMRI-activation patterns in the FFA and PPA which could be discriminated via classification analysis ([Wang et al., 2019](#)). In other words, just following a typical face-related or house-related gaze path, in the absence of a face or house image, differentially activated high-level visual areas that are well-known to be activated by images of faces, respectively houses. Thus, these areas appear to contain category-specific object representations including information about typical gaze sequences used for looking at them.

The PPA is particularly strongly activated by images of houses or scenes. Free viewing of scenes, as compared to forced central fixation, led to enhanced activation of the PPA and the HC as well as enhanced functional connectivity between these two structures ([Liu et al., 2020](#)). These activation changes went along with improved subsequent recognition memory. Moreover, activation clusters modulated by number of fixations overlapped with clusters modulated by subsequent memory. These data suggest that MTL and ventral temporal structures are commonly involved in visual memory. It has even been suggested that fixations may be the information units on which HC binding processes operate to form new memories ([Liu et al., 2020](#)).

The entorhinal cortex contains grid cells that respond in an allocentric triangular grid to the spatial location of the animal ([Hafting et al., 2005](#)). This grid-like representation has also been observed with respect to the direction of human eye movements, in the sense that eye movements aligned with the grid elicit stronger fMRI signals

than eye movements that are not aligned with the grid (Killian et al., 2015; Julian et al., 2018; Nau et al., 2018). Given the evidence that EC may serve as a visual WM buffer, it appears quite likely that visuospatial WM contents may also be represented in a grid-like fashion. However, this needs to be investigated in future research.

WM, LTM, and active sampling for visual search: Evidence for MTL contributions from contextual cueing studies

Visual search is often guided by memory. We have already reported evidence that MTL is involved in the guidance of eye movements during active sampling, often without conscious control. A prominent experimental paradigm for studying such processes is contextual cueing (Chun and Jiang, 1998). It refers to memory-guided visual search by incidentally and often implicitly learned information. In this paradigm, search performance is compared between repeatedly presented and newly generated displays. Repeated and new displays are randomly intermixed, and participants are not informed about the repetition. They are also unaware that memory is tested, as they are instructed only to search for a target item among distractors. Nevertheless, after a number of repetitions, search times become faster for the repeated than for the new displays, accompanied by more efficient gaze paths (Peterson and Kramer, 2001; Tseng and Li, 2004; Brockmole and Henderson, 2006; Manginelli and Pollmann, 2009). Postexperimental tests typically show no explicit memory for the repeated displays, although the reliability of these measures is under debate (Colagiuri and Livesey, 2016; Vadillo et al., 2016). However, in those cases where explicit memory could be shown for individual displays, it did not lead to increased contextual cueing (Geyer et al., 2012; Spaak and de Lange, 2020). Thus, contextual cueing appears to be an example of nonconscious (nonreportable) search guidance by incidentally learned spatial configurations. In line with this, it was initially reported that contextual cueing does not depend on visual working-memory capacity (Vickery et al., 2010). In this study, the search experiment was carried out during the delay of a visual DMS task. When the repeated displays were presented again in a subsequent test phase without working-memory load, the typical search time advantage for repeated displays was observed. In subsequent studies, however, it became apparent that the search time advantage for repeated displays was lost when—after initial training with or without WM load—displays had to be searched under working-memory load (Manginelli et al., 2012, 2013; Annac et al., 2013; Travis et al., 2013).

Thus, learning must be distinguished from the expression of learning (Frensch et al., 1998), i.e., the utilization

of the learned patterns for memory-guided search. While the former can occur without working-memory demands in the sense of active processing within the capacity-limited part, the latter depends on working-memory capacity. More specifically, revealing contextual cueing effects depends on visuospatial working memory but not on nonspatial visual working-memory load (Manginelli et al., 2012, 2013). Furthermore, the dependence on working memory of memory-guided search, but not initial learning, in the contextual cueing paradigm is in good agreement with reports showing that attending to the repeated configurations is not necessary for learning, but it is necessary for later memory-guided search (Jiang and Leung, 2005).

What is the contribution of temporal lobe structures to contextual cueing? An initial patient study failed to report a contextual cueing effect (i.e., the search time advantage for repeated displays) in patients with MTL lesions (Chun and Phelps, 1999). Two of the four patients of this study had suffered from anoxic episodes, which were expected to have led to hippocampal damage, confirmed by MR in one of them. The other two patients had more widespread lesions of the MTL and neighboring structures caused by encephalitis. This contrasted with another study that investigated patients with isolated hippocampal damage (Manns and Squire, 2001). Their patients had lesions restricted to the hippocampal region (CA fields, dentate gyrus, and subicular complex), and in 2 of the 5 patients extending into the parahippocampal gyrus. In contrast to the patients of Chun and Phelps, they showed normal contextual cueing. Manns and Squire also tested a group of patients with extensive MTL lesions due to encephalitis and replicated the loss of contextual cueing in these patients. These data show that the MTL is necessary for contextual cueing to occur. The contribution of the hippocampus, in contrast, remains unclear. The intact contextual cueing effect observed after selective hippocampal lesions may suggest that the hippocampus is not crucial for contextual cueing. However, Manns and Squire noted that the hippocampal lesions of their patients led to MR-defined volume loss ranging from 22% to 46%, so it cannot be completely ruled out that residual hippocampal function may have contributed to the successful contextual cueing.

Recently, a study in healthy participants reported a positive correlation between hippocampal volume and the size of the contextual cueing effect (Rosero et al., 2019). However, there were also significant correlations between volume and contextual cueing size for the entorhinal cortex and the parahippocampal gyrus. Unfortunately, no analyses were reported that tried to disambiguate the contribution of these MTL structures to contextual cueing. Therefore, this study also yielded no evidence for a selective role of the hippocampus in contextual cueing.

The contribution of MTL structures to contextual cueing has also been investigated with functional MRI. Consistently, stronger MTL activation was observed for new relative to repeated displays following learning (Greene et al., 2007; Preston and Gabrieli, 2008; Geyer et al., 2012; Giesbrecht et al., 2013; Kasper et al., 2015). Activations related to the strength of contextual cueing were observed in the left entorhinal and perirhinal cortices (Preston and Gabrieli, 2008; Geyer et al., 2012).

Two studies took advantage of the fact that participants can sometimes explicitly remember some search displays and compared explicitly learned to implicitly learned displays. Displays with higher hit rates in an explicit recognition task led to stronger activations in the hippocampus (Preston and Gabrieli, 2008). Likewise, explicitly remembered displays led to increased activation in anterior parahippocampal cortex relative to new displays after learning, whereas decreased activation was observed for implicitly learned displays (Geyer et al., 2012). No differential activation for repeated vs new displays was observed in the early learning phase in this study. The lack of differential activation early in learning does not necessarily mean that MTL structures do not contribute to context learning, since they could just be comparably active for new and repeated displays. In fact, before learning, all displays are novel and the hippocampus is well known to respond to novelty (Kumaran and Maguire, 2007, 2009). Furthermore, the strength of individual participants' hippocampal activation early in training correlated with individual contextual cueing strength at the end of the experiment in one study (Giesbrecht et al., 2013). Perhaps the strongest evidence for a contribution of the hippocampus to contextual cueing comes from a study that compared the trial-wise activation of the hippocampus with the search time for the next repetition of the same display (Goldfarb et al., 2016). It was found that hippocampal activation significantly predicted search time facilitation, particularly in the early part of the experiment. Lower hippocampal activation predicted shorter search time for the next display repetition. This effect was selective—for a simple S-R learning task it did not predict performance. In contrast, the latter task, but not contextual cueing, could be predicted by striatal activation.

There are a few reports of increased activation for repeated displays, based on behavioral measures. Stronger HC activation for repeated displays was reported for trials with fast responses (Greene et al., 2007). Similarly, reduced number of fixations over repeated presentation of the same displays was correlated with increasing HC activation (Manelis and Reder, 2012). However, it was not reported whether this correlation was stronger for repeated than for novel displays. Further research needs to show if there is a consistent increase of

hippocampal activation with increasing search efficiency, and how its topography relates to the location of repetition suppression.

To summarize, these imaging studies agree in that more medial temporal activation was observed early in learning, subsequently declining for repeated displays, i.e., a pattern of repetition suppression. The reverse, increasing activation was only observed for explicitly remembered configurations in later phases of the task (Preston and Gabrieli, 2008; Geyer et al., 2012). Of course, these correlative findings allow no causal interpretation. However, the consistent finding of repetition suppression may suggest that we primarily see reduced hippocampal involvement in the case of accurate implicit learning of a configuration. This is in line with the view that the MTL may be particularly engaged when novel, complex stimuli implying demanding relational bindings are encountered, for which no established LTM representations exist (Ranganath, 2006) and rapid ad hoc encoding is asked for (Henke, 2010).

In line with this WM involvement, the stronger hippocampal activation for novel stimuli would be predicted by the model of Lisman and Grace (2005), who posited a role for the hippocampus as a comparator between sensory input and memory—a classical WM function. According to this model, when the hippocampus detects new information, not yet stored in LTM, an HC-ventral tegmental loop becomes activated, leading to HC-dopamine release, in turn enhancing long-term potentiation and learning.

In contrast, increased MTL involvement was observed after configurations had been explicitly learned. Thus, the same anatomical structures appear to serve two distinct processes underlying the expression of implicitly and explicitly learned configurations.

While the exact processes underlying these differences are still unknown, similar repetition suppression vs repetition enhancement patterns have been reported in many brain areas. A recent meta-analysis (Kim, 2017) concluded that the brain topography of repetition-suppression effects is strikingly similar to that of subsequent memory effects, suggesting that repetition suppression may be due to reduced memory encoding, which would fit our interpretation of the contribution of MTL to implicit configuration learning. Repetition enhancement, in contrast, was observed in regions that also showed retrieval success effects, thereby suggesting that repetition enhancement may be related to explicit retrieval processes. Thus, it may be that the MTL primarily supports encoding or retrieval processes depending on the implicit or explicit nature of contextual learning, a hypothesis that needs confirmation by future studies.

The MTL decisively contributes to contextual cueing, as shown by the absence of cueing in patients with extensive MTL damage. Patient studies give us no indication

of the stage at which contextual cueing is deficient in the patients (e.g., [Sisk et al., 2019](#)). If we consider the imaging studies, however, we would conclude that initial learning rather than expression of learning may be deficient in the patients. Until now, no “reversible lesion” studies could be carried out to address this question, because the MTL is out of the reach of transcranial magnetic stimulation. In the future, transcranial focused ultrasound stimulation may be used to investigate this question by selectively disrupting MTL activity during learning or subsequent test phases.

Whereas contextual cueing is typically investigated with semantically meaningless, symbolic search displays like the T-among-L search, search facilitation for repeated target-distractor configurations can also be observed in naturalistic scenes ([Brockmole and Henderson, 2006](#); [Pollmann et al., 2020](#)). In such a naturalistic contextual cueing task, using scenes instead of spatial configurations, MTL activation was modulated by the explicit knowledge of scene repetition. Explicit knowledge, induced per instruction, led to increased activation in several MTL areas, whereas without this instruction, activation was reduced ([Westerberg et al., 2011](#)), analogous to the findings for contextual cueing in symbolic search displays ([Geyer et al., 2012](#)). In a similar task, amnesic patients were at chance when detecting location changes of objects across repetitions of complex scenes ([Hannula et al., 2006](#)). Therefore, it is likely that MTL dysfunction will also have implications for contextual cueing in everyday life.

In summary, intact MTLs appear to be necessary for contextual cueing. It is still less well known which MTL structures are vital for context learning and later memory-guided search in the contextual cueing paradigm.

WORKING MEMORY AND ACTIVE SAMPLING: ROLE OF MTL

The studies reviewed so far demonstrate that the MTL is involved in guiding active sampling in the service of efficient memory encoding on the one hand and in guiding the efficient exploration of already encountered images on the other hand. In line with earlier reviews (e.g., [Aly and Turk-Browne, 2017](#); [Voss et al., 2017](#); [Ryan et al., 2020](#)), we emphasize the role of memory-based knowledge for the control of active sampling by eye movements (e.g., knowledge about objects and their locations within a current scene; e.g., [Torralba et al., 2006](#); [Chun et al., 2011](#)) and conclude that MTL structures are crucially involved in certain forms of sampling. However, should we consider these as working-memory processes? Traditionally, WM has been defined as an STM store whose contents are manipulated by a central executive ([Baddeley and Hitch, 1974](#)). Executive processes, nowadays more often called cognitive control operations

(e.g., [Badre, 2020](#)), become necessary if the task goals cannot be achieved by relying on habit-based thought and action, by just retrieving precompiled pieces of LTM contents for its control ([Norman and Shallice, 1986](#); [Schneider et al., 2020](#)). In these situations, cognitive control should require the computational space of capacity-limited WM (e.g., [Badre, 2020](#); [Schneider et al., 2020](#)). However, the eye movement patterns during scene and object viewing (Sections “[LTM, working memory, and active sampling: Evidence for MTL contributions from scene and object inspection studies](#),” “[LTM, working memory, and active sampling: Evidence for MTL contributions from scene and object studies with strong cognitive control requirements](#),” and “[Relationships of MTL with inferior temporal cortex in active sampling](#)”), modulated by the MTL, will largely be carried out without conscious control. Humans and other primates can make several saccadic eye movements per second without noticing them (e.g., [Deubel et al., 1999](#)). Nevertheless, even without conscious control, eye movements, e.g., the refixations between aspects of a scene, help us deal with the capacity limits imposed by visual WM capacity, and this process is more efficient with an intact MTL. Models that formalize WM as an activated part of LTM posit a set of LTM contents that become activated by their association with a current situation. Out of this—theoretically unlimited—set a severely limited (3–4 items) set is in a consciously accessible state (Section “[Long-term memory, short-term memory, and working memory](#)”). We posit that the MTL is crucially involved in selecting which items out of the large set of activated LTM contents enter the capacity-limited WM region by comparing the sensory input provided by a fixation with the memory items from activated LTM ([Fig. 20.2](#)).

This suggestion is in line with the proposed comparator function of the HC and explains why novelty is particularly processed by the MTL, because novel items or changes in the environment are particularly informative for the individual. Novelty detection requires a mismatch with stored LTM contents. Processes of pattern completion and pattern separation, subserved by the MTL ([Hunsaker and Kesner, 2013](#)), are particularly suited to find structure in complex environments, such as the sensory input provided by a fixation or a sequence of fixations. This may explain why the MTL contributes crucially to the short-term maintenance of complex inter-related configurations. Thus, the debate whether the MTL is involved in WM or only in LTM may not be fruitful—the MTL compares sensory input derived from active sampling with selected contents activated in LTM, to influence the contents that have direct access to consciousness (e.g., that can be reported). This suggestion also yields a solution to the subspan vs supraspan debate—the MTL accesses a large number of activated

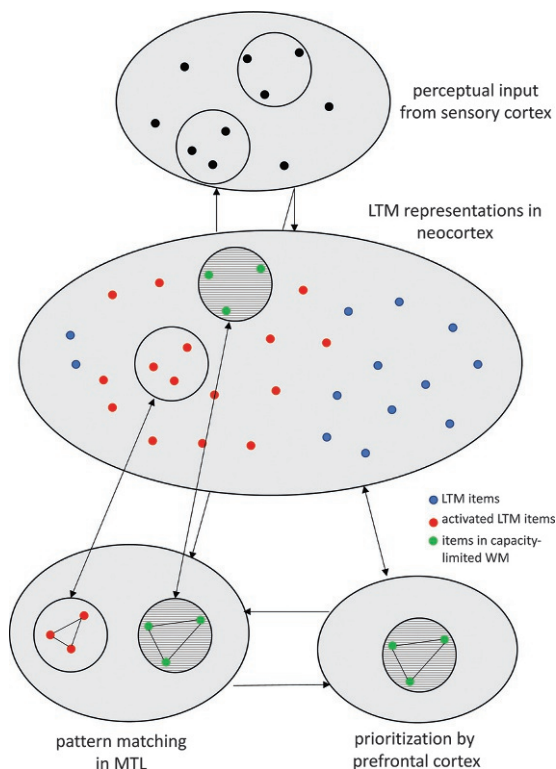


Fig. 20.2. MTL supports the selection of task-relevant information into capacity-limited WM. Visual input (from a fixation or sequence of fixations) activates LTM representations in neocortex. The MTL compares perceptual input to activated LTM representation. Via pattern separation and pattern completion processes, it extracts relational patterns from the activated LTM representations. In interaction with other cortical areas, notably prefrontal cortex which may contain a search template, one relational pattern is selected to be attentively processed in capacity-limited WM (indicated by *horizontal line pattern*). Note that the figure is schematic and does not contain an exhaustive depiction of areal connectivity.

LTM contents in the service of optimal information allocation to the limited-capacity, consciously accessible part of WM.

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ABBREVIATIONS

CA, cornu ammonis; DAT, dementia of the Alzheimer type; DMS, delayed matching to sample; fMRI, functional magnetic resonance imaging; HC, hippocampus; LTM, long-term memory; MTL, medial temporal lobe; STM, short-term memory; WM, working memory.

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