The Hippocampal Horizon: Constructing and Segmenting Experience for Episodic Memory

T. W. Ross[1,2]* & A. Easton[1,2]

1. Department of Psychology, Durham University, South Road, Durham, DH1 3LE, United Kingdom.

2. Centre for Learning and Memory Processes, Durham University, United Kingdom.

*Corresponding author: tyler.w.ross@durham.ac.uk; Department of Psychology, Durham University, South Road, Durham, DH1 3LE, United Kingdom

Highlights:

- Event segmentation can be externally or internally driven.

- Externally driven event segmentation on shorter versus longer timescales reflects distinct cognitive and hippocampal mechanisms.

- Hippocampal Sharp-Wave Ripples can subserve an intrinsic event segmentation function.

- Hippocampal coding during specific event boundaries may be necessary for episodic recollection.

Abstract

How do we recollect specific events that have occurred during continuous ongoing experience? There is converging evidence from non-human animals that spatially modulated cellular activity of the hippocampal formation supports the construction of ongoing events. On the other hand, recent human oriented event cognition models have outlined that our experience is segmented into discrete units, and that such segmentation can operate on shorter or longer timescales. Here, we describe a unification of how these dynamic physiological mechanisms of the hippocampus relate to ongoing externally and internally driven event segmentation, facilitating the demarcation of specific moments during experience. Our cross-species interdisciplinary approach offers a novel perspective in the way we construct and remember specific events, leading to the generation of many new hypotheses for future research.

Table of Contents

1. Introduction

Since the first reporting of hippocampal place cells (O'Keefe & Dostrovsky, 1971), we have developed a clearer understanding of the nature of spatial representations within the medial temporal lobe (MTL; e.g., Poulter, Hartley & Lever, 2018; Moser, Moser & McNaughton, 2017) and their relation to episodic memory, which is itself so clearly reliant on the hippocampus (e.g., Eacott & Easton, 2010; Vargha-Khadem et al., 1997). However, only recently have we begun to consider fully the nature of the events being recollected in episodic memory. Whilst an event can be understood in the laboratory as a discrete, controlled period distinct from any other, in real life events merge into one another and their boundaries can change over time. Here, we discuss a model of event segmentation in cognitive studies, how it relates to hippocampal formation mechanisms on shorter versus longer timescales and how this may result in the recollection of specific events from ongoing experience.

2. The Event Horizon Model

There is an extensive literature on event and situation cognition in humans (Altmann & Ekves, 2019; Zwaan, 2016; Zacks, 2020; Richmond & Zacks, 2017), and in recent years the event horizon model (EHM) has developed to address how ongoing experience is encoded in long-term human event memory, how those event representations are subsequently accessed and may link to each other (Radvansky & Zacks, 2014; Radvansky, 2012). The EHM is discussed in fuller detail elsewhere (Radvansky & Zacks, 2014, 2017), but here we seek to highlight key aspects of the model relating to event segmentation and link these to understood neural mechanisms.

The starting assumption of the EHM is that events in everyday life are continually segmented into discrete meaningful units (Zacks, Speer, Swallow, Braver & Reynolds, 2007;

Kurby & Zacks, 2008). The event of 'getting ready in the morning' might include meaningful units such as 'getting washed', 'getting dressed', 'brushing teeth', rather than less meaningful units such as 'putting toothpaste on the toothbrush' or 'pouring mouthwash' etc. In such a model, an event boundary reflects the cognitive 'border' separating one event from another, i.e., separating 'getting ready in the morning' from 'having breakfast' (Radvansky & Zacks, 2014). Moreover, the EHM outlines that recurrent neural activity maintains a given working event model (i.e., an active mental representation of the current ongoing event) and is predictive, needing regular updating when error of predictions accumulates, typically at event boundaries (Zacks et al., 2007; Radvansky & Zacks, 2014).

The segmentation of events can be explored experimentally, by allowing people to watch movies and instructing them to press a button when they feel a meaningful unit of activity finishes and another starts (Newtson, 1973; Newtson & Engquist, 1976). Indeed, people can adjust the level at which they consider a meaningful unit of activity, by reporting event boundaries at different temporal grains, with finer-grained event boundaries grouped into coarser-grained event boundaries, indicating a partonomic hierarchy (Zacks, 2020). For instance, as one goes to purchase a coffee from a shop, they may broadly segment this experience: entering, ordering, receiving the coffee and leaving the shop (*coarse-grained*). Equivalent to broader segmentation in 'getting ready for in the morning': getting dressed, brushing teeth… However, if one attends to the steps undertaken by the barista, they may segment by each detailed action of the coffee making process (i.e., adding the beans, grinding them, heating the milk etc., *fine-grained*), in addition to the coarser boundaries. Thus, brushing one's teeth may consist of finer-grained segmentations: putting toothpaste on the toothbrush and pouring mouthwash, which also contributes to the overall event of 'getting ready in the morning', demonstrating the partonomic hierarchy.

Work based on these passive viewing paradigms has found good inter- and intra-

subjective agreement on event boundaries (Speer, Swallow & Zacks, 2003; Zacks, Speer, Swallow & Maley, 2010). Moreover, regardless of whether a video of the same actions was filmed in first person or third person (with visual features differing over time) there was also similarity in segmentation, suggesting it is changes in meaningful content that underlies event segmentation (Swallow, Kemp & Simsek, 2018). Thus, our perspective highlights the critical importance of this event boundary heterogeneity on the cognitive level, as we later outline evidence indicating that this heterogeneity is underpinned by various differing albeit interacting neural mechanisms. Yet, in order for us to consider the physiology of how events are segmented for memory, we first have to discuss how they are constructed. One way to do so is to perceive scenes, which can efficiently package spatially organised content (what-where information). And indeed, it is easier to remember multiple objects in a single location, as opposed to remembering a single object in multiple locations (Radvansky, Andrea & Fisher, 2017).

3. The Hippocampal Formation and Event Construction

The hippocampal formation of the MTL is highly conserved across mammalian species (Insausti, 1993) and homologies are seen across birds and reptiles (Allen & Fortin, 2013). Historically, it has been functionally ascribed to declarative memory and spatial navigation cognition in such species (Scoville & Milner, 1957; Squire & Zola-Morgan, 1991; O'Keefe & Dostrovsky, 1971; Rodríguez et al., 2002; Moser et al., 2017). Accumulating evidence from episodic memory tasks in rodents strongly supports that the hippocampus proper, fornices, lateral entorhinal cortex, perirhinal cortex and the medial prefrontal cortex (and interaction between these areas) are critical for good performance on these tasks (Eacott & Norman, 2004; Langston & Wood, 2010; Langston, Stevenson, Wilson, Saunders & Wood, 2010; Chao, Nikolaus, Brandão, Huston & de Souza Silva, 2017; Chao, Huston, Li,

Wang & de Souza Silva, 2016; de Souza Silva, Huston, Wang, Petri & Chao, 2015; Wilson, Watanabe, Milner & Ainge, 2013; Vandrey et al., 2020; Barker & Warburton, 2020). On the other hand, converging evidence from neuropsychological patients with MTL pathology suggests that the hippocampus contributes to many cognitive functions namely: episodic memory, spatial navigation, imagining personal future experiences and fictitious scenes (Vargha-Khadem et al., 1997; Hassabis, Kumaran, Vann & Maguire, 2007; Race, Keane & Verfaellie, 2011), all unified by the capacity of the hippocampus to construct internally spatially coherent scenes (Maguire & Mullally, 2013; Hassabis & Maguire, 2007).

One paradigm that explores this perceptual role of scenes by the hippocampus in humans is the boundary extension effect (Intraub & Richardson, 1989). Boundary extension is a rapidly occurring cognitive phenomenon, where we implicitly visualise and extrapolate beyond the borders of a scene stimulus and subsequently misremember the original scene input due to the internalised extended scene representation (Intraub & Richardson, 1989). It was reported that MTL damaged participants paradoxically performed better than healthy controls by displaying fewer boundary extension related recognition errors (Mullally, Intraub & Maguire, 2012). Later, using neuroimaging in healthy participants, the hippocampus and parahippocampal cortex (PHC) were seen to be markedly activated, 2-4s after a 250ms scene stimulus onset in trials where boundary extension errors were made (Chadwick, Mullally & Maguire, 2013). Notably, the human PHC and monkey PHC homolog also display robust activation to scene stimuli (Epstein & Kanwisher, 1998; Epstein, Harris, Stanley & Kanwisher, 1999; Baldassano, Beck & Fei-Fei, 2013; Rajimehr, Devaney, Bilenko, Young & Tootell, 2011). Moreover, Aly, Ranganath and Yonelinas (2013) support this perceptual function of the hippocampus by reporting that MTL patients have deficits in perceiving the strength of relational match between scene stimuli, but not when discrete details can differentiate similar images. They also describe that hippocampal activity in healthy

participants monitored the strength of the scene perception as measured by neuroimaging, becoming increasingly active when participants were more confident of stimuli change (Aly et al., 2013).

Together, this provides evidence for a perceptual role of the hippocampus in scene construction and monitoring. Yet, as shown by event segmentation, scenes can be dynamic and temporally bound (events), and intuitively we as agents are always inside events and interact with the outside of objects (Cheng, Walther, Park & Dilks, 2021). Therefore, we tend to view and experience ourselves as part of events that unfold from our egocentric perspective (Rubin & Umanath, 2015; Langston et al., 2010; Zaman & Russell, 2021). If the hippocampal formation mentally constructs events, we should expect a dynamic neural code that binds the self and event content into a spatially coherent representation over time (see Table 1; also Eichenbaum et al., 2012; Sugar & Moser, 2019; Clewett, DuBrow & Davachi, 2019).

3.1. Cellular Representations of Self Position and Viewpoint

Hippocampal principal cells can fire in one or more localised areas of space in environments, constituting a cell's place field(s), hence named place cells (O'Keefe & Dostrovsky, 1971). Place cells, and other hippocampal cells can display temporal organisation of their firing pattern in relation to the local field potential of the theta oscillation (~4-12Hz in rats; O'Keefe & Reece, 1993; Skaggs, McNaughton, Wilson & Barnes, 1996; Valero & de la Prida, 2018). The temporal discharge relationship between given place cells allows good decoding of the animal's position in space as during locomotion the co-firing of place cells can trigger one another depending on the animal's trajectory, indicating that place fields are overlapping (Kubie, Levy & Fenton, 2020; O'Neill, Senior, Allen, Huxter & Csicsvari, 2008; Kay et al., 2020; Harris, Csicsvari, Hirase, Dragoi & Buzsáki, 2003). When an animal is slowly moving or immobile, the self-position

representation is understood to be signalled by a subset of cornu ammonis 2 (CA2) place cells, in which their firing rate displays an atypical negative correlation with speed compared to other place cells (Kay et al., 2016). Furthermore, in a multi-pathway environment, spiking of subicular neurons have been found to represent the current axis of travel along space and time in a given corridor (Olson, Tongprasearth & Nitz, 2017), and this activity was distinguished from head-direction tuning (Taube, Muller & Ranck, 1990).

Despite much of the place cell research being conducted in rodents, it is clear that these findings extend to other species. Cross-species comparisons of place cell activity have been made in bats (Ulanovsky & Moss, 2007; Yartsev & Ulanovsky, 2013; Eliav et al., 2021) and place cell activity exists in the hippocampal homolog of several bird species (Payne, Lynch & Aronov, 2021; Bingman & Sharp, 2006). However, spatially modulated activity recorded from single MTL cells of primates have yielded a different insight to that of rodent work. Spatial view cells have been described in the hippocampus which display localised firing activity when the animals look at a particular location in space. This activity persists even when the visual space is occluded suggesting a mnemonic component (Rolls, 1999; Rueckemann & Buffalo, 2017).

Recordings from the MTL of human patients navigating virtual environments echoes both the primate and rodent data, showing both place-like activity and spatial view activity (Ekstrom et al., 2003; Miller et al., 2013; Tsitsiklis et al., 2020). Analogous to the axis of current travel activity found in rodent subiculum (Olson et al., 2017), there is a primate spatial view cell equivalent, where posterior entorhinal cortex (EC) cells were modulated by the saccade direction during viewing of complex images (Killian, Potter & Buffalo, 2015). In fact, subgroups of saccade direction EC cells differed in activity, with some predicting future saccade trajectories, others reflecting previous saccade movements, and some not uniformly classifying into the latter groups (Killian et al., 2015). Such data reveals that attention plays a

prominent role in primate MTL spatially modulated cellular activity and highlights that attentional control likely also influences place cell activity in rodents (Keleman & Fenton, 2016).

A cue-mismatch paradigm that rotated distal cues relative to local cues in an environment, hinted at the employment of two different spatial frames of reference in place coding (Shapiro, Tanila & Eichenbaum, 1997; Lee, Yoganarasimha, Rao & Knierim, 2004). Most of the CA3 place fields rotated with local cues, whereas CA1 place cells displayed little preference for rotation amongst distal versus local cues, being more selective across sessions or displaying ambiguous activity compared to more coherent CA3 activity (Lee et al., 2004). However, Kelemen and Fenton (2010) more explicitly demonstrated attentional control in CA1 place cell coding using a two-frame place avoidance task where rats were trained to avoid two shock areas. Importantly, distal visual landmarks defined a room-guided spatial frame of reference, whereas rotating olfactory and visual cues marked an immediate arena spatial frame. Within a session it was shown that CA1 activity dynamically switched between the two spatial frames of reference, with given coactive cell ensembles displaying a tendency to exhibit the same frame of reference on a scale from milliseconds to minutes (Kelemen & Fenton, 2010). More recently, it has been argued that place field tuning only accounts for a small variance of a given place cell's spikes, suggesting there may be alternative sources for firing activity (Jercog et al., 2019). Indeed, heading direction to a specific reference point in an environment can influence place cell activity (Jercog et al., 2019). In other words, single CA1 cells are conjunctively driven by multiple coding factors that can include attentional modulation, a finding mirrored across different mammalian species (Nieh et al., 2021; Wirth, Baraduc, Planté, Pinède & Duhamel, 2017; Ulanovsky & Moss, 2011; Keleman & Fenton, 2016). Therefore, there is strong evidence that cells of the hippocampal formation not only place the self within the spatial context of events, but at least in primates, do so with an 'own

eyes' perspective concomitant with the phenomenological aspect of conscious episodic recollection (Zaman & Russell, 2021).

3.2. Cellular Representations of Content

In addition to placing ourselves within the spatial context of events, our day-to-day experiences are naturally filled with things that happen, as we interact with objects and people. Early work recording from CA1 showed that when a 3D barrier, transparent or opaque, was placed into a familiar environment some of the place fields in the vicinity of the barrier were suppressed (Muller & Kubie, 1987); an early indication that the hippocampal place code is sensitive to objects in the local environment. Furthermore, some CA1 firing fields moved with the barrier when the barrier was translated, rotated when the barrier rotated, were abolished when the barrier was removed and were context-invariant when the global environment was changed (Rivard, Li, Lenck-Santini, Poucet & Muller, 2004).

Landmark vector cells found in CA1 exhibit a more complex spatial relationship to objects, forming firing fields at certain vectors to objects and have a propensity to establish new firing fields to other objects at the same vector relationship as the previous objects (Deshmukh & Knierim, 2013). Unlike superficial medial EC (MEC) object-vector cells which are readily present within environments (Høydal, Skytøen, Andersson, Moser & Moser, 2019), landmark vector cells take more time to be established (Deshmukh & Knierim, 2013). Even virtual visual cues upon a linear track can increase the CA1 spatial coding resolution, with a larger portion of place cells with smaller place fields (Bourboulou et al., 2019). Moreover, vector trace cells found in the distal subiculum of rats, displayed trace firing fields at allocentric vector relationships after objects were removed, and these were seen to persist for hours (Poulter, Lee, Dachtler, Wills & Lever, 2021). Of remarkable note, is the distinguishable yet complementary object-vector coding scheme in the various subregions of the hippocampal formation with robust vector object-location memory in subiculum,

which is regarded as an area that outputs information from the hippocampus to the neocortex (Deshmukh & Knierim, 2013; Høydal et al., 2019; Poulter et al., 2021; Kim & Spruston, 2012; Graves et al., 2012; Niztan et al., 2020). As well as firing in particular locations in an environment, the firing rate of CA1 and CA3 pyramidal neurons can also be used to identify specific objects and object-location memories (Geiller, Fattahi, Choi & Royer, 2017; Deshmukh & Knierim, 2013) and the heterogeneity of hippocampal formation anatomy contributes to object-location coding (Vandrey, Duncan & Ainge, 2021; Fernández-Ruiz et al., 2021). Overall, whether given stimuli are mainly tactile, olfactory, gustatory or auditory, the hippocampal formation can represent 'what' information (Anderson & Jeffery, 2003; Herzog et al., 2019; Wang, Monaco, Knierim, 2020; Woods et al., 2020; Sakurai, 1994; Aronov, Nevers & Tank, 2017), highlighting a necessary polymodal nature supporting the idea that the hippocampus constructs events.

When using conspecifics instead of objects, hippocampal areas CA2 and ventral CA1 were critical for successful social recognition memory (Hitti & Siegelbaum, 2014; Okuyama, Kitamura, Roy, Itohara & Tonegawa, 2016). Indeed, ventral CA1 excitatory neurons respond greatly to the presence of conspecifics over minutes and are modulated by conspecific facial whisker stimulations and vocalisations (Rao, von Heimendahl, Bahr & Brecht, 2019). Firing rate in males could also be used to discriminate the identity of females in single neurons (Rao et al., 2019). Interestingly, dorsal CA2 social place cells can shift their place fields relative to the identity of specific conspecifics in a trial-by-trial manner (Oliva, Fernández-Ruiz, Leroy & Siegelbaum, 2020). Furthermore, social place cells have also been observed in CA1 of the rat and bat, where neuronal firing fields were established by the position of the conspecific separate to the self (Danjo, Toyoizumi & Fujisawa, 2018; Omer, Maimon, Las & Ulanovsky, 2018). Therefore, similarly to the situation for inanimate objects as described above, there is

a cellular level hippocampal representation for 'who' and 'who-where' information. The final

content representation relates to affective experiences and behavioural prediction or outcome.

Reward-associated cells in CA1 and subiculum were found to be either active at the

location after reward delivery or strikingly, before obtaining the reward (reward-predictive

cells; Gauthier & Tank, 2018). Such reward-associated cells were context-dependent or

context-invariant to the external virtual environment and the reward-predictive neurons were

correlated with slowed running behaviour indictive of reward anticipation (Gauthier & Tank,

2018). Moreover, shifting of intermediate CA1 place field locations were observed in

response to palatable changes in reward value (Jin & Lee, 2021). Again, such reward-location

activation is not unique to rodents but can also be seen in other species (e.g., Pigeons;

Bingman & Sharp, 2006).

In terms of adverse stimuli, a recent fear acquisition-extinction experiment reported

elevated CA1 place cell activity during freezing bouts (Schuette et al., 2020). Surveying the

calcium-related activity across this population of place cells indicated that their firing was

located at a significant difference from individual freeze locations, suggesting that these place

cells co-jointly encoded defensive freezing behaviour (Schuette et al., 2020). Similarly,

basolateral amygdala projecting ventral CA1 cells can be shock-responsive after brief

environment exploration, with these cells later responding during tone-shock pairs in the

same environment (i.e., context-dependent), but not in a novel environment when the tones

were repeated (Jimenez et al., 2020). Finally, in a jump avoidance task, single cell CA1 firing

activity in rats was triggered by dropping or jumping, with some cells sensitive to both

occurrences (Lenck-Santini, Fenton & Muller, 2008). Collectively this evidence highlights

the diversity of cellular content representations in the hippocampus, particularly in CA1.

It was initially posited that hippocampal scene construction may be an atemporal

process (Maguire & Mullally, 2013), yet time can also play an essential role in hippocampal

formation functioning, especially when considering the process of monitoring changes in event content over time (Maurer & Nadel, 2021; Griffiths & Fuentemilla, 2020; Clewett et al., 2019; Eichenbaum, 2004; Yonelinas, Ranganath, Ekstrom & Wiltgen, 2019; Ameen-Ali, Easton & Eacott, 2015; Aly et al., 2013).

3.3. Cellular Representations of Time

Hippocampal damage in rodent models indicates that it is necessary for elapsed time discrimination beyond 10 seconds (Sabariego et al., 2020; Kesner, Hunsaker & Gilbert, 2005), and memory for high resolution elapsed time discriminations on short (1 vs 1.5 minutes) and longer timescales (8 vs 12 minutes; Jacobs, Allen, Nguyen & Fortin, 2013). Additionally, remembering the sequential order of items in events was seen to be hippocampus dependent, yet recognising a task item versus a novel stimulus was intact in these same hippocampus lesioned animals (Fortin, Agster & Eichenbaum, 2002; Kesner, Gilbert & Barua, 2002).

These lesion studies allude to a possible hippocampal cellular assembly mechanism for temporal coding, and indeed, CA1 and CA3 pyramidal neurons can function as 'time cells' firing sequentially in temporally structured experiences (Eichenbaum, 2014; Salz et al., 2016). Such activity can be triggered after the onset or offset of a stimulus and can bridge stimuli across delays, until the temporal firing fields gradually become broader and lesser in number, similarly to place cells relative to landmarks (Eichenbaum, 2014; Sheehan, Charczynski, Fordyce, Hasselmo & Howard, 2021). Time cell activity in rodents and primates, can be scalable and is seen on the scale of milliseconds to minutes (Modi, Dhawale & Bhalla, 2014; Shimbo, Izawa & Fujisawa, 2021; Naya & Suzuki, 2011; Shikano, Ikegaya & Sasaki, 2021; Umbach et al., 2020; Reddy et al., 2021). Another reported temporal hippocampal phenomenon was termed event-specific rate remapping (ESR) activity (Sun,

Yang, Martin & Tonegawa, 2020). Mice were trained to run four consecutive laps in a square maze, the environment and task was identical, apart from the first lap being rewarded in a start box, acting as a temporal marker. Calcium imaging indicated that ~30% of the given CA1 cells had a peak activity rate for a given lap number that was preserved across days, hence termed ESR, and these cells conjunctively represented place coding, but this was separable from ESR activity (Sun et al., 2020). Crucially, when each lap was rewarded following a previous day of the standard one-in-four lap reward experiment i.e., removal of the temporal marker, ESR activity was abolished. Furthermore, some cell's activity could be described as 'counting', in that they had ESR activity for lap four (the last lap before a new trial) yet showed a progressive increase across laps until displaying maximal rate for lap four (Sun et al., 2020), similar to the ramp-like activity reported in CA1 minute time cells (Shikano et al., 2021).

Emerging evidence also highlights that the EC contributes to temporal coding (Robinson et al., 2017; Miao et al., 2015; Suh, Rivest, Nakashiba, Tominaga & Tonegawa, 2011; Kitamura et al., 2014; Tsao et al., 2018; Heys & Dombeck, 2018; Chenani et al., 2019). For example, extensive optogenetic inactivation of the MEC has led to disruption of CA1 temporal coding, whereas spatial coding was largely preserved (Robinson et al., 2017). Likewise in the ESR experiment, MEC optogenetic inactivation evoked remapping in ESR activity, whilst place field location remained stable (Sun et al., 2020). Interestingly, a recent computational model predicts that the MEC should also be capable of producing ESR representations (Whittington et al., 2020). The persistent activity of layer 3 MEC neurons, which project directly to CA1, make it a good candidate area for temporal related coding and communication between the neocortex and hippocampus (Hahn, McFarland, Berberich, Sakmann & Mehta, 2012; Kitamura et al., 2014; Beed et al., 2020; Isomura et al., 2006). In fact, a revised continuous attractor network model describes that a synergetic relationship

between the hippocampus and the MEC underlies the sequential temporal order of ongoing event construction (Rueckemann, Sosa, Giocomo & Buffalo, 2021). However, it is important to note that the temporal activity reported above encapsulates relative time and may require learning of the repeated regularity in the event structure, which likely requires recruitment of other brain regions (Paz et al., 2010; Shikano et al., 2021; Sun et al., 2020).

In summary, there is convincing evidence on the cellular level that the hippocampal formation binds event content and the self's position (and viewpoint in primates) to construct spatially coherent event representations over time (Rueckemann et al., 2021). This leads us to how the heterogeneity in behaviourally reported event boundaries is differentially yet complementarily represented by the brain. More specifically, how does this relate to the aforementioned hippocampal dynamics of event construction to facilitate the discrimination of certain moments in event memory. Interestingly, many of the neuronal coding phenomena discussed in this section overlap with dimensions relating to event representations from text narratives, as outlined by event-indexing theory, namely: time, space, entity, causation, and motivation (Zwaan, Langston & Graesser, 1995; Zwaan, 2016), which may enact as features of experience that cue segmentation.

4. Working Event Memory and Event Horizons

Neuroimaging and electrophysiological recordings in humans have shown that hippocampal neurons (and other MTL neurons) contribute to working memory of complex images (e.g., people and scenes) over short maintenance periods (Luck et al., 2010; Ranganath, DeGutis & D'Esposito, 2004; Kornblith, Quiroga, Koch, Fried & Mormann, 2017; Kamiński et al., 2017). This has shed light upon the existing mixed evidence for an impairment of working memory in patients with MTL pathology (Allen, Vargha-Khadem & Baddeley, 2014; Duff, Hengst, Tranel & Cohen, 2006; Zuo et al., 2020; Jonin et al., 2019; Nichols, Kao, Verfaellie & Gabrieli, 2006; Olson, Moore, Stark & Chatterjee, 2006;

Goodrich & Yonelinas, 2016; Goodrich, Baer, Quent & Yonelinas, 2019). Indeed, this working memory hippocampal activity was stimuli specific, building upon prior research of concept cells in the human MTL, whereby single neurons were seen to fire selectively to multiple images of the same person and to their written and spoken name (Kamiński et al., 2017; Kornblith et al., 2017, Quiroga, Reddy, Kreiman, Koch & Fried, 2005; Quiroga, 2020).

Concepts cells have provided important corroboration for semantic information as well as episodic information contributing to hippocampal activity, it is therefore somewhat surprising that amnesic patients with hippocampal damage can communicate efficiently with a partner in a collaborative goal-directed communication game, showing rapid learning over time, within and across sessions, comparably to controls (Duff et al., 2006).

Moment-by-moment brain activity in the default mode network (DMN) between an amnesic patient and controls was seen to be similar in response to complex auditory-based narrative information (Zuo et al., 2020). Likewise, there was similar brain activity in DMN regions during watching of video stimuli between an amnestic patient and age-matched controls (Oedekoven, Keidel, Anderson, Nisbet & Bird, 2019). However, an exception of reduced functional connectivity between the posterior midline cortex (of the DMN) and left hippocampus was noted (Oedekoven et al., 2019). Human studies such as these have led to argument that the DMN can retain some comprehension of narratives and communitive interactions in ongoing events over the span of minutes without the hippocampus (Yeshurun, Nguyen & Hassan, 2021; Hasson, Chen & Honey, 2015; Zuo et al., 2020; Oedekoven et al., 2019), and generally contend against the notion of specialised memory systems (Hasson et al., 2015; Gaffan, 2002). It is yet to be determined how these added complexities in human event construction may relate to non-human animals. However, numerous reports of amnesic patients with hippocampal damage consistently highlight the forgetting of momentary information during ongoing experience, particularly when delayed retention or distraction is

involved (Vargha-Khadem et al., 1997; Tulving, 1985; Corkin, 1984; Duff et al., 2006; Scoville & Milner, 1957). This suggests that there is a dynamic functional relationship between working memory and hippocampal dependent episodic memory to continuously maintain some coherence in our experience, within and across events (Beukers, Buschman, Cohen & Norman, 2021; Maurer & Nadel, 2021; Schneider et al., 2021; Clewett et al., 2019). To this end, we employ the term 'event horizons' defining them as coarse-grained hippocampal-dependent event boundary activations, which we view as distinct from finer-grained event boundary activity. This can more clearly realise the transition of an event representation from working memory into 'long'-term episodic memory (Zacks, 2021; Richmond & Zacks, 2017; Baldassano et al., 2017).

4.1. Long Timescales

An emerging body of research in humans have made use of naturalistic stimuli to investigate how we segment and remember events (Bird, 2020). For example, Ben-Yakov and Dudai (2011) used short realistic audiovisual clips (8-16s) and found peak bilateral hippocampal activity following offset of the stimuli. They further show that this response persisted when two clips were presented consecutively (Ben-Yakov, Eshel & Dudai, 2013). In this context, event horizons reflected the rapid termination of the brief clips, indicating that each clip was encoded as a discrete episode, yet due to the length of the videos in these studies it remained unanswered how the brain responded to longer continuous naturalistic input.

Comparable brain activity in DMN regions within and across participants was observed between watching a long episode of Sherlock (~50mins), and subsequently verbally recalling aspects from said episode (Chen et al., 2017). However, it was later shown using the same stimuli, that there was dynamic, hierarchically structured activity in the hippocampus and neocortex (including the DMN) in response to the passive exposure of this continuous

input (Baldassano et al., 2017). Primary visual and auditory cortex were active to more fine-grained event boundaries on shorter timescales, whereas coarser-grained event boundaries were represented at longer timescales by stable activity in DMN regions, such as the posterior medial cortex and angular gyrus, matching behaviourally reported event boundaries from independent scorers (Baldassano et al., 2017). Importantly, along with cortically represented long-time scale event boundaries, there was also peak hippocampal activity (Baldassano et al., 2017). This has been corroborated by other long movie data sets, finding that the more observers uniformly referenced a given event boundary, the stronger the magnitude of the post-boundary hippocampal activation (Ben-Yakov & Henson, 2018). Therefore, there is good evidence to support the distinction of event horizons which tend occur on longer timescales, relating to coarser-gained event boundaries (Ben-Yakov & Henson, 2018; Cooper & Ritchey, 2020; Baldassano et al., 2017; Ben-Yakov & Dudai, 2011; Ben-Yakov et al., 2013; Zacks et al., 2010; Stawarczyk, Bezdek & Zacks, 2021). Further work will be needed to characterise event horizon activity in humans on the cellular level (Zheng et al., 2021; Yoo, Umbach, Lega, 2021) and investigate how aging and pathology impacts event boundaries and horizons (Reagh, Delarazan, Garber & Ranganath, 2020; Bailey et al., 2013). Finally, it will be critical to further understand how the relevant aspects from event-index theory (Zwaan, 2016; Zwaan et al, 1995) e.g., space, time, narrative (of protagonists) and causality drives evocation of event horizons and hippocampal activity across event horizons (Cutting, 2014; Chang, Lazaridi, Yeshurun, Norman & Hasson, 2021; Cohn-Sheehy et al., 2021a; Cohn-Sheehy et al., *in press*; Lee & Chen, 2021; Clewett et al., 2019; Song, Finn & Rosenberg, 2021).

4.2. Short Timescales

Implementation of long continuous naturalistic stimuli in neuroimaging studies has been extremely insightful, yet they are not without their limitations. One being that in real-

world events we are not always passively perceiving the events that unfold before us, but our own bodily actions can be instrumental to how events develop, hence we can be actively engaged in the events we experience. This distinction has been realised by a recent virtual reality experiment in humans, showing that memory recall for words was better when participants actively explored a novel virtual environment, as opposed to passively experiencing the input of another participant (Schomaker & Wittmann, 2021). In a similar vein, passive transport training of hippocampal-lesioned and sham rats in a Morris water maze task led the control group to perform worse than the lesioned group on probe-trials when rats had to actively swim to the goal location (Poulter et al., 2019). This is echoed neurally, as when rats were passively transported in a car instead of self-generated movement, their place cell activity was degraded in number and resolution (Terrazas et al., 2005). In this way, the formerly described hippocampal place and spatial view cell ensemble dynamics (and other hippocampal activity) that operate on much faster timescales, are left unaccounted for in the previous section.

Taking a different approach to movie viewing paradigms, a momentary burst of arousal was observed (as measured by increased pupil dilation) in response to auditory-based event boundaries versus non boundaries (Clewett, Gasser & Davachi, 2020). Moreover, making revisitation saccade movements to previous focal points in novel scene imagery (presented for 3s) was seen to enhance scene memory formation (Kragel, Schuele, VanHaerents, Rosenow & Voss, 2021). Crucially, prevalence of hippocampal theta oscillations after the revisitation fixation was increased relative to other saccade movements and there was top-down hippocampal modulation of the visual network specifically for revisitation saccades (Kragel et al., 2021). Indeed, hippocampal-lesioned mice are unable to produce learning induced plasticity in primary visual cortex when exposed to sequential visual grating stimuli, which also affect their predictive capabilities relative to sham controls

(Finnie, Komorowski & Bear, 2021).

Returning to movie stimuli, a wide distributed network of brain areas including the hippocampus were seen to be active following blink-onset during video watching, with the hippocampus displaying peak activation 4-6s after blink-onset (Nakano, 2015). Additionally, increases in mean between-participant eye movement synchrony correlates with increases in the proportion of movie-recalled episodic details (Davis, Chemnitz, Collins, Geerligs & Campbell, 2021). And in fact, a general increase in eye fixation rate at recall is also correlated with an increase of episodic recollection details in those with high autobiographical recollection ability (Armson, Diamond, Levesque, Ryan & Levine, 2021).

This highlights that one's own volition on shorter timescales are an important factor to consider within the scheme of unfolding events. Thus, it is necessary to further establish whether theta organised hippocampal cellular activity exists in humans and in relation to event boundaries and event horizons (which preliminary evidence supports that it does, e.g., Qasim, Fried & Jacobs, 2021; Zheng et al., 2021; Yoo et al., 2021). For example, Zheng and colleagues (2021) asked patients to watch a continuous movie clip with no boundary, a movie clip with a soft boundary (cutting to new scene in the same movie) or with a hard boundary (cutting to a different movie; an event horizon). They reported 'boundary' and 'event' cells in the MTL, wherein the onset of soft boundaries or event horizons triggered increased firing rate respectively, with event cells being entrained by local theta oscillations (Zheng et al., 2021). Therefore, as events evolve, hippocampal activity (particularly stemming from the visual domain) can operate on shorter timescales, impact memory formation (Kragel et al., 2021) and is more concomitant with finer-grained event boundaries (Baldassano et al., 2017; Zacks, 2020).

4.3. Spatial Context

Another issue arising from the use of movie stimuli to investigate the neural mechanisms of event segmentation, is that cinematic techniques applied by filmmakers are aimed to facilitate viewer event segmentation (Cutting, 2014; Cutting & Iricinschi, 2015). Cutting to a new scene with a camera shot and expressing a novel spatiotemporal context or character inclusion may indicate an event boundary (Cutting, 2014), whereas in real-world situations it is unlikely that there are such definitive transitions. However, some have argued that the context of spatial environments and physical boundaries in space may enact as cues for event segmentation in real-world scenarios (Radvansky, 2012; Brunec, Moscovitch & Barense, 2018).

The location-updating effect paradigm explores spatially driven event segmentation by making human participants experience (or virtually experience) a spatial shift by walking through a doorway from one distinct room to another with a memory task (Radvansky & Copeland, 2006; Radvansky, Krawietz & Tamplin, 2011). It was initially found that people took longer and were more erroneous in reporting the object they were carrying when there had been spatial shifts compared to when there were no shifts in a virtual environment (Radvansky & Copeland, 2006). Additionally, this forgetting effect was shown to increase by how many shifts there were to new rooms and not by the number of spatial shifts (i.e., returning to a room; Radvansky et al., 2011) and equally was seen to impact long-term temporal memory for sequentially presented items (Horner, Bisby, Wang, Bogus & Burgess, 2016). Critically, experiencing a spatial shift decreases the number of high confident correct reports associated with subjective remembering, whereas the feeling of knowing remains unaffected by a spatial shift (Seel, Easton, McGregor, Buckley & Eacott, 2019).

If we expect that experiencing a spatial shift is sufficient to trigger event boundaries or event horizons, for example, by walking through a doorway into contextually different rooms, we should therefore expect a hippocampal-dependent physiological mechanism to reflect this. Indeed, this is known as global remapping, referring to the phenomenon whereby place fields of given place cells will drastically change their spatial tuning such that population level representations of different environments become distinguished (Kubie et al., 2020; Sanders, Wilson & Gershman, 2020; Alme et al., 2014). However, we note that changes in one's use of sensory modality to achieve a goal has equally elicited global remapping in an otherwise stable environment with fixed sensory cues (Radvansky, Oh, Climer & Dombeck, 2021; Geva-Sagiv, Romani, Las & Ulanovksy, 2016). Such remapping in rodents can be modulated by environment novelty and prior experience (Frank, Stanley & Brown, 2004; Barry, Ginzberg, O'Keefe & Burgess, 2012; Duszkiewicz, McNamara, Takeuchi & Genzel, 2019; Bulkin, Law & Smith, 2016; Plitt & Giocomo, 2021) and is underpinned by differential coding dynamics from hippocampal subareas and cell populations (Dong, Madar & Sheffield, 2021; Hainmueller & Bartos, 2018; Grosmark & Buzsáki, 2016; Gava et al., 2021). Interestingly, when recording in a multicompartment environment (connected by a single corridor), place cells displayed a tendency to cluster around the doorways (Spiers, Hayman, Jovalekic, Marozzi & Jeffery, 2015; Grieves, Jenkins, Harland, Wood & Dudchenko, 2016) and remapped when there was a local contextual change to one out of the four rooms (Spiers et al., 2015). Moreover, when rats were 'teleported' from one familiar environment to another (via manipulation of light cues), there was prolonged flickering of alternate CA3 ensemble environment representations in rhythm with theta (less so in CA1; Jezek et al., 2011). In this way, interference between past and present hippocampal spatial representations and novelty-evoked responses likely contribute

to the cognitive manifestations from the location-updating effect in humans (Radvansky et al., 2011; Seel et al., 2019).

Theta-paced sequential place cell activity in rats showed the capability to segment various parts of an environment, by representing past and future trajectories in space differentially to maze turn points and reward landmarks (Gupta, van der Meer, Touretzky & Redish, 2012). Similar relevant activity for segmenting space has also been observed at arising choice-points (Kay et al., 2020; Kinsky et al., 2020) and as previously mentioned, along corridors (Olson et al., 2017). Upstream from the hippocampus, segmentation of space by turns also affects superficial MEC grid cells, that typically display spatially organised hexagonal firing fields and provide input to the hippocampus (Hafting, Fyhn, Molden, Moser & Moser, 2005; Jacobs et al., 2013). When an environment was divided into spatially equal corridors (a hairpin maze), MEC grid cells were reset at turning points resulting in discrete submaps for a given corridor (Derdikman et al., 2009). This corresponds to human phenomenological work, where it was found that when navigating and waiting before a turn compared to the route midpoint, people's memories for scenes at pre-turn stop points were more associated with 're-experiencing' compared to just knowing (Brunec et al., 2020).

The above evidence spanning from a neural level to a cognitive-experiential level, provides a compelling argument that shifts in spatial context and physical boundaries not only contribute to event segmentation but differentially impact subsequent episodic recollection (Seel et al., 2019; Brunec et al., 2020; Tulving, 1985), paralleling the work from naturalistic stimuli (Ben-Yakov & Henson, 2018; Baldassano et al., 2017; Zheng et al., 2021). Moreover, hippocampal predictive coding in rodents (Gauthier & Tank, 2018; Liu, Sibille & Dragoi, 2021; Stachenfeld, Botvinick & Gershman, 2017) can also relate to important elements regarding predictive cognition from the EHM, namely that increasing prediction error in what to expect in situations can lead to segmentation and is reliant on

one's prior knowledge about such situations (Radvansky & Zacks, 2014; Zacks, 2020). For example, when mice were presented with changes in their currently experienced contextual information their hippocampal activity remapped (suggestive of segmentation) in either a continuous or discontinuous manner, dependant on whether the animal was trained in a frequently morphing context versus a rarely morphing context respectively (Plitt & Giocomo, 2021). In other words, when the mice faced increasing prediction error during their experience, their prior knowledge in what to expect in such events impacted how the hippocampus reacted to the prediction error. Therefore, operationalising event segmentation by physical means (e.g., spatial context), as opposed to conceptual means (e.g., narrative/semantic causality) may allow the start of a clearer framework to bridge the EHM from humans to nonhuman animals. Finally, given the aforementioned evidence of dynamic hippocampal processing on shorter timescales (sections 3, 4.2), we argue that this further supports the necessity of distinguishing event horizons, as we speculate that several bidirectional hippocampal-cortical interactions may occur (Beukers et al., 2021; Maurer & Nadel, 2021; Kragel et al., 2021) before a given event horizon. Returning to the coffee shop example, while many visual fixations may be made during the diligence of barista's coffee making process (finer-grained event boundaries), only upon receiving the coffee and leaving the shop (change in spatial context), may an event horizon be afforded.

5. Intrinsically Driven Event Segmentation

Insofar we have mostly discussed event segmentation in terms of external stimulus-driven change, yet are external changes always necessary for event segmentation, i.e., in the absence of external change does event segmentation still occur? Many event boundary studies encapsulate high inter-participant agreement upon given boundaries, implying homogeneity in subsequent memory performance. Yet, there is in fact great individual variance in episodic recollective abilities (Palombo, Sheldon & Levine, 2018) and while

many factors may give rise to this variance, one being oculomotor-hippocampal interactions during encoding as previously discussed (Davis et al., 2021; Armson et al., 2021; Kragel et al., 2021; Meister & Buffalo, 2016), there remains an explanatory gap between event encoding, segmentation and recollection.

Recent reports indicate that our daily mental experiences are frequently punctuated by periods of spontaneous thoughts, such as mind-wandering (Christoff, Irving, Fox, Spreng & Andrews-Hanna, 2016) or stimulus-independent perceptions (Waters, Barnby & Blom, 2020), with the former recruiting similar neural machinery as we have already mentioned e.g., the hippocampus, wider MTL and the DMN (Christoff et al., 2016; Stawarczyk et al., 2021; O'Callaghan, Shine, Hodges, Andrews-Hanna & Irish, 2019; McCormick, Rosenthal, Miller & Maguire, 2018; Karapanagiotidis, Bernhardt, Jefferies & Smallwood, 2017; Ellamil et al., 2016). The methodology of the aforementioned event segmentation studies do not address these introspective interruptions during ongoing events, which we posit are equally likely to elicit a form of 'internal' event boundary. The core of this argument relies on the postulation that event segmentation in itself is an inherent property of the brain, as a result of the mechanisms of intrinsically generated neural activity and transition between network states (Honey, Newman & Schapiro, 2017; Kay & Frank, 2019; Buzsáki & Draguhn, 2004). We elaborate this idea by focusing upon hippocampal sharp-wave ripples (SWRs), which have recently been discussed in relation to event boundaries (Bilkey & Jenson, 2021). Notably, similar approaches to cognition based on intrinsic function have been raised in the context of the hippocampus (Buzsáki & Tingley, 2018; Nieh et al., 2021; Kay & Frank, 2019; Mau, Hasselmo & Cai, 2020; Bittner, Milstein, Grienberger, Romani & Magee, 2017; Josselyn & Frankland, 2018). Importantly, this view does not invalidate externally modulated event boundaries or horizons but proposes that externally driven and inherent event segmentation can act both separably and complementarily to one another.

5.1. Features and Ontogeny of Sharp-Wave Ripples

Sharp waves can be characterised as large negative amplitudes seen in the local field potential of the CA1 *stratum radiatum* layer, where afferents from the dentate gyrus-CA3 performant pathway reside (Witter et al., 2000; Buzáski, 2015). These usually coincide with 'ripples' (~110–220 Hz), transient events containing a series of wavelets (Buzsáki, 2015). Together sharp waves and ripples form a complex, SWRs, observed frequently in slow wave sleep and wakeful still behaviours (Kay & Frank, 2018; Joo & Frank, 2018; Poulter et al., 2018; Buzáski, 2015) and are prevalent, albeit less often during exploratory active behaviour (O'Neill, Senior & Csicsvari, 2006; Leonard et al., 2015; Leonard & Hoffman, 2017). Moreover, SWRs can be accompanied by slower gamma oscillations (~20-50 Hz) in the hippocampus and cortex (Carr, Karlsson & Frank, 2012; Remondes & Wilson, 2015). Critically, even in a decorticated mammalian brain SWRs internally arise in the hippocampus (Buzáski, 2015), with regions CA3, CA2, subiculum and EC all contributing to the generation of SWRs typically in low cholinergic states (Hunt, Linaro, Si, Romani & Spruston, 2018; Davoudi & Foster, 2019; Hwaun & Colgin, 2019; Oliva, Fernández-Ruiz, Buzsáki & Berényi, 2016; Imbrosci et al., 2021; Norimoto, Matsumoto, Miyawaki, Matsuki & Ikegaya, 2013; Yamamoto & Tonegawa, 2017; Chenani et al., 2019; Vandecasteele et al., 2014; Zhang et al., 2021).

The earliest emergent oscillatory activity of the rodent hippocampus are early SWs at postnatal day 4±2 (Leinekugel et al., 2002). They are highly spatiotemporally coordinated, originating in part from synchronous CA3 burst activity that can be preceded by EC layer 3 burst activity, paw twitches or startles (Leinekugel et al., 2002; Karlsson, Mohns, di Prisco & Blumber, 2006; Valeeva et al., 2019; Valeeva, Rychkova. Vinokurova, Nasretdinov &

Khazipov, 2020). Whole cell patch experiments in 5±1 day old rats have shown that CA1 pyramidal cells are driven by both gamma-aminobutyric acid (GABA) and glutamatergic synaptic input during early SWs (Leinekugel et al., 2002). Notably, GABA has an excitatory affect during development and can induce calcium influx in synergy with N-Methyl-D-Aspartate receptors (Ben-Ari, Gaiarsa, Tyzio & Khazipov, 2007; Leinekugel, Medina, Khalilov, Ben-Ari & Khazipov, 1997; Valeeva, Tressard, Mukhtarov, Baude & Khazipov, 2016). Interestingly, although early SWs occur within the rodent's first postnatal week, CA1 ripples develop toward the end of the second postnatal week, seemingly around the time of eye-opening and the earliest reports of operational CA1 place cells (Buhl & Buzsáki, 2005; Wills et al., 2010; Langston et al., 2010). However, ripple-like activity (140-200 Hz) and fast-gamma activity (60-100 Hz) has been described as early as postnatal day 7±1 (Mohns, Karlsson & Blumberg, 2007). Thus, before the emergence of place cells and complex externally driven experience SWRs are present, contributing to synchronous hippocampal activity which is theorised to facilitate network maturation at this stage (Ben-Ari, 2001), underlying further development of more complex spatial and event cognition (Tan, Wills & Cacucci, 2017; Donato et al., 2021).

5.1. Cognitive Functions of Sharp-Wave Ripples

A substantial body of evidence supports that SWRs serve a memory consolidatory function of recent experience, commonly referred to as 'replay' (See Pfeiffer, 2020; Foster, 2017; Joo & Frank, 2018). For example, Lee and Wilson (2002) showed that CA1 sequential place cell firing during SWRs in slow wave sleep were forwardly replayed after rats traversed a linear track, temporally compressing the place cell firing sequence by approximately 20-fold. During wakeful rest periods, place cell sequences have also been observed to be reversely and forwardly replayed (Foster & Wilson, 2006; Diba & Buzsáki, 2007), which

may underlie different functions (Pfeiffer, 2020). Furthermore, disruption of SWRs in rodents has led to impaired performance on spatial and social memory tasks (Girardeau, Benchenane, Wiener, Buzsáki & Zugaro, 2009; van de Ven, Trouche, McNamara, Allen & Dupret, 2016; Oliva et al., 2020), whereas in converse, optogenetically prolonging or triggering SWRs has increased performance on such tasks (Fernández-Ruiz et al., 2019; Oliva et al., 2020). Likewise, to that of rodent work, the number of human SWRs (in parahippocampal areas) during an afternoon sleep have been positively correlated with the number of successfully recognised image items, as measured by intracranial recordings (Axmacher, Elger & Fell, 2008). This is corroborated by a recent neuroimaging study in healthy participants, finding that sequential hippocampal activity during wakeful rest periods (proxy for SWRs), replayed the ordered hippocampal activity when completing a non-spatial decision-making task (Schuck & Niv, 2019). Primate SWRs are also temporally coupled with neocortical oscillations much like in rodents (Staresina et al., 2015; Abadchi et al., 2020; Logothetis et al., 2012; Oyanedel, Durán, Niethard, Inostroza & Born, 2020; Remondes & Wilson, 2015), which has provided further support for long-term memory models incorporating systems consolidation; the transfer of information from the hippocampus to the neocortex (Squire, 1992; Barry & Maguire, 2019).

'Pre-play' as opposed to replay, describes the hippocampal phenomenon whereby during SWRs of sleep and rest periods *prior* to novel experience, place cell sequences can emerge that are subsequently recruited during ongoing experience (Dragoi & Tonegawa, 2011, 2013). The ontogeny of this occurrence has recently been explored, reporting that pre-play develops around postnatal day 17, before the development of theta entrained sequential place cell activity and complex extended replay around day 23 (Farooq & Dragoi, 2019). Importantly, within single CA1 cells, those that went on to form place cells versus silent cells in a novel track, displayed more propensity to burst fire and had a lower first action potential

threshold during exploration (Epsztein, Brecht & Lee, 2011), suggesting that intrinsic dynamics contribute to place cell selection and cell allocation for memory formation (Lee, Lin & Lee, 2012; McKenzie et al., 2021; Park et al., 2016; Sekeres, Neve, Frankland & Josselyn, 2010; Josselyn & Frankland, 2018). The future oriented role of SWRs also complies with more direct cognitive demands. For instance, sequential activity during SWRs can represent novel spatial trajectories of shortcuts rarely or never even physically experienced (Gupta, van der Meer, Touretzky & Redish, 2010). Indeed, increased pre-play activity of unexperienced space was found when rats observed that the space was goal-baited as opposed to unrewarded (Ólafsdóttir, Barry, Saleem, Hassabis & Spiers, 2015). In this way, hippocampal SWRs not only reflect experience-dependent consolidatory activity but contribute to preconfigured activity (which can also be shaped by experience), allowing the network to flexibly prepare for future experience.

Memory retrieval is the final function of SWRs that we will highlight. In humans, Vaz and colleagues (2019) described an increased number of MTL ripples and coupled MTL-temporal association cortex ripples relative to successful verbally reported paired-word association retrievals. Similarly in the visual domain, the rate of SWRs increased prior to verbal retrieval (describing visual details) of previously viewed faces and places (Norman et al., 2019). Recently, increased ripple rate was also seen in relation to long-term episodic recollections and past and future oriented thought (Norman, Raccah, Liu, Parvizi & Malach, 2021; Chen et al., 2021). Comparatively in nonhuman animals, when macaques searched for target objects during repeated visual scene stimuli, SWR rate increased as a function of gaze distance to the target location (Leonard & Hoffman, 2017). Furthermore, when rats learned to avoid a shock zone by making avoiding turns, awake SWRs before rats made the turn, preferentially reactivated sequential place cell activity in the shock zone learned previously, indicative of memory retrieval (Wu, Haggerty, Kemere & Ji, 2017). Collectively, the above

cross-species evidence highlights a range of putative cognitive functions for SWRs.

While the estimated probability of a single cell spiking during SWRs is ~0-40% (Ylinen et al., 1995), the activity of many cells in the waking state is typically organised into cell assemblies (Malvache, Reichinnek, Villette, Haimerl & Cossart, 2016). Moreover, the variance in single CA1 cell's membrane potential during spontaneous wakeful SWRs can largely be characterised by three components: depolarisation, intracellular ripples and hyperpolarisation (Hulse, Moreaux, Lubenov & Siapas, 2016), reflecting heterogeneity in a given hippocampal cells response during SWRs (Hulse et al., 2016; Valero et al., 2015; Böhm et al., 2015). Such evidence suggests that the synaptic weights of the vast majority of cells in the immediate network vicinity are likely modulated by SWRs (Buzsáki, 2015; Norimoto et al., 2018), indicating that a given awake SWR may simultaneously serve a dual cognitive function of consolidating and for example, retrieving information (see Joo & Frank, 2018), or even consolidating and providing a non-cognitive function (Tingley, McClain, Kaya, Carpenter & Buzsáki, 2021). Importantly, similar SWR-like high frequency oscillations are also observed in other regions of the mammalian brain, during sleep in the claustrum homolog of reptiles and the hippocampal homolog in birds (Buzsáki, 2015; Norimoto et al., 2020; Payne et al., 2021; Yeganegi, Luksch & Ondracek, 2019).

Based on (i) the hippocampus constructs events (section 3), (ii) the ontogeny of SWRs and (iii) the combinatory functions of SWRs, we argue that SWR activity inherently segments events. This novel perspective leads to several working hypotheses, firstly, the temporal onset of SWRs should correlate within a temporal window of some externally driven event horizons and finer-grained event boundaries (see Bilkey & Jenson, 2021). Secondly, heterogeneity in SWR activations may differentially reflect event boundaries from event horizons, in which we highlight long duration ripples and concatenating ripples as candidate phenomena (Fernández-Ruiz et al., 2019; Buzsáki, 2015; Yamamoto & Tonegawa,

2017; Pfeiffer, 2020). Thirdly, if mind wandering and episodic past/future oriented thought modulates SWRs (O'Callaghan, Walpola & Shine, 2021; Chen et al., 2021) eliciting internal event boundaries, we thus expect that it will impact subsequent memory. This may especially be tested in the absence of external change or at least minimal external change. Previous evidence (with external change) supports that mind wandering or 'zoning out' during a lecture, critical moments in a narrative and a cued task-switching protocol negatively affects learning and memory performance (Risko, Anderson, Sarwal, Engelhardt & Kingstone, 2012; Smallwood, McSpadden & Schooler, 2008; Whitehead, Mahmoud, Seli & Egner, 2021). As opposed to traditional approaches to event segmentation that describe high inter-subject agreement on given event boundaries (Baldassano et al., 2017; Ben-Yakov & Henson, 2018; Zacks, 2020), our view speculates that individual differences in episodic memory may arise due to subjective differences in intrinsically driven event segmentation. In this way, theorising that event segmentation can be externally and internally driven allows the EHM and other human-oriented models to further account for nonhuman mammals.

6. Beyond the Event Horizon

Events are not experienced in isolation, they evolve sequentially upon our subjective temporal continuum (Tulving, 2002; Eichenbaum, 2004). Hence, once an event model passes an event horizon threshold, it likely crosses into 'long'-term episodic memory (Zacks, 2020) and according to EHM, a given event model is updated (Radvansky & Zacks, 2014, 2017). To this end, the hippocampus and the entorhinal-hippocampal circuit should be able to maintain event relevant information via recurrent network activity, such that when recent previous event information is experienced, the circuit can conjunctively represent long-term episodic past and present information to formulate coherent meaning (Rueckemann et al.,

2021; Maurer & Nadel, 2021; Griffiths & Fuentemilla, 2020; Hasselmo, 2006; Clewett et al., 2019; Morris & Frey, 1997; McKenzie et al., 2014; Eichenbaum, 2004).

6.1. Relation of Information Across Events

Myriad anatomical evidence demonstrates that the hippocampus and entorhinal-hippocampal circuit have numerous recurrent connections both intra-regionally and inter-regionally (Nilssen, Doan, Nigro, Ohara & Witter, 2019; Sun et al., 2019; Ohara et al., 2018; Ohara et al., 2021; Rozov et al., 2020; Beed et al., 2020; Tsoi et al., 2021; Lin et al., 2021). For example, it is well described that pyramidal cells of distal CA3 display strong recurrent connectivity, which is theorised to computationally subserve pattern completion (autocompleting a representation when given a partial cue) and contribute to SWR generation (Cembrowski & Spruston, 2019; Hunt et al., 2018; Guzman, Schlögl, Frotscher & Jonas, 2016; Rolls, 2013; Jezek et al., 2011; Alme et al., 2014). Recently, the micro-circuitry of hippocampal output to the EC has also been explored in depth (Ohara et al., 2018; Ohara et al., 2021; Tsoi et al., 2021) and of note, is that SWRs can propagate to the deeper layers of MEC (Ólafsdóttir, Carpenter & Barry, 2016; Gardner Lu, Wernle, Moser & Moser, 2019; Chrobak & Buzsáki, 1994). This becomes especially important given that hippocampal firing during SWRs was seen to underlie inference between separate but related information that ultimately led to a reward (Barron et al., 2020), and that information can recirculate back into the hippocampus via functional connectivity between the entorhinal layers (Koster et al., 2018). Furthermore, subicular vector-trace cells as previously mentioned, can retain representations of allocentric object-location memory lasting for hours (Poulter et al., 2021). These cells were found to be topographically biased in distal subiculum, a region which exhibits bidirectional connectivity with the MEC (Kim & Spruston, 2012; Graves et al., 2012; Cembrowski et al., 2018), suggesting another functional entorhinal-hippocampal

recurrent pathway for the relation of information across events.

In regards to more complex naturalistic work, emerging evidence utilising auditory-based narratives and neuroimaging has described that human hippocampal activity not only tracks context-specific narratives, but is necessary to bridge previous narrative information across event boundaries and one-day delays to form globally coherent narratives (Chang et al., 2021; Chen et al., 2016; Milivojevic et al., 2016; Cohn-Sheehy et al., *in press*). Another recent neuroimaging experiment showed that the hippocampus was more active during encoding after the offset of event boundaries with high, but not low, causal or semantic connectivity to other events (Lee & Chen, 2021), yet further work will be needed to corroborate this finding. Nevertheless, this remains an interesting avenue of research given that causal and semantic relations to other event features is also a prominent aspect of episodic recollection on the timescale of days to months, to even more remote timescales, where hippocampal-prefrontal cortex interactions may be crucial (Greenberg & Rubin, 2003; Horner, Bisby, Bush, Lin & Burgess, 2015; Eacott & Easton, 2010; Clewett et al., 2019; McCormick, Barry, Jafarian, Barnes & Maguire, 2020).

6.2. Episodic Recollection

The present review has mostly focused upon the cognition of events through the lens of recency, however remote episodic memory is an especially reconstructive process, scaffolded by schema and context (Simons, Ritchey, Fernyhough, *in press*; Bartlett, 1932; Eacott & Easton, 2010). Human neuroimaging evidence has outlined a vast distributed network of interacting brain regions during episodic retrieval including the DMN and hippocampus, in the phenomenologically associated re-experiencing that Tulving originally envisioned (Nyberg, Kim, Habib, Levine & Tulving, 2010; Jacques, Kragel & Rubin, 2011; Fandakova, Johnson & Ghetti, 2021; Ritchey & Cooper, 2020; Richter, Cooper, Bays &

Simons, 2016; McCormick et al., 2020; Tulving 2002). On the micro level, several studies have now demonstrated that despite the stability of some spatially modulated hippocampal cells over long periods of time there is high cellular turnover (Ziv et al., 2013; Rubin, Geva, Sheintuch & Ziv, 2015; Kinsky et al., 2020; Hayashi, 2019; Hainmueller & Bartos, 2018), mirrored in synaptic turnover (Attardo, Fitzgerald & Schnitzer, 2015). This has led to discussion of memory models accounting for this synaptic volatility (Langille & Gallistel, 2020; Mau, Hasselmo & Cai, 2020; Barry & Maguire, 2019; Ziv & Brenner, 2018; Mongillo, Rumpel & Loewenstein, 2017). Here, we seek to unite how the mechanisms we raised in event construction (section 3) and event segmentation (sections 4 & 5) may facilitate subjective episodic recollection.

Memory can be phenomenologically distinguished as remembering (recollection) versus knowing (familiarity), subserved by separate neuronal structures (Tulving, 1985; Brown & Aggleton, 2001; Yonelinas, 2002; Ameen-Ali et al., 2015). With episodic recollection being critically reliant upon the hippocampus and fornices, as evidenced by non-human animal models and neuropsychological cases (Easton, Zinkivskay & Eacott, 2009; Eichenabaum et al., 2012; Aggleton & Brown 1999). Likewise for healthy participants, where successful recollection also depended on hippocampal activity (Richter et al., 2016), whereby the hippocampus can be necessary for cortical reinstatement (i.e., reinstatement of the content-specific activity at retrieval that is observed during encoding; Gordon, Rissman, Kiani & Wagner, 2014; Horner et al., 2015; Bone & Buchsbaum, 2021). However, cortical reinstatement may still occur without hippocampal involvement, although critically, the success of recollection is substantially reduced (Elward, Rugg & Vargha-Khadem, 2021). The experiential component is further realised by MTL patients being unable to vividly construct scenes, often describing a feeling of 'blankness' in doing so (Maguire & Mullally, 2013; Tulving, 1985), and therefore, some have posited that recollection by the hippocampus

is a threshold or index dependent process (Yonelinas, 2002; Teyler & DiScenna, 1986).

Some rodent CA1 place cells do not remap across environments and may indeed be indexing specific environmental experiences (Tanaka et al., 2018; Goode, Tanaka, Sahay & McHugh, 2020). These place cells are characterised by expressing the activity-dependent immediate early gene cellular feline osteosarcoma (c-Fos), which can be used as a biomarker for subsequent morphological and functional long-term synaptic plasticity (Yap & Greenberg, 2018; Choi et al., 2018). Moreover, c-Fos[+] double projecting ventral CA1 cells (to the basolateral amygdala and medial prefrontal cortex) were found to be preferentially activated during fear conditioning (Kim & Cho, 2017) and are markedly activated during environment exploration (Kim & Cho, 2017; Kinnavane, Amin, Olarte-Sánchez & Aggleton, 2017). In this way, a fundamental question is whether c-Fos^{+} CA1 cells are indexing specific events within a spatially stable environment. If so, such activity may be comparable to the event cells recorded in humans (Zheng et al., 2021; Yoo et al., 2021). It is also notable that triple projecting ventral CA1 task-responsive neurons were preferentially recruited during SWRs (Ciocchi, Passecker, Malagon-Vina, Mikus & Klausberger, 2015). To this end, a working hypothesis can be constructed for episodic recollection of *recent* experience: (i) primate spatial view cells and the hippocampal-oculomotor related activity (Rolls, 1999; Rueckemann & Buffalo, 2017; see sections 3.1. and 4.2) offers the necessary foundations to lay trace to an 'own eyes' perspective during event encoding (Zaman & Russell, 2021). (ii) A subset of event or c-Fos^{+} CA1 cells may enact as indices (including place cells; Tanaka et al., 2018) underlying event boundaries and especially event horizons to demarcate specific moments during ongoing events. (iii) These may formulise cellular assemblies which can be consolidated via SWRs (Malvache et al., 2016; Ciocchi et al., 2015) and further segment ongoing events. (iv) Subsequent recollection of these recently experienced events will require activation of the hippocampal index (Bone & Buchsbaum, 2021; Goode et al., 2020),

coordinating cortical reinstatement (Gordon et al.,2014; Bone & Buchsbaum, 2021; Richter et al., 2016; Horner et al., 2015).

6.3. Aging, Pathology and Individual Differences

This review and its resulting working hypotheses have addressed event cognition largely in the absence of aging, pathology (e.g., dementia), and individual differences, which are undoubtedly important disciplines of active research. We will therefore briefly describe some relevant findings which may act as a guide for future research. Recent work has suggested that older adults segment less, and rely more upon semantic knowledge to aid their segmentation and subsequent memory (Pitts, Smith, Newberry & Bailey, 2021). This is potentially underpinned by observed age-related changes in brain activity during event segmentation (Reagh et al., 2020). Moreover, as we have argued that SWRs may play a key role in event segmentation, it is noticeable that aged rats display a reduced SWR rate during wakeful task performance and rest (Wiegand et al., 2016; Cowen, Gray, Wiegand, Schimanski & Barnes, 2020).

In a similar vein, several non-human animal *in vivo* models of Alzheimer's disease pathology also display a reduced abundance of SWRs (Sanchez-Aguilera & Quintanilla, 2021; Jones, Gillespie, Yoon, Frank & Huang, 2019) and importantly, are impaired at an episodic memory task compared to age-matched controls (Davis, Eacott, Easton & Gigg, 2013a; Davis, Easton, Eacott & Gigg, 2013b). However, naturally aged mice at around 12 months show an impairment on an episodic memory task too (Davis et al., 2013a). We therefore suggest that future work should explore the relationship between SWRs and behaviour on episodic tasks in aging rodents and more Alzheimer's disease models. Additionally, examining individual differences in aging (Santangelo et al., 2021; Reagh et al., 2020) and mild cognitive impairment (Serra et al., 2020) may further elucidate processes of

event segmentation and episodic memory.

Finally, while we have briefly touched upon some contributing factors relating to individual variability of episodic memory, we acknowledge that the picture is far more complicated than what has insofar been discussed. For example, many molecular (Redondo & Morris, 2011; Lisman, Cooper, Sehgal & Silva. 2018) and neuromodulatory mechanisms (Duszkiewicz et al., 2019; O'Callaghan et al., 2021) contribute to the formation and persistence of a hippocampal index and may be influenced by variability that is biologically determined (Lee & Silva, 2009), or by one's experience before and after the time of event encoding (Yonelinas et al., 2019; Redondo & Morris, 2011; Gava et al., 2021; Plitt & Giocomo, 2021). Also, emerging research regarding system interactions during recollection in people with highly superior autobiographical memory have found differing neural activation compared to that of typical controls (Santangelo, Pedale, Macrì & Campolongo, 2020; Mazzoni et al., 2019; Santangelo et al., 2018). Therefore, given such evidence and known variability in humans (Palombo et al., 2018), there is a pressing need to refine behavioural measures of episodic memory in non-human animals that should become more sensitive to individual differences. This will ultimately allow us to utilise the increasingly complex invasive technologies at our disposal to further understand how aging, pathology and individual differences impact the neural mechanisms of episodic memory.

7. Conclusion

In order to holistically understand complex cognition such as episodic memory evidence spanning from molecular, cellular resolutions to meso-circuit, system levels, to cognition and behaviour (and even the experiential level) needs to be assimilated. In this review, we have united elements of the cognitive EHM with hippocampal formation physiological mechanisms, to allow development of a neurocognitive framework addressing event construction, monitoring, discrimination and subsequent episodic recollection of recent experience. Such a cross-species approach is necessary to link the rapidly developing human oriented and non-human based research fields in the episodic and spatial domains. Moreover, we have argued that hippocampal activity during event segmentation on shorter timescales (fine-grained event boundaries) is distinct from event horizons; hippocampal related activity during event segmentation on longer timescales (coarse-grained event boundaries). Also, we have challenged the typical 'outside-in' perspective (Buzsáki, 2019) up-held in the event segmentation literature, by proposing that the brain inherently segments events due to transitions in network states. We reiterate that this viewpoint does not invalidate externally driven event segmentation but envisages that external and internal segmentation operates in tandem to facilitate episodic memory, raising many novel hypotheses regarding episodic cognition in various fields.

Declaration of Competing Interest

Authors declare no conflict of interest to disclose.

Acknowledgements

References

Abadchi, J. K., Nazari-Ahangarkolaee, M., Gattas, S., Bermudez-Contreras, E., Luczak, A., McNaughton, B. L., & Mohajerani, M. H. (2020). Spatiotemporal patterns of neocortical activity around hippocampal sharp-wave ripples. *Elife*, *9*, e51972.

Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia, and the hippocampal–anterior thalamic axis. *Behavioral and brain sciences*, *22*(3), 425-444.

Allen, T. A., & Fortin, N. J. (2013). The evolution of episodic memory. *Proceedings of the National Academy of Sciences*, *110*(Supplement 2), 10379-10386.

Allen, R. J., Vargha-Khadem, F., & Baddeley, A. D. (2014). Item-location binding in working memory: Is it hippocampus-dependent?. *Neuropsychologia*, *59*, 74-84.

Alme, C. B., Miao, C., Jezek, K., Treves, A., Moser, E. I., & Moser, M. B. (2014). Place cells in the hippocampus: eleven maps for eleven rooms. *Proceedings of the National Academy of Sciences*, *111*(52), 18428-18435.

Altmann, G., & Ekves, Z. (2019). Events as intersecting object histories: A new theory of event representation. *Psychological Review*, *126*(6), 817.

Aly, M., Ranganath, C., & Yonelinas, A. P. (2013). Detecting changes in scenes: The hippocampus is critical for strength-based perception. *Neuron*, *78*(6), 1127-1137.

Ameen-Ali, K. E., Easton, A., & Eacott, M. J. (2015). Moving beyond standard procedures to assess spontaneous recognition memory. *Neuroscience & Biobehavioral Reviews*, *53*, 37-51.

Anderson, M. I., & Jeffery, K. J. (2003). Heterogeneous modulation of place cell firing by changes in context. *Journal of Neuroscience*, *23*(26), 8827-8835.

Armson, M. J., Diamond, N. B., Levesque, L., Ryan, J. D., & Levine, B. (2021). Vividness of recollection is supported by eye movements in individuals with high, but not low trait autobiographical memory. *Cognition*, *206*, 104487.

Aronov, D., Nevers, R., & Tank, D. W. (2017). Mapping of a non-spatial dimension by the hippocampal–entorhinal circuit. *Nature*, *543*(7647), 719-722.

Attardo, A., Fitzgerald, J. E., & Schnitzer, M. J. (2015). Impermanence of dendritic spines in live adult CA1 hippocampus. *Nature*, *523*(7562), 592-596.

Axmacher, N., Elger, C. E., & Fell, J. (2008). Ripples in the medial temporal lobe are relevant for human memory consolidation. *Brain*, *131*(7), 1806-1817.

Bailey, H. R., Zacks, J. M., Hambrick, D. Z., Zacks, R. T., Head, D., Kurby, C. A., & Sargent, J. Q. (2013). Medial temporal lobe volume predicts elders' everyday memory. *Psychological science*, *24*(7), 1113-1122.

Baldassano, C., Beck, D. M., & Fei-Fei, L. (2013). Differential connectivity within the parahippocampal place area. *NeuroImage*, *75*, 228-237.

Baldassano, C., Chen, J., Zadbood, A., Pillow, J. W., Hasson, U., & Norman, K. A. (2017). Discovering event structure in continuous narrative perception and memory. *Neuron*, *95*(3), 709- 721.

Barker, G. R. I., & Warburton, E. C. (2020). Putting objects in context: A prefrontal– hippocampal perirhinal cortex network. *Brain and Neuroscience Advances*, *4*, 1-11.

Barron, H. C., Reeve, H. M., Koolschijn, R. S., Perestenko, P. V., Shpektor, A., Nili, H., ... & Dupret, D. (2020). Neuronal computation underlying inferential reasoning in humans and mice. *Cell*, *183*(1), 228-243.

Barry, C., Ginzberg, L. L., O'Keefe, J., & Burgess, N. (2012). Grid cell firing patterns signal nvironmental novelty by expansion. *Proceedings of the National Academy of Sciences*, *109*(43), 17687-17692.

Barry, D. N., & Maguire, E. A. (2019). Remote memory and the hippocampus: A constructive critique. *Trends in cognitive sciences*, *23*(2), 128-142.

Bartlett, F.C. (1932). Remembering: A Study in Experimental and Social Psychology. Cambridge University Press.

Beed, P., de Filippo, R., Holman, C., Johenning, F. W., Leibold, C., Caputi, A., ... & Schmitz, D. (2020). Layer 3 pyramidal cells in the medial entorhinal cortex orchestrate up-down states and entrain the deep layers differentially. *Cell Reports*, *33*(10), 108470.

Ben-Ari, Y. (2001). Developing networks play a similar melody. *Trends in neurosciences*, *24*(6), 353 360.

Ben-Ari, Y., Gaiarsa, J. L., Tyzio, R., & Khazipov, R. (2007). GABA: a pioneer transmitter that excites immature neurons and generates primitive oscillations. *Physiological reviews*, *87*(4), 1215-1284.

Ben-Yakov, A., & Dudai, Y. (2011). Constructing realistic engrams: poststimulus activity of hippocampus and dorsal striatum predicts subsequent episodic memory. *Journal of Neuroscience*, *31*(24), 9032-9042.

Ben-Yakov, A., Eshel, N., & Dudai, Y. (2013). Hippocampal immediate poststimulus activity in the encoding of consecutive naturalistic episodes. *Journal of Experimental Psychology: General*, *142*(4), 1255.

Ben-Yakov, A., & Henson, R. N. (2018). The hippocampal film editor: sensitivity and specificity to event boundaries in continuous experience. *Journal of Neuroscience*, *38*(47), 10057- 10068.

Beukers, A. O., Buschman, T. J., Cohen, J. D., & Norman, K. A. (2021). Is Activity Silent Working Memory Simply Episodic Memory?. *Trends in Cognitive Sciences*, *25*(4), 284-293.

Bilkey, D. K., & Jensen, C. (2021). Neural markers of event boundaries. *Topics in cognitive science*, *13*(1), 128-141.

Bingman, V. P., & Sharp, P. E. (2006). Neuronal implementation of hippocampal-mediated spatial behavior: a comparative evolutionary perspective. *Behavioral and Cognitive Neuroscience Reviews*, *5*(2), 80-91.

Bird, C. M. (2020). How do we remember events?. *Current Opinion in Behavioral Sciences*, *32*, 120 125.

Bittner, K. C., Milstein, A. D., Grienberger, C., Romani, S., & Magee, J. C. (2017). Behavioral time scale synaptic plasticity underlies CA1 place fields. *Science*, *357*(6355), 1033-1036.

Böhm, C., Peng, Y., Maier, N., Winterer, J., Poulet, J. F., Geiger, J. R., & Schmitz, D. (2015). Functional diversity of subicular principal cells during hippocampal ripples. *Journal of Neuroscience*, *35*(40), 13608-13618.

Bone, M. B., & Buchsbaum, B. R. (2021). Detailed Episodic Memory Depends on Concurrent Reactivation of Basic Visual Features within the Posterior Hippocampus and Early Visual Cortex. *Cerebral cortex communications*, *2*(3), tgab045.

Bourboulou, R., Marti, G., Michon, F. X., El Feghaly, E., Nouguier, M., Robbe, D., ... & Epsztein, J. (2019). Dynamic control of hippocampal spatial coding resolution by local visual cues. *Elife*, *8*, e44487.

Brown, M. W., & Aggleton, J. P. (2001). Recognition memory: what are the roles of the perirhinal cortex and hippocampus?. *Nature Reviews Neuroscience*, *2*(1), 51-61.

Brunec, I. K., Moscovitch, M., & Barense, M. D. (2018). Boundaries shape cognitive representations of spaces and events. *Trends in cognitive sciences*, *22*(7), 637-650.

Brunec, I. K., Ozubko, J. D., Ander, T., Guo, R., Moscovitch, M., & Barense, M. D. (2020). Turns during navigation act as boundaries that enhance spatial memory and expand time estimation. *Neuropsychologia*, *141*, 107437.

Buhl, D. L., & Buzsáki, G. (2005). Developmental emergence of hippocampal fast-field "ripple" oscillations in the behaving rat pups. *Neuroscience*, *134*(4), 1423-1430.

Bulkin, D. A., Law, L. M., & Smith, D. M. (2016). Placing memories in context: Hippocampal representations promote retrieval of appropriate memories. *Hippocampus*, *26*(7), 958-971.

Buzsáki, G. (2019). *The brain from inside out*. Oxford University Press.

Buzsáki, G. (2015). Hippocampal sharp wave-ripple: A cognitive biomarker for episodic memory and planning. *Hippocampus*, *25*(10), 1073-1188.

Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science*, *304*(5679), 1926-1929.

Buzsáki, G., & Tingley, D. (2018). Space and time: The hippocampus as a sequence generator. *Trends in cognitive sciences*, *22*(10), 853-869.

Carr, M. F., Karlsson, M. P., & Frank, L. M. (2012). Transient slow gamma synchrony underlies hippocampal memory replay. *Neuron*, *75*(4), 700-713.

Cembrowski, M. S., Phillips, M. G., DiLisio, S. F., Shields, B. C., Winnubst, J., Chandrashekar, J., ... & Spruston, N. (2018). Dissociable structural and functional hippocampal outputs via distinct subiculum cell classes. *Cell*, *173*(5), 1280-1292.

Cembrowski, M. S., & Spruston, N. (2019). Heterogeneity within classical cell types is the rule: lessons from hippocampal pyramidal neurons. *Nature Reviews Neuroscience*, *20*(4), 193- 204.

Chadwick, M. J., Mullally, S. L., & Maguire, E. A. (2013). The hippocampus extrapolates beyond the view in scenes: an fMRI study of boundary extension. *Cortex*, *49*(8), 2067-2079.

Chang, C. H., Lazaridi, C., Yeshurun, Y., Norman, K. A., & Hasson, U. (2021). Relating the past with the present: Information integration and segregation during ongoing narrative processing. *Journal of Cognitive Neuroscience*, *33*(6), 1106-1128.

Chao, O. Y., Huston, J. P., Li, J. S., Wang, A. L., & de Souza Silva, M. A. (2016). The medial prefrontal cortex—Lateral entorhinal cortex circuit is essential for episodic-like memory and associative object-recognition. *Hippocampus*, *26*(5), 633-645.

Chao, O. Y., Nikolaus, S., Brandão, M. L., Huston, J. P., & de Souza Silva, M. A. (2017). Interaction between the medial prefrontal cortex and hippocampal CA1 area is essential for episodic-like memory in rats. *Neurobiology of Learning and Memory*, *141*, 72-77.

Chen, Y. Y., Aponik-Gremillion, L., Bartoli, E., Yoshor, D., Sheth, S. A., & Foster, B. L. (2021). Stability of ripple events during task engagement in human hippocampus. *Cell reports*, *35*(13), 109304.

Chen, J., Honey, C. J., Simony, E., Arcaro, M. J., Norman, K. A., & Hasson, U. (2016). Accessing real-life episodic information from minutes versus hours earlier modulates hippocampal and high-order cortical dynamics. *Cerebral cortex*, *26*(8), 3428-3441.

Chen, J., Leong, Y. C., Honey, C. J., Yong, C. H., Norman, K. A., & Hasson, U. (2017). Shared memories reveal shared structure in neural activity across individuals. *Nature neuroscience*, *20*(1), 115-125.

Chenani, A., Sabariego, M., Schlesiger, M. I., Leutgeb, J. K., Leutgeb, S., & Leibold, C. (2019). Hippocampal CA1 replay becomes less prominent but more rigid without inputs from medial entorhinal cortex. *Nature communications*, *10*(1), 1-13.

Cheng, A., Walther, D. B., Park, S., & Dilks, D. D. (2021). Concavity as a diagnostic feature of visual scenes. *NeuroImage*, *232*, 117920.

Christoff, K., Irving, Z. C., Fox, K. C., Spreng, R. N., & Andrews-Hanna, J. R. (2016). Mind wandering as spontaneous thought: a dynamic framework. *Nature Reviews Neuroscience*, *17*(11), 718-731.

Chrobak, J. J., & Buzsáki, G. (1994). Selective activation of deep layer (V-VI) retrohippocampal cortical neurons during hippocampal sharp waves in the behaving rat. *Journal of Neuroscience*, *14*(10), 6160-6170.

Choi, J. H., Sim, S. E., Kim, J. I., Choi, D. I., Oh, J., Ye, S., ... & Kaang, B. K. (2018). Interregional synaptic maps among engram cells underlie memory formation. *Science*, *360*(6387), 430-435.

Ciocchi, S., Passecker, J., Malagon-Vina, H., Mikus, N., & Klausberger, T. (2015). Selective information routing by ventral hippocampal CA1 projection neurons. *Science*, *348*(6234), 560-563.

Clewett, D., Gasser, C., & Davachi, L. (2020). Pupil-linked arousal signals track the temporal organization of events in memory. *Nature communications*, *11*(1), 1-14.

Clewett, D., DuBrow, S., & Davachi, L. (2019). Transcending time in the brain: How event memories are constructed from experience. *Hippocampus*, *29*(3), 162-183.

Cohn-Sheehy, B. I., Delarazan, A. I., Crivelli-Decker, J. E., Reagh, Z. M., Mundada, N. S., Yonelinas, A. P., ... & Ranganath, C. (2021). Narratives bridge the divide between distant events in episodic memory. *Memory & Cognition*, 1-17.

Cohn-Sheehy, B. I., Delarazan, A. I., Reagh, Z. M., Crivelli-Decker, J. E., Kim, K., Barnett, A. J., Zacks, J. M., & Ranganath, C. (in press). The hippocampus constructs narrative memories across distant events. *Current Biology*. https://doi.org/10.1016/j.cub.2021.09.013

Cooper, R. A., & Ritchey, M. (2020). Progression from feature-specific brain activity to hippocampal binding during episodic encoding. *Journal of Neuroscience*, *40*(8), 1701-1709.

Corkin, S. (1984). Lasting consequences of bilateral medial temporal lobectomy: Clinical course and experimental findings in HM. In Seminars in Neurology (Vol. 4, No. 2, pp. 249-259)

Cowen, S. L., Gray, D. T., Wiegand, J. P. L., Schimanski, L. A., & Barnes, C. A. (2020). Age-associated changes in waking hippocampal sharp-wave ripples. *Hippocampus*, *30*(1), 28-38.

Cutting, J. E. (2014). Event segmentation and seven types of narrative discontinuity in popular movies. *Acta psychologica*, *149*, 69-77.

Cutting, J., & Iricinschi, C. (2015). Re-presentations of space in hollywood movies: An event indexing analysis. *Cognitive Science*, *39*(2), 434-456.

Danjo, T., Toyoizumi, T., & Fujisawa, S. (2018). Spatial representations of self and other in the hippocampus. *Science*, *359*(6372), 213-218.

Davis, E. E., Chemnitz, E., Collins, T. K., Geerligs, L., & Campbell, K. L. (2021). Looking the same, but remembering differently: Preserved eye-movement synchrony with age during movie watching. *Psychology and Aging*, *36*(5), 604-615.

Davis, K. E., Eacott, M. J., Easton, A., & Gigg, J. (2013). Episodic-like memory is sensitive to both Alzheimer's-like pathological accumulation and normal ageing processes in mice. *Behavioural brain research*, *254*, 73-82.

Davis, K. E., Easton, A., Eacott, M. J., & Gigg, J. (2013). Episodic-like memory for what-where-which occasion is selectively impaired in the 3xTgAD mouse model of Alzheimer's disease. *Journal of Alzheimer's Disease*, *33*(3), 681-698.

Davoudi, H., & Foster, D. J. (2019). Acute silencing of hippocampal CA3 reveals a dominant role in place field responses. *Nature neuroscience*, *22*(3), 337-342.

de Souza Silva, M. A., Huston, J. P., Wang, A. L., Petri, D., & Chao, O. Y. H. (2015). Evidence for a specific integrative mechanism for episodic memory mediated by AMPA/kainate receptors in a circuit involving medial prefrontal cortex and hippocampal CA3 region. *Cerebral Cortex*, *26*(7), 3000-3009.

Derdikman, D., Whitlock, J. R., Tsao, A., Fyhn, M., Hafting, T., Moser, M. B., & Moser, E. I. (2009). Fragmentation of grid cell maps in a multicompartment environment. *Nature neuroscience*, *12*(10), 1325-1332.

Deshmukh, S. S., & Knierim, J. J. (2013). Influence of local objects on hippocampal representations: Landmark vectors and memory. *Hippocampus*, *23*(4), 253-267.

Diba, K., & Buzsáki, G. (2007). Forward and reverse hippocampal place-cell sequences during ripples. *Nature neuroscience*, *10*(10), 1241-1242.

Donato, F., Alberini, C. M., Amso, D., Dragoi, G., Dranovsky, A., & Newcombe, N. S. (2021). The ontogeny of hippocampus-dependent memories. *Journal of Neuroscience*, *41*(5), 920-926.

Dong, C., Madar, A. D., & Sheffield, M. E. (2021). Distinct place cell dynamics in CA1 and CA3 encode experience in new environments. *Nature communications*, *12*(1), 1-13.

Dragoi, G., & Tonegawa, S. (2011). Preplay of future place cell sequences by hippocampal cellular assemblies. *Nature*, *469*(7330), 397-401.

Dragoi, G., & Tonegawa, S. (2013). Distinct preplay of multiple novel spatial experiences in the rat. *Proceedings of the National Academy of Sciences*, *110*(22), 9100-9105.

Duff, M. C., Hengst, J., Tranel, D., & Cohen, N. J. (2006). Development of shared information in communication despite hippocampal amnesia. *Nature neuroscience*, *9*(1), 140-146.

Duszkiewicz, A. J., McNamara, C. G., Takeuchi, T., & Genzel, L. (2019). Novelty and dopaminergic modulation of memory persistence: a tale of two systems. *Trends in neurosciences*, *42*(2), 102-114.

Eacott, M. J., & Easton, A. (2010). Episodic memory in animals: remembering which occasion. *Neuropsychologia*, *48*(8), 2273-2280.

Eacott, M. J., & Norman, G. (2004). Integrated memory for object, place, and context in rats: a possible model of episodic-like memory?. *Journal of Neuroscience*, *24*(8), 1948-1953.

Easton, A., Zinkivskay, A., & Eacott, M. J. (2009). Recollection is impaired, but familiarity remains intact in rats with lesions of the fornix. *Hippocampus*, *19*(9), 837-843.

Eichenbaum, H. (2004). Hippocampus: cognitive processes and neural representations that underlie declarative memory. *Neuron*, *44*(1), 109-120.

Eichenbaum, H. (2014). Time cells in the hippocampus: a new dimension for mapping memories. *Nature Reviews Neuroscience*, *15*(11), 732-744.

Eichenbaum, H., Sauvage, M., Fortin, N., Komorowski, R., & Lipton, P. (2012). Towards a functional organization of episodic memory in the medial temporal lobe. *Neuroscience & Biobehavioral Reviews*, *36*(7), 1597-1608.

Ekstrom, A. D., Kahana, M. J., Caplan, J. B., Fields, T. A., Isham, E. A., Newman, E. L., & Fried, I. 2003). Cellular networks underlying human spatial navigation. *Nature*, *425*(6954), 184-188.

Eliav, T., Maimon, S. R., Aljadeff, J., Tsodyks, M., Ginosar, G., Las, L., & Ulanovsky, N. (2021). Multiscale representation of very large environments in the hippocampus of flying bats. *Science*, *372*(6545).

Ellamil, M., Fox, K. C., Dixon, M. L., Pritchard, S., Todd, R. M., Thompson, E., & Christoff, K. (2016). Dynamics of neural recruitment surrounding the spontaneous arising of thoughts in experienced mindfulness practitioners. *NeuroImage*, *136*, 186-196.

Elward, R. L., Rugg, M. D., & Vargha-Khadem, F. (2021). When the brain, but not the person, remembers: Cortical reinstatement is modulated by retrieval goal in developmental amnesia. *Neuropsychologia*, *154*, 107788.

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*(6676), 598-601.

Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: recognition, navigation, or encoding?. *Neuron*, *23*(1), 115-125.

Epsztein, J., Brecht, M., & Lee, A. K. (2011). Intracellular determinants of hippocampal CA1 place and silent cell activity in a novel environment. *Neuron*, *70*(1), 109-120.

Fandakova, Y., Johnson, E. G., & Ghetti, S. (2021). Distinct neural mechanisms underlie subjective and objective recollection and guide memory-based decision making. *Elife*, *10*, e62520.

Farooq, U., & Dragoi, G. (2019). Emergence of preconfigured and plastic time-compressed sequences in early postnatal development. *Science*, *363*(6423), 168-173.

Fernández-Ruiz, A., Oliva, A., de Oliveira, E. F., Rocha-Almeida, F., Tingley, D., & Buzsáki, G. (2019). Long-duration hippocampal sharp wave ripples improve memory. *Science*, *364*(6445), 1082-1086.

Fernández-Ruiz, A., Oliva, A., Soula, M., Rocha-Almeida, F., Nagy, G. A., Martin-Vazquez, G., & Buzsáki, G. (2021). Gamma rhythm communication between entorhinal cortex and dentate gyrus neuronal assemblies. *Science*, *372*(6537).

Finnie, P., Komorowski, R., & Bear, M. (2021). The spatiotemporal organization of experience dictates hippocampal involvement in primary visual cortical plasticity. *Current Biology*, *31*(18), 3996-4008.

Fortin, N. J., Agster, K. L. & Eichenbaum, H. Critical role of the hippocampus in memory for sequences of events. *Nature Neuroscience*. **5**, 458–462 (2002).

Foster, D. J. (2017). Replay comes of age. *Annual review of neuroscience*, *40*, 581-602.

Foster, D. J., & Wilson, M. A. (2006). Reverse replay of behavioural sequences in hippocampal place cells during the awake state. *Nature*, *440*(7084), 680-683.

Frank, L. M., Stanley, G. B., & Brown, E. N. (2004). Hippocampal plasticity across multiple days of exposure to novel environments. *Journal of Neuroscience*, *24*(35), 7681-7689.

Gaffan, D. (2002). Against memory systems. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *357*(1424), 1111-1121.

Gardner, R. J., Lu, L., Wernle, T., Moser, M. B., & Moser, E. I. (2019). Correlation structure of grid cells is preserved during sleep. *Nature neuroscience*, *22*(4), 598-608.

Gauthier, J. L., & Tank, D. W. (2018). A dedicated population for reward coding in the hippocampus. *Neuron*, *99*(1), 179-193.

Gava, G. P., McHugh, S. B., Lefèvre, L., Lopes-dos-Santos, V., Trouche, S., El-Gaby, M., ... & Dupret, D. (2021). Integrating new memories into the hippocampal network activity space. *Nature neuroscience*, *24*(3), 326-330.

Geiller, T., Fattahi, M., Choi, J. S., & Royer, S. (2017). Place cells are more strongly tied to landmarks in deep than in superficial CA1. *Nature communications*, *8*(1), 1-11.

Geva-Sagiv, M., Romani, S., Las, L., & Ulanovsky, N. (2016). Hippocampal global remapping for different sensory modalities in flying bats. *Nature neuroscience*, *19*(7), 952-958.

Girardeau, G., Benchenane, K., Wiener, S. I., Buzsáki, G., & Zugaro, M. B. (2009). Selective suppression of hippocampal ripples impairs spatial memory. *Nature neuroscience*, *12*(10), 1222-1223.

Goode, T. D., Tanaka, K. Z., Sahay, A., & McHugh, T. J. (2020). An integrated index: Engrams, place cells, and hippocampal memory. *Neuron*, *107*(5), 805-820.

Goodrich, R. I., Baer, T. L., Quent, J. A., & Yonelinas, A. P. (2019). Visual working memory impairments for single items following medial temporal lobe damage. *Neuropsychologia*, *134*, 107227.

Goodrich, R. I., & Yonelinas, A. P. (2016). The medial temporal lobe supports sensing-based visual working memory. *Neuropsychologia*, *89*, 485-494.

Gordon, A. M., Rissman, J., Kiani, R., & Wagner, A. D. (2014). Cortical reinstatement mediates the relationship between content-specific encoding activity and subsequent recollection decisions. *Cerebral Cortex*, *24*(12), 3350-3364.

Graves, A. R., Moore, S. J., Bloss, E. B., Mensh, B. D., Kath, W. L., & Spruston, N. (2012). Hippocampal pyramidal neurons comprise two distinct cell types that are countermodulated by metabotropic receptors. *Neuron*, *76*(4), 776-789.

Greenberg, D. L., & Rubin, D. C. (2003). The neuropsychology of autobiographical memory. *Cortex*, *39*(4-5), 687-728.

Grieves, R. M., Jenkins, B. W., Harland, B. C., Wood, E. R., & Dudchenko, P. A. (2016). Place field repetition and spatial learning in a multicompartment environment. *Hippocampus*, *26*(1), 118 134.

Griffiths, B. J., & Fuentemilla, L. (2020). Event conjunction: How the hippocampus integrates episodic memories across event boundaries. *Hippocampus*, *30*(2), 162-171.

Grosmark, A. D., & Buzsáki, G. (2016). Diversity in neural firing dynamics supports both rigid and learned hippocampal sequences. *Science*, *351*(6280), 1440-1443.

Gupta, A. S., van der Meer, M. A., Touretzky, D. S., & Redish, A. D. (2010). Hippocampal replay is not a simple function of experience. *Neuron*, *65*(5), 695-705.

Gupta, A. S., van der Meer, M. A., Touretzky, D. S., & Redish, A. D. (2012). Segmentation of spatial experience by hippocampal theta sequences. *Nature neuroscience*, *15*(7), 1032-1039.

Guzman, S. J., Schlögl, A., Frotscher, M., & Jonas, P. (2016). Synaptic mechanisms of pattern completion in the hippocampal CA3 network. *Science*, *353*(6304), 1117-1123.

Hahn, T. T., McFarland, J. M., Berberich, S., Sakmann, B., & Mehta, M. R. (2012). Spontaneous persistent activity in entorhinal cortex modulates cortico-hippocampal interaction in vivo. *Nature neuroscience*, *15*(11), 1531-1538.

Hainmueller, T., & Bartos, M. (2018). Parallel emergence of stable and dynamic memory engrams in the hippocampus. *Nature*, *558*(7709), 292-296.

Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, *436*(7052), 801-806.

Harris, K. D., Csicsvari, J., Hirase, H., Dragoi, G., & Buzsáki, G. (2003). Organization of cell assemblies in the hippocampus. *Nature*, *424*(6948), 552-556.

Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences*, *104*(5), 1726-1731.

Hassabis, D., & Maguire, E. A. (2007). Deconstructing episodic memory with construction. *Trends in cognitive sciences*, *11*(7), 299-306.

Hasselmo, M. E. (2006). The role of acetylcholine in learning and memory. *Current opinion in neurobiology*, *16*(6), 710-715.

Hasson, U., Chen, J., & Honey, C. J. (2015). Hierarchical process memory: memory as an integral component of information processing. *Trends in cognitive sciences*, *19*(6), 304-313.

Hayashi, Y. (2019). NMDA receptor-dependent dynamics of hippocampal place cell ensembles. *Journal of Neuroscience*, *39*(26), 5173-5182.

Herzog, L. E., Pascual, L. M., Scott, S. J., Mathieson, E. R., Katz, D. B., & Jadhav, S. P. (2019). Interaction of taste and place coding in the hippocampus. *Journal of Neuroscience*, *39*(16), 3057-3069.

Heys, J. G., & Dombeck, D. A. (2018). Evidence for a subcircuit in medial entorhinal cortex representing elapsed time during immobility. *Nature neuroscience*, *21*(11), 1574-1582.

Hitti, F. L., & Siegelbaum, S. A. (2014). The hippocampal CA2 region is essential for social memory. *Nature*, *508*(7494), 88-92.

Honey, C. J., Newman, E. L., & Schapiro, A. C. (2017). Switching between internal and external modes: a multiscale learning principle. *Network Neuroscience*, *1*(4), 339-356.

Horner, A. J., Bisby, J. A., Bush, D., Lin, W. J., & Burgess, N. (2015). Evidence for holistic episodic recollection via hippocampal pattern completion. *Nature communications*, *6*(1), 1-11.

Horner, A. J., Bisby, J. A., Wang, A., Bogus, K., & Burgess, N. (2016). The role of spatial boundaries in shaping long-term event representations. *Cognition*, *154*, 151-164.

Høydal, Ø. A., Skytøen, E. R., Andersson, S. O., Moser, M. B., & Moser, E. I. (2019). Object-vector coding in the medial entorhinal cortex. *Nature*, *568*(7752), 400-404.

Hulse, B. K., Moreaux, L. C., Lubenov, E. V., & Siapas, A. G. (2016). Membrane potential dynamics of CA1 pyramidal neurons during hippocampal ripples in awake mice. *Neuron*, *89*(4), 800 813.

Hunt, D. L., Linaro, D., Si, B., Romani, S., & Spruston, N. (2018). A novel pyramidal cell type promotes sharp-wave synchronization in the hippocampus. *Nature neuroscience*, *21*(7), 985 995.

Hwaun, E., & Colgin, L. L. (2019). CA3 place cells that represent a novel waking experience are preferentially reactivated during sharp wave-ripples in subsequent sleep. *Hippocampus*, *29*(10), 921-938.

Imbrosci, B., Nitzan, N., McKenzie, S., Donoso, J. R., Swaminathan, A., Böhm, C., ... & Schmitz, D. (2021). Subiculum as a generator of sharp wave-ripples in the rodent hippocampus. *Cell Reports*, *35*(3), 109021.

Insausti, R. (1993). Comparative anatomy of the entorhinal cortex and hippocampus in mammals. *Hippocampus*, *3*(S1), 19-26.

Intraub, H., & Richardson, M. (1989). Wide-angle memories of close-up scenes. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *15*(2), 179.

Isomura, Y., Sirota, A., Özen, S., Montgomery, S., Mizuseki, K., Henze, D. A., & Buzsáki, G. (2006). Integration and segregation of activity in entorhinal-hippocampal subregions by neocortical slow oscillations. *Neuron*, *52*(5), 871-882.

Jacobs, N. S., Allen, T. A., Nguyen, N., & Fortin, N. J. (2013). Critical role of the hippocampus in memory for elapsed time. *Journal of Neuroscience*, *33*(34), 13888-13893.

Jacobs, J., Weidemann, C. T., Miller, J. F., Solway, A., Burke, J. F., Wei, X. X., ... & Kahana, M. J. (2013). Direct recordings of grid-like neuronal activity in human spatial navigation. *Nature neuroscience*, *16*(9), 1188-1190.

Jacques, P. L. S., Kragel, P. A., & Rubin, D. C. (2011). Dynamic neural networks supporting memory retrieval. *NeuroImage*, *57*(2), 608-616.

Jercog, P. E., Ahmadian, Y., Woodruff, C., Deb-Sen, R., Abbott, L. F., & Kandel, E. R. (2019). Heading direction with respect to a reference point modulates place-cell activity. *Nature communications*, *10*(1), 1-8.

Jezek, K., Henriksen, E. J., Treves, A., Moser, E. I., & Moser, M. B. (2011). Theta-paced flickering between place-cell maps in the hippocampus. *Nature*, *478*(7368), 246-249.

Jimenez, J. C., Berry, J. E., Lim, S. C., Ong, S. K., Kheirbek, M. A., & Hen, R. (2020). Contextual fear memory retrieval by correlated ensembles of ventral CA1 neurons. *Nature communications*, *11*(1), 1-11.

Jin, S. W., & Lee, I. (2021). Differential encoding of place value between the dorsal and intermediate hippocampus. *Current Biology*, *31*(14), 3053-3072.

Jones, E. A., Gillespie, A. K., Yoon, S. Y., Frank, L. M., & Huang, Y. (2019). Early hippocampal sharp-wave ripple deficits predict later learning and memory impairments in an Alzheimer's disease mouse model. *Cell reports*, *29*(8), 2123-2133.

Jonin, P. Y., Calia, C., Muratot, S., Belliard, S., Duché, Q., Barbeau, E. J., & Parra, M. A. (2019). Refining understanding of working memory buffers through the construct of binding: Evidence from a single case informs theory and clinical practise. *Cortex*, *112*, 37-57.

Joo, H. R., & Frank, L. M. (2018). The hippocampal sharp wave–ripple in memory retrieval for immediate use and consolidation. *Nature Reviews Neuroscience*, *19*(12), 744-757.

Josselyn, S. A., & Frankland, P. W. (2018). Memory allocation: mechanisms and function. *Annual review of neuroscience*, *41*, 389-413.

Kamiński, J., Sullivan, S., Chung, J. M., Ross, I. B., Mamelak, A. N., & Rutishauser, U. (2017). Persistently active neurons in human medial frontal and medial temporal lobe support working memory. *Nature neuroscience*, *20*(4), 590-601.

Karapanagiotidis, T., Bernhardt, B. C., Jefferies, E., & Smallwood, J. (2017). Tracking thoughts: Exploring the neural architecture of mental time travel during mind wandering. *NeuroImage*, *147*, 272-281.

Karlsson, K. Æ., Mohns, E. J., di Prisco, G. V., & Blumberg, M. S. (2006). On the co-occurrence of startles and hippocampal sharp waves in newborn rats. *Hippocampus*, *16*(11), 959-965.

Kay, K., Chung, J. E., Sosa, M., Schor, J. S., Karlsson, M. P., Larkin, M. C., ... & Frank, L. M. (2020). Constant sub-second cycling between representations of possible futures in the hippocampus. *Cell*, *180*(3), 552-567.

Kay, K., & Frank, L. M. (2019). Three brain states in the hippocampus and cortex. *Hippocampus*, *29*(3), 184-238.

Kay, K., Sosa, M., Chung, J. E., Karlsson, M. P., Larkin, M. C., & Frank, L. M. (2016). A hippocampal network for spatial coding during immobility and sleep. *Nature*, *531*(7593), 185- 190.

Kelemen, E., & Fenton, A. A. (2010). Dynamic grouping of hippocampal neural activity during cognitive control of two spatial frames. *PLoS biology*, *8*(6), e1000403.

Kelemen, E., & Fenton, A. A. (2016). Coordinating different representations in the hippocampus. *Neurobiology of learning and memory*, *129*, 50-59.

Kesner, R. P. Gilbert, P. E. & Barua, L. A. The role of the hippocampus in memory for the temporal order of a sequence of odors. *Behavioral. Neuroscience.* **116**, 286–290 (2002).

Kesner, R. P., Hunsaker, M. R., & Gilbert, P. E. (2005). The role of CA1 in the acquisition of an object-trace-odor paired associate task. *Behavioral neuroscience*, *119*(3), 781.

Killian, N. J., Potter, S. M., & Buffalo, E. A. (2015). Saccade direction encoding in the primate entorhinal cortex during visual exploration. *Proceedings of the National Academy of Sciences*, *112*(51), 15743-15748.

Kim, W. B., & Cho, J. H. (2017). Synaptic targeting of double-projecting ventral CA1 hippocampal neurons to the medial prefrontal cortex and basal amygdala. *Journal of Neuroscience*, *37*(19), 4868-4882.

Kim, Y., & Spruston, N. (2012). Target-specific output patterns are predicted by the distribution of regular-spiking and bursting pyramidal neurons in the subiculum. *Hippocampus*, *22*(4), 693 706.

Kinnavane, L., Amin, E., Olarte-Sánchez, C. M., & Aggleton, J. P. (2017). Medial temporal pathways for contextual learning: Network c-fos mapping in rats with or without perirhinal cortex lesions. *Brain and neuroscience advances*, *1*, 2398212817694167.

Kinsky, N. R., Mau, W., Sullivan, D. W., Levy, S. J., Ruesch, E. A., & Hasselmo, M. E. (2020). Trajectory-modulated hippocampal neurons persist throughout memory-guided navigation. *Nature communications*, *11*(1), 1-14.

Kitamura, T., Pignatelli, M., Suh, J., Kohara, K., Yoshiki, A., Abe, K., & Tonegawa, S. (2014). Island cells control temporal association memory. *Science*, *343*(6173), 896-901.

Kornblith, S., Quiroga, R. Q., Koch, C., Fried, I., & Mormann, F. (2017). Persistent single-neuron activity during working memory in the human medial temporal lobe. *Current Biology*, *27*(7), 1026-1032.

Koster, R., Chadwick, M. J., Chen, Y., Berron, D., Banino, A., Düzel, E., ... & Kumaran, D. (2018). Big-loop recurrence within the hippocampal system supports integration of information across episodes. *Neuron*, *99*(6), 1342-1354.

Kragel, J. E., Schuele, S., VanHaerents, S., Rosenow, J. M., & Voss, J. L. (2021). Rapid coordination of effective learning by the human hippocampus. *Science Advances*, *7*(25), eabf7144.

Kubie, J. L., Levy, E. R., & Fenton, A. A. (2020). Is hippocampal remapping the physiological basis for context?. *Hippocampus*, *30*(8), 851-864.

Kurby, C. A., & Zacks, J. M. (2008). Segmentation in the perception and memory of events. *Trends in cognitive sciences*, *12*(2), 72-79.

Langille, J. J., & Gallistel, C. R. (2020). Locating the engram: Should we look for plastic synapses or information-storing molecules?. *Neurobiology of learning and memory*, *169*, 107164.

Langston, R. F., Ainge, J. A., Couey, J. J., Canto, C. B., Bjerknes, T. L., Witter, M. P., ... & Moser, M. B. (2010). Development of the spatial representation system in the rat. *Science*, *328*(5985), 1576-1580.

Langston, R. F., Stevenson, C. H., Wilson, C. L., Saunders, I., & Wood, E. R. (2010). The role of hippocampal subregions in memory for stimulus associations. *Behavioural brain research*, *215*(2), 275-291.

Langston, R. F., & Wood, E. R. (2010). Associative recognition and the hippocampus: Differential effects of hippocampal lesions on object-place, object-context and object-place-context memory. *Hippocampus*, *20*(10), 1139-1153.

Lee, H., & Chen, J. (2021). Narratives as Networks: Predicting Memory from the Structure of Naturalistic Events. *bioRxiv*. https://doi.org/10.1101/2021.04.24.441287

Lee, D., Lin, B. J., & Lee, A. K. (2012). Hippocampal place fields emerge upon single-cell manipulation of excitability during behavior. *Science*, *337*(6096), 849-853.

Lee, Y. S., & Silva, A. J. (2009). The molecular and cellular biology of enhanced cognition. *Nature Reviews Neuroscience*, *10*(2), 126-140.

Lee, A. K., & Wilson, M. A. (2002). Memory of sequential experience in the hippocampus during slow wave sleep. *Neuron*, *36*(6), 1183-1194.

Lee, I., Yoganarasimha, D., Rao, G., & Knierim, J. J. (2004). Comparison of population coherence of place cells in hippocampal subfields CA1 and CA3. *Nature*, *430*(6998), 456-459.

Leinekugel, X., Khazipov, R., Cannon, R., Hirase, H., Ben-Ari, Y., & Buzsáki, G. (2002). Correlated bursts of activity in the neonatal hippocampus in vivo. *Science*, *296*(5575), 2049-2052.

Leinekugel, X., Medina, I., Khalilov, I., Ben-Ari, Y., & Khazipov, R. (1997). Ca2+ oscillations mediated by the synergistic excitatory actions of GABAA and NMDA receptors in the neonatal hippocampus. *Neuron*, *18*(2), 243-255.

Lenck-Santini, P. P., Fenton, A. A., & Muller, R. U. (2008). Discharge properties of hippocampal neurons during performance of a jump avoidance task. *Journal of Neuroscience*, *28*(27), 6773-6786.

Leonard, T. K., & Hoffman, K. L. (2017). Sharp-wave ripples in primates are enhanced near remembered visual objects. *Current Biology*, *27*(2), 257-262.

Leonard, T. K., Mikkila, J. M., Eskandar, E. N., Gerrard, J. L., Kaping, D., Patel, S. R., ... & Hoffman, K. L. (2015). Sharp wave ripples during visual exploration in the primate hippocampus. *Journal of Neuroscience*, *35*(44), 14771-14782.

Lin, X., Amarlraj, M., Blanton, C., Avila, B., Todd, H., Nitz, D., & Xu, X. (2021). Non- canonical projections from ventral CA1 and subicular complex to CA3 augments the feedforward hippocampal trisynaptic pathway. *bioRxiv*. https://doi.org/10.1101/2021.02.01.429124

Lisman, J., Cooper, K., Sehgal, M., & Silva, A. J. (2018). Memory formation depends on both synapse-specific modifications of synaptic strength and cell-specific increases in excitability. *Nature neuroscience*, *21*(3), 309-314.

Liu, K., Sibille, J., & Dragoi, G. (2021). Orientation selectivity enhances context generalization and generative predictive coding in the hippocampus. *Neuron*, *109*(22) 3688-3698.

Logothetis, N. K., Eschenko, O., Murayama, Y., Augath, M., Steudel, T., Evrard, H. C., ... & Oeltermann, A. (2012). Hippocampal–cortical interaction during periods of subcortical silence. *Nature*, *491*(7425), 547-553.

Luck, D., Danion, J. M., Marrer, C., Pham, B. T., Gounot, D., & Foucher, J. (2010). The right parahippocampal gyrus contributes to the formation and maintenance of bound information in working memory. *Brain and cognition*, *72*(2), 255-263.

Maguire, E. A., & Mullally, S. L. (2013). The hippocampus: a manifesto for change. *Journal of Experimental Psychology: General*, *142*(4), 1180.

Malvache, A., Reichinnek, S., Villette, V., Haimerl, C., & Cossart, R. (2016). Awake hippocampal reactivations project onto orthogonal neuronal assemblies. *Science*, *353*(6305), 1280-1283.

Mau, W., Hasselmo, M. E., & Cai, D. J. (2020). The brain in motion: How ensemble fluidity drives memory-updating and flexibility. *Elife*, *9*, e63550.

Maurer, A. P., & Nadel, L. (2021). The continuity of context: A role for the hippocampus. *Trends in Cognitive Sciences*, *25*(3), 187-199.

Mazzoni, G., Clark, A., De Bartolo, A., Guerrini, C., Nahouli, Z., Duzzi, D., ... & Venneri, A. (2019). Brain activation in highly superior autobiographical memory: the role of the precuneus in the autobiographical memory retrieval network. *Cortex*, *120*, 588-602.

McCormick, C., Barry, D. N., Jafarian, A., Barnes, G. R., & Maguire, E. A. (2020). vmPFC drives hippocampal processing during autobiographical memory recall regardless of remoteness. *Cerebral Cortex*, *30*(11), 5972-5987.

McCormick, C., Rosenthal, C. R., Miller, T. D., & Maguire, E. A. (2018). Mind-wandering in people with hippocampal damage. *Journal of Neuroscience*, *38*(11), 2745-2754.

McKenzie, S., Frank, A. J., Kinsky, N. R., Porter, B., Rivière, P. D., & Eichenbaum, H. (2014). Hippocampal representation of related and opposing memories develop within distinct, hierarchically organized neural schemas. *Neuron*, *83*(1), 202-215.

McKenzie, S., Huszár, R., English, D. F., Kim, K., Christensen, F., Yoon, E., & Buzsáki, G. (2021). Preexisting hippocampal network dynamics constrain optogenetically induced place fields. *Neuron*, *109*(6), 1040-1054.

Meister, M. L., & Buffalo, E. A. (2016). Getting directions from the hippocampus: The neural connection between looking and memory. *Neurobiology of learning and memory*, *134*, 135-144.

Miao, C., Cao, Q., Ito, H. T., Yamahachi, H., Witter, M. P., Moser, M. B., & Moser, E. I. (2015). Hippocampal remapping after partial inactivation of the medial entorhinal cortex. *Neuron*, *88*(3), 590-603.

Milivojevic, B., Varadinov, M., Grabovetsky, A. V., Collin, S. H., & Doeller, C. F. (2016). Coding of event nodes and narrative context in the hippocampus. *Journal of Neuroscience*, *36*(49), 12412-12424.

Miller, J. F., Neufang, M., Solway, A., Brandt, A., Trippel, M., Mader, I., ... & Schulze-Bonhage, A. (2013). Neural activity in human hippocampal formation reveals the spatial context of retrieved memories. *Science*, *342*(6162), 1111-1114.

Modi, M. N., Dhawale, A. K., & Bhalla, U. S. (2014). CA1 cell activity sequences emerge after reorganization of network correlation structure during associative learning. *Elife*, *3*, e01982.

Mohns, E. J., Karlsson, K. A., & Blumberg, M. S. (2007). Developmental emergence of transient and persistent hippocampal events and oscillations and their association with infant seizure susceptibility. *European Journal of Neuroscience*, *26*(10), 2719-2730.

Mongillo, G., Rumpel, S., & Loewenstein, Y. (2017). Intrinsic volatility of synaptic connections—a challenge to the synaptic trace theory of memory. *Current opinion in neurobiology*, *46*, 7-13.

Morris, R. G., & Frey, U. (1997). Hippocampal synaptic plasticity: role in spatial learning or the automatic recording of attended experience?. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *352*(1360), 1489-1503.

Moser, E. I., Moser, M. B., & McNaughton, B. L. (2017). Spatial representation in the hippocampal formation: a history. *Nature neuroscience*, *20*(11), 1448-1464.

Mullally, S. L., Intraub, H., & Maguire, E. A. (2012). Attenuated boundary extension produces a paradoxical memory advantage in amnesic patients. *Current Biology*, *22*(4), 261-268.

Muller, R. U., & Kubie, J. L. (1987). The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *Journal of Neuroscience*, *7*(7), 1951-1968.

Nakano, T. (2015). Blink-related dynamic switching between internal and external orienting networks while viewing videos. *Neuroscience Research*, *96*, 54-58.

Naya, Y., & Suzuki, W. A. (2011). Integrating what and when across the primate medial temporal lobe. *Science*, *333*(6043), 773-776.

Newtson, D. (1973). Attribution and the unit of perception of ongoing behavior. *Journal of Personality and Social Psychology*, *28*(1), 28.

Newtson, D., & Engquist, G. (1976). The perceptual organization of ongoing behavior. *Journal of Experimental Social Psychology*, *12*(5), 436-450.

Nichols, E. A., Kao, Y. C., Verfaellie, M., & Gabrieli, J. D. (2006). Working memory and long-term memory for faces: Evidence from fMRI and global amnesia for involvement of the medial temporal lobes. *Hippocampus*, *16*(7), 604-616.

Nieh, E. H., Schottdorf, M., Freeman, N. W., Low, R. J., Lewallen, S., Koay, S. A., ... & Tank, D. W. (2021). Geometry of abstract learned knowledge in the hippocampus. *Nature*, 595, 80-84. https://doi.org/10.1038/s41586-021-03652-7

Nilssen, E. S., Doan, T. P., Nigro, M. J., Ohara, S., & Witter, M. P. (2019). Neurons and networks in the entorhinal cortex: A reappraisal of the lateral and medial entorhinal subdivisions mediating parallel cortical pathways. *Hippocampus*, *29*(12), 1238-1254.

Nitzan, N., McKenzie, S., Beed, P., English, D. F., Oldani, S., Tukker, J. J., ... & Schmitz, D. (2020). Propagation of hippocampal ripples to the neocortex by way of a subiculum-retrosplenial pathway. *Nature communications*, *11*(1), 1-17.

Norimoto, H., Fenk, L. A., Li, H. H., Tosches, M. A., Gallego-Flores, T., Hain, D., ... & Laurent, G. (2020). A claustrum in reptiles and its role in slow-wave sleep. *Nature*, *578*(7795), 413-418.

Norimoto, H., Makino, K., Gao, M., Shikano, Y., Okamoto, K., Ishikawa, T., ... & Ikegaya, Y. (2018). Hippocampal ripples down-regulate synapses. *Science*, *359*(6383), 1524-1527.

Norimoto, H., Matsumoto, N., Miyawaki, T., Matsuki, N., & Ikegaya, Y. (2013). Subicular activation preceding hippocampal ripples in vitro. *Scientific reports*, *3*(1), 1-4.

Norman, Y., Raccah, O., Liu, S., Parvizi, J., & Malach, R. (2021). Hippocampal ripples and their coordinated dialogue with the default mode network during recent and remote recollection. *Neuron*, *107*(17), 2767-2780.

Norman, Y., Yeagle, E. M., Khuvis, S., Harel, M., Mehta, A. D., & Malach, R. (2019). Hippocampal sharp-wave ripples linked to visual episodic recollection in humans. *Science*, *365*(6454).

Nyberg, L., Kim, A. S., Habib, R., Levine, B., & Tulving, E. (2010). Consciousness of subjective time in the brain. *Proceedings of the National Academy of Sciences*, *107*(51), 22356-22359.

Oedekoven, C. S., Keidel, J. L., Anderson, S., Nisbet, A., & Bird, C. M. (2019). Effects of amnesia on processing in the hippocampus and default mode network during a naturalistic memory task: A case study. *Neuropsychologia*, *132*, 107104.

Ohara, S., Blankvoort, S., Nair, R. R., Nigro, M. J., Nilssen, E. S., Kentros, C., & Witter, M. P. (2021). Local projections of layer Vb-to-Va are more prominent in lateral than in medial entorhinal cortex. *Elife*, *10*, e67262.

Ohara, S., Onodera, M., Simonsen, Ø. W., Yoshino, R., Hioki, H., Iijima, T., ... & Witter, M. P (2018). Intrinsic projections of layer Vb neurons to layers Va, III, and II in the lateral and medial entorhinal cortex of the rat. *Cell Reports*, *24*(1), 107-116.

Okuyama, T., Kitamura, T., Roy, D. S., Itohara, S., & Tonegawa, S. (2016). Ventral CA1 neurons store social memory. *Science*, *353*(6307), 1536-1541.

Ólafsdóttir, H. F., Barry, C., Saleem, A. B., Hassabis, D., & Spiers, H. J. (2015). Hippocampal place cells construct reward related sequences through unexplored space. *Elife*, *4*, e06063.

Ólafsdóttir, H. F., Carpenter, F., & Barry, C. (2016). Coordinated grid and place cell replay during rest. *Nature neuroscience*, *19*(6), 792-794.

Oliva, A., Fernández-Ruiz, A., Buzsáki, G., & Berényi, A. (2016). Role of hippocampal CA2 region in triggering sharp-wave ripples. *Neuron*, *91*(6), 1342-1355.

Oliva, A., Fernández-Ruiz, A., Leroy, F., & Siegelbaum, S. A. (2020). Hippocampal CA2 sharp-wave ripples reactivate and promote social memory. *Nature*, *587*(7833), 264-269.

Olson, I. R., Moore, K. S., Stark, M., & Chatterjee, A. (2006). Visual working memory is impaired when the medial temporal lobe is damaged. *Journal of cognitive neuroscience*, *18*(7), 1087 1097.

Olson, J. M., Tongprasearth, K., & Nitz, D. A. (2017). Subiculum neurons map the current axis of travel. *Nature neuroscience*, *20*(2), 170-172.

Omer, D. B., Maimon, S. R., Las, L., & Ulanovsky, N. (2018). Social place-cells in the bat hippocampus. *Science*, *359*(6372), 218-224.

Oyanedel, C. N., Durán, E., Niethard, N., Inostroza, M., & Born, J. (2020). Temporal associations between sleep slow oscillations, spindles and ripples. *European Journal of Neuroscience*, *52*(12), 4762-4778.

O'Callaghan, C., Shine, J. M., Hodges, J. R., Andrews-Hanna, J. R., & Irish, M. (2019). Hippocampal atrophy and intrinsic brain network dysfunction relate to alterations in mind wandering in neurodegeneration. *Proceedings of the National Academy of Sciences*, *116*(8), 3316-3321.

O'Callaghan, C., Walpola, I. C., & Shine, J. M. (2021). Neuromodulation of the mind-wandering brain state: the interaction between neuromodulatory tone, sharp wave-ripples and spontaneous thought. *Philosophical Transactions of the Royal Society B*, *376*(1817), 20190699.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: preliminary evidence from unit activity in the freely-moving rat. *Brain research*, 34, 171-175.

O'Keefe, J., & Recce, M. L. (1993). Phase relationship between hippocampal place units and the EEG theta rhythm. *Hippocampus*, *3*(3), 317-330.

O'Neill, J., Senior, T. J., Allen, K., Huxter, J. R., & Csicsvari, J. (2008). Reactivation of experience dependent cell assembly patterns in the hippocampus. *Nature neuroscience*, *11*(2), 209-215.

O'Neill, J., Senior, T., & Csicsvari, J. (2006). Place-selective firing of CA1 pyramidal cells during sharp wave/ripple network patterns in exploratory behavior. *Neuron*, *49*(1), 143-155.

Palombo, D. J., Sheldon, S., & Levine, B. (2018). Individual differences in autobiographical memory. *Trends in cognitive sciences*, *22*(7), 583-597.

Park, S., Kramer, E. E., Mercaldo, V., Rashid, A. J., Insel, N., Frankland, P. W., & Josselyn, S. A. (2016). Neuronal allocation to a hippocampal engram. *Neuropsychopharmacology*, *41*(13), 2987-2993.

Payne, H. L., Lynch, G. F., & Aronov, D. (2021). Neural representations of space in the hippocampus of a food-caching bird. *Science*, *373*(6552), 343-348.

Paz, R., Gelbard-Sagiv, H., Mukamel, R., Harel, M., Malach, R., & Fried, I. (2010). A neural substrate in the human hippocampus for linking successive events. *Proceedings of the National Academy of Sciences*, *107*(13), 6046-6051.

Pfeiffer, B. E. (2020). The content of hippocampal "replay". *Hippocampus*, *30*(1), 6-18.

Pitts, B. L., Smith, M. E., Newberry, K. M., & Bailey, H. R. (2021). Semantic knowledge attenuates age-related differences in event segmentation and episodic memory. *Memory & cognition*, 1 15.

Plitt, M. H., & Giocomo, L. M. (2021). Experience-dependent contextual codes in the hippocampus. *Nature neuroscience*, *24*(5), 705-714.

Poulter, S., Austen, J. M., Kosaki, Y., Dachtler, J., Lever, C., & McGregor, A. (2019). En route to delineating hippocampal roles in spatial learning. *Behavioural brain research*, *369*, 111936.

Poulter, S., Hartley, T., & Lever, C. (2018). The neurobiology of mammalian navigation. *Current Biology*, *28*(17), R1023-R1042.

Poulter, S., Lee, S. A., Dachtler, J., Wills, T. J., & Lever, C. (2021). Vector trace cells in the subiculum of the hippocampal formation. *Nature neuroscience*, *24*(2), 266-275.

Qasim, S. E., Fried, I., & Jacobs, J. (2021). Phase precession in the human hippocampus and entorhinal cortex. *Cell*, *184*(12), 3242-3255.

Quiroga, R. Q. (2020). No pattern separation in the human hippocampus. *Trends in cognitive sciences*.

Quiroga, R. Q., Reddy, L., Kreiman, G., Koch, C., & Fried, I. (2005). Invariant visual representation by single neurons in the human brain. *Nature*, *435*(7045), 1102-1107.

Race, E., Keane, M. M., & Verfaellie, M. (2011). Medial temporal lobe damage causes deficits in episodic memory and episodic future thinking not attributable to deficits in narrative construction. *Journal of Neuroscience*, *31*(28), 10262-10269.

Radvansky, G. A. (2012). Across the event horizon. *Current Directions in Psychological Science*, *21*(4), 269-272.

Radvansky, G. A., Andrea, E. O., & Fisher, J. S. (2017). Event models and the fan effect. *Memory & cognition*, *45*(6), 1028-1044.

Radvansky, G. A., & Copeland, D. E. (2006). Walking through doorways causes forgetting: Situation models and experienced space. *Memory & cognition*, *34*(5), 1150-1156.

Radvansky, G. A., Krawietz, S. A., & Tamplin, A. K. (2011). Walking through doorways causes forgetting: Further explorations. *Quarterly journal of experimental psychology*, *64*(8), 1632 1645.

Radvansky, B. A., Oh, J. Y., Climer, J. R., & Dombeck, D. A. (2021). Behavior determines the hippocampal spatial mapping of a multisensory environment. *Cell reports*, *36*(5), 109444.

Radvansky, G. A., & Zacks, J. M. (2014). *Event cognition*. Oxford University Press.

Radvansky, G. A., & Zacks, J. M. (2017). Event boundaries in memory and cognition. *Current opinion in behavioral sciences*, *17*, 133-140.

Rajimehr, R., Devaney, K. J., Bilenko, N. Y., Young, J. C., & Tootell, R. B. (2011). The "parahippocampal place area" responds preferentially to high spatial frequencies in human and monkeys. *PLoS Biology*, *9*(4), e1000608.

Ranganath, C., DeGutis, J., & D'Esposito, M. (2004). Category-specific modulation of inferior temporal activity during working memory encoding and maintenance. *Cognitive Brain Research*, *20*(1), 37-45.

Rao, R. P., von Heimendahl, M., Bahr, V., & Brecht, M. (2019). Neuronal responses to conspecifics in the ventral CA1. *Cell reports*, *27*(12), 3460-3472.

Reagh, Z. M., Delarazan, A. I., Garber, A., & Ranganath, C. (2020). Aging alters neural activity at event boundaries in the hippocampus and Posterior Medial network. *Nature communications*, *11*(1), 1-12.

Reddy, L., Zoefel, B., Possel, J. K., Peters, J., Dijksterhuis, D. E., Poncet, M., ... & Self, M. W. (2021). Human hippocampal neurons track moments in a sequence of events. *Journal of Neuroscience*, *41*(31), 6714-6725.

Redondo, R. L., & Morris, R. G. (2011). Making memories last: the synaptic tagging and capture hypothesis. *Nature Reviews Neuroscience*, *12*(1), 17-30.

Remondes, M., & Wilson, M. A. (2015). Slow-γ rhythms coordinate cingulate cortical responses to hippocampal sharp-wave ripples during wakefulness. *Cell reports*, *13*(7), 1327-1335.

Richmond, L. L., & Zacks, J. M. (2017). Constructing experience: Event models from perception to action. *Trends in cognitive sciences*, *21*(12), 962-980.

Richter, F. R., Cooper, R. A., Bays, P. M., & Simons, J. S. (2016). Distinct neural mechanisms underlie the success, precision, and vividness of episodic memory. *Elife*, *5*, e18260.

Risko, E. F., Anderson, N., Sarwal, A., Engelhardt, M., & Kingstone, A. (2012). Everyday attention: Variation in mind wandering and memory in a lecture. *Applied Cognitive Psychology*, *26*(2), 234-242.

Ritchey, M., & Cooper, R. A. (2020). Deconstructing the posterior medial episodic network. *Trends in cognitive sciences*, *24*(6), 451-465.

Rivard, B., Li, Y., Lenck-Santini, P. P., Poucet, B., & Muller, R. U. (2004). Representation of objects in space by two classes of hippocampal pyramidal cells. *The Journal of general physiology*, *124*(1), 9-25.

Robinson, N. T., Priestley, J. B., Rueckemann, J. W., Garcia, A. D., Smeglin, V. A., Marino, F. A., & Eichenbaum, H. (2017). Medial entorhinal cortex selectively supports temporal coding by hippocampal neurons. *Neuron*, *94*(3), 677-688.

Rodrıguez, F., López, J. C., Vargas, J. P., Broglio, C., Gómez, Y., & Salas, C. (2002). Spatial memory and hippocampal pallium through vertebrate evolution: insights from reptiles and teleost fish. *Brain research bulletin*, *57*(3-4), 499-503.

Rolls, E. T. (1999). Spatial view cells and the representation of place in the primate hippocampus. *Hippocampus*, *9*(4), 467-480.

Rolls, E. T. (2013). The mechanisms for pattern completion and pattern separation in the hippocampus. *Frontiers in systems neuroscience*, *7*, 74.

Rozov, A., Rannap, M., Lorenz, F., Nasretdinov, A., Draguhn, A., & Egorov, A. V. (2020).' Processing of hippocampal network activity in the receiver network of the medial entorhinal cortex layer V. *Journal of Neuroscience*, *40*(44), 8413-8425.

Rubin, A., Geva, N., Sheintuch, L., & Ziv, Y. (2015). Hippocampal ensemble dynamics timestamp events in long-term memory. *Elife*, *4*, e12247.

Rubin, D. C., & Umanath, S. (2015). Event memory: A theory of memory for laboratory, autobiographical, and fictional events. *Psychological review*, *122*(1), 1.

Rueckemann, J. W., & Buffalo, E. A. (2017). Spatial responses, immediate experience, and memory in the monkey hippocampus. *Current opinion in behavioral sciences*, *17*, 155-160.

Rueckemann, J. W., Sosa, M., Giocomo, L. M., & Buffalo, E. A. (2021). The grid code for ordered experience. *Nature Reviews Neuroscience*, 1-13. https://doi.org/10.1038/s41583-021 00499-9

Sabariego, M., Tabrizi, N. S., Marshall, G. J., McLagan, A. N., Jawad, S., & Hales, J. B. (2021). In the temporal organization of episodic memory, the hippocampus supports the experience of elapsed time. *Hippocampus*, *31*(1), 46-55.

Sakurai, Y. (1994). Involvement of auditory cortical and hippocampal neurons in auditory working memory and reference memory in the rat. *Journal of Neuroscience*, *14*(5), 2606-2623.

Salz, D. M., Tiganj, Z., Khasnabish, S., Kohley, A., Sheehan, D., Howard, M. W., & Eichenbaum, H. (2016). Time cells in hippocampal area CA3. *Journal of Neuroscience*, *36*(28), 7476-7484.

Sanchez-Aguilera, A., & Quintanilla, J. P. (2021). Sharp Wave Ripples in Alzheimer's Disease: In Search of Mechanisms. *Journal of Neuroscience*, *41*(7), 1366-1370.

Sanders, H., Wilson, M. A., & Gershman, S. J. (2020). Hippocampal remapping as hidden state inference. *Elife*, *9*, e51140.

Santangelo, V., Cavallina, C., Colucci, P., Santori, A., Macrì, S., McGaugh, J. L., & Campolongo, P. (2018). Enhanced brain activity associated with memory access in highly superior autobiographical memory. *Proceedings of the National Academy of Sciences*, *115*(30), 7795-7800.

Santangelo, V., Pedale, T., Colucci, P., Giulietti, G., Macrì, S., & Campolongo, P. (2021). Highly Superior Autobiographical Memory in Aging: A single case study. *Cortex*, *143*, 267-280.

Santangelo, V., Pedale, T., Macrì, S., & Campolongo, P. (2020). Enhanced cortical specialization to distinguish older and newer memories in highly superior autobiographical memory. *Cortex*, *129*, 476-483.

Schneider, E., Züst, M. A., Wuethrich, S., Schmidig, F., Klöppel, S., Wiest, R., ... & Henke, K. (2021). Larger capacity for unconscious versus conscious episodic memory. *Current Biology*, *31*(16), 3551-3563

Schomaker, J., & Wittmann, B. C. (2021). Effects of active exploration on novelty-related declarative memory enhancement. *Neurobiology of Learning and Memory*, *179*, 107403.

Schuck, N. W., & Niv, Y. (2019). Sequential replay of nonspatial task states in the human hippocampus. *Science*, *364*(6447).

Schuette, P. J., Reis, F. M., Maesta-Pereira, S., Chakerian, M., Torossian, A., Blair, G. J., ... & Adhikari, A. (2020). Long-term characterization of hippocampal remapping during contextual fear acquisition and extinction. *Journal of Neuroscience*, *40*(43), 8329-8342.

Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of neurology, neurosurgery, and psychiatry*, *20*(1), 11.

Seel, S. V., Easton, A., McGregor, A., Buckley, M. G., & Eacott, M. J. (2019). Walking through doorways differentially affects recall and familiarity. *British Journal of Psychology*, *110*(1), 173-184.

Sekeres, M. J., Neve, R. L., Frankland, P. W., & Josselyn, S. A. (2010). Dorsal hippocampal CREB is both necessary and sufficient for spatial memory. *Learning & memory*, *17*(6), 280-283.

Serra, L., Bozzali, M., Fadda, L., De Simone, M. S., Bruschini, M., Perri, R., ... & Carlesimo, G. A. (2020). The role of hippocampus in the retrieval of autobiographical memories in patients with amnestic Mild Cognitive Impairment due to Alzheimer's disease. *Journal of Neuropsychology*, *14*(1), 46-68.

Shapiro, M. L., Tanila, H., & Eichenbaum, H. (1997). Cues that hippocampal place cells encode: dynamic and hierarchical representation of local and distal stimuli. *Hippocampus*, *7*(6), 624 642.

Sheehan, D. J., Charczynski, S., Fordyce, B. A., Hasselmo, M. E., & Howard, M. W. (2021). A compressed representation of spatial distance in the rodent hippocampus. *bioRxiv*. https://doi.org/10.1101/2021.02.15.431306

Shikano, Y., Ikegaya, Y., & Sasaki, T. (2021). Minute-encoding neurons in hippocampal- striatal circuits. *Current Biology*, *31*(7), 1438-1449.

Shimbo, A., Izawa, E. I., & Fujisawa, S. (2021). Scalable representation of time in the hippocampus. *Science Advances*, *7*(6), eabd7013.

Simons, J. S., Ritchey, M., & Fernyhough, C. (in press). Brain Mechanisms underlying the subjective experience of remembering. *Annual review of psychology.* https://doi.org/10.1146/annurev psych-030221-025439

Skaggs, W. E., McNaughton, B. L., Wilson, M. A., & Barnes, C. A. (1996). Theta phase precession in hippocampal neuronal populations and the compression of temporal sequences. *Hippocampus*, *6*(2), 149-172.

Smallwood, J., McSpadden, M., & Schooler, J. W. (2008). When attention matters: The curious incident of the wandering mind. *Memory & cognition*, *36*(6), 1144-1150.

Song, H., Finn, E. S., & Rosenberg, M. D (2021) Neural signatures of attentional engagement during narratives and its consequences for event memory. *Proceedings of the National Academy of Sciences*, *118*(33) e2021905118.

Speer, N. K., Swallow, K. M., & Zacks, J. M. (2003). Activation of human motion processing areas during event perception. *Cognitive, Affective, & Behavioral Neuroscience*, *3*(4), 335-345.

Spiers, H. J., Hayman, R. M., Jovalekic, A., Marozzi, E., & Jeffery, K. J. (2015). Place field repetition and purely local remapping in a multicompartment environment. *Cerebral Cortex*, *25*(1), 10 25.

Squire, L. R. (1992). Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychological review*, *99*(2), 195.

Squire, L. R., & Zola-Morgan, S. (1991). The medial temporal lobe memory system. *Science*, *253*(5026), 1380-1386.

Stachenfeld, K. L., Botvinick, M. M., & Gershman, S. J. (2017). The hippocampus as a predictive map. *Nature neuroscience*, *20*(11), 1643-1653.

Staresina, B. P., Bergmann, T. O., Bonnefond, M., Van Der Meij, R., Jensen, O., Deuker, L., ... & Fell, J. (2015). Hierarchical nesting of slow oscillations, spindles and ripples in the human hippocampus during sleep. *Nature neuroscience*, *18*(11), 1679-1686.

Stawarczyk, D., Bezdek, M. A., & Zacks, J. M. (2021). Event representations and predictive processing: The role of the midline default network core. *Topics in cognitive science*, *13*(1), 164-186.

Sugar, J., & Moser, M. B. (2019). Episodic memory: Neuronal codes for what, where, and when. *Hippocampus*, *29*(12), 1190-1205.

Suh, J., Rivest, A. J., Nakashiba, T., Tominaga, T., & Tonegawa, S. (2011). Entorhinal cortex layer III input to the hippocampus is crucial for temporal association memory. *Science*, *334*(6061), 1415-1420.

Sun, Y., Jin, S., Lin, X., Chen, L., Qiao, X., Jiang, L., ... & Xu, X. (2019). CA1-projecting subiculum neurons facilitate object–place learning. *Nature neuroscience*, *22*(11), 1857-1870.

Sun, C., Yang, W., Martin, J., & Tonegawa, S. (2020). Hippocampal neurons represent events as transferable units of experience. *Nature neuroscience*, *23*(5), 651-663.

Swallow, K. M., Kemp, J. T., & Simsek, A. C. (2018). The role of perspective in event segmentation. *Cognition*, *177*, 249-262.

Tan, H. M., Wills, T. J., & Cacucci, F. (2017). The development of spatial and memory circuits in the rat. *Wiley Interdisciplinary Reviews: Cognitive Science*, *8*(3), e1424.

Tanaka, K. Z., He, H., Tomar, A., Niisato, K., Huang, A. J., & McHugh, T. J. (2018). The hippocampal engram maps experience but not place. *Science*, *361*(6400), 392-397.

Taube, J. S., Muller, R. U., & Ranck, J. B. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience*, *10*(2), 420-435.

Terrazas, A., Krause, M., Lipa, P., Gothard, K. M., Barnes, C. A., & McNaughton, B. L. (2005). Self motion and the hippocampal spatial metric. *Journal of Neuroscience*, *25*(35), 8085-8096.

Teyler, T. J., & DiScenna, P. (1986). The hippocampal memory indexing theory. *Behavioral neuroscience*, *100*(2), 147.

Tingley, D., McClain, K., Kaya, E., Carpenter, J., & Buzsáki, G. (2021) A metabolic function of the hippocampal sharp wave-ripple. *Nature*. https://doi.org/10.1038/s41586-021-03811-w

Tsao, A., Sugar, J., Lu, L., Wang, C., Knierim, J. J., Moser, M. B., & Moser, E. I. (2018). Integrating time from experience in the lateral entorhinal cortex. *Nature*, *561*(7721), 57-62.

Tsitsiklis, M., Miller, J., Qasim, S. E., Inman, C. S., Gross, R. E., Willie, J. T., ... & Jacobs, J. (2020). Single-neuron representations of spatial targets in humans. *Current Biology*, *30*(2), 245-253.

Tsoi, S. Y., Öncül, M., Svahn, E., Robertson, M., Bogdanowicz, Z., McClure, C., & Sürmeli, G. (2021). Telencephalic outputs from the medial entorhinal cortex are copied directly to the hippocampus. *bioRxiv*. https://doi.org/10.1101/2021.03.10.434566

Tulving, E. (2002). Episodic memory: From mind to brain. *Annual review of psychology*, *53*(1), 1-25.

Tulving, E. (1985). Memory and consciousness. *Canadian Psychology/Psychologie canadienne*, *26*(1), 1.

Ulanovsky, N., & Moss, C. F. (2007). Hippocampal cellular and network activity in freely moving echolocating bats. *Nature neuroscience*, *10*(2), 224-233.

Ulanovsky, N., & Moss, C. F. (2011). Dynamics of hippocampal spatial representation in echolocating bats. *Hippocampus*, *21*(2), 150-161.

Umbach, G., Kantak, P., Jacobs, J., Kahana, M., Pfeiffer, B. E., Sperling, M., & Lega, B. (2020). Time cells in the human hippocampus and entorhinal cortex support episodic memory. *Proceedings of the National Academy of Sciences*, *117*(45), 28463-28474.

Valeeva, G., Janackova, S., Nasretdinov, A., Rychkova, V., Makarov, R., Holmes, G. L., ... & Lenck Santini, P. P. (2019). Emergence of coordinated activity in the developing entorhinal hippocampal network. *Cerebral Cortex*, *29*(2), 906-920.

Valeeva, G., Rychkova, V., Vinokurova, D., Nasretdinov, A., & Khazipov, R. (2020). Early sharp wave synchronization along the septo-temporal axis of the neonatal rat hippocampus. *Neuroscience and Behavioral Physiology*, *50*(9), 1195-1202.

Valeeva, G., Tressard, T., Mukhtarov, M., Baude, A., & Khazipov, R. (2016). An optogenetic approach for investigation of excitatory and inhibitory network GABA actions in mice expressing channelrhodopsin-2 in GABAergic neurons. *Journal of Neuroscience*, *36*(22), 5961-5973.

Valero, M., Cid, E., Averkin, R. G., Aguilar, J., Sanchez-Aguilera, A., Viney, T. J., ... & De La Prida, L. M. (2015). Determinants of different deep and superficial CA1 pyramidal cell dynamics during sharp-wave ripples. *Nature neuroscience*, *18*(9), 1281-1290.

Valero, M., & de la Prida, L. M. (2018). The hippocampus in depth: a sublayer-specific perspective of entorhinal–hippocampal function. *Current opinion in neurobiology*, *52*, 107-114.

van de Ven, G. M., Trouche, S., McNamara, C. G., Allen, K., & Dupret, D. (2016). Hippocampal offline reactivation consolidates recently formed cell assembly patterns during sharp wave ripples. *Neuron*, *92*(5), 968-974.

Vandecasteele, M., Varga, V., Berényi, A., Papp, E., Barthó, P., Venance, L., ... & Buzsáki, G. (2014). Optogenetic activation of septal cholinergic neurons suppresses sharp wave ripples and enhances theta oscillations in the hippocampus. *Proceedings of the National Academy of Sciences*, *111*(37), 13535-13540.

Vandrey, B., Duncan, S., & Ainge, J. A. (2021). Object and object-memory representations across the proximodistal axis of CA1. *Hippocampus*, *31*(8), 881-896.

Vandrey, B., Garden, D. L., Ambrozova, V., McClure, C., Nolan, M. F., & Ainge, J. A. (2020). Fan cells in layer 2 of the lateral entorhinal cortex are critical for episodic-like memory. *Current Biology*, *30*(1), 169-175.

Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science*, *277*(5324), 376-380.

Vaz, A. P., Inati, S. K., Brunel, N., & Zaghloul, K. A. (2019). Coupled ripple oscillations between the medial temporal lobe and neocortex retrieve human memory. *Science*, *363*(6430), 975-978.

Wang, C. H., Monaco, J. D., & Knierim, J. J. (2020). Hippocampal place cells encode local surface texture boundaries. *Current Biology*, *30*(8), 1397-1409.

Waters, F., Barnby, J. M., & Blom, J. D. (2021). Hallucination, imagery, dreaming: reassembling stimulus-independent perceptions based on Edmund Parish's classic misperception framework. *Philosophical Transactions of the Royal Society B*, *376*(1817), 20190701.

Whitehead, P.S., Mahmoud, Y., Seli, P., & Egner, T. (2021) Mind wandering at encoding, but not at retrieval, disrupts one-shot stimulus-control learning. *Attention, Perception, Psychophysics,* 83, 2968–2982.

Whittington, J. C., Muller, T. H., Mark, S., Chen, G., Barry, C., Burgess, N., & Behrens, T. E. (2020). The Tolman-Eichenbaum machine: Unifying space and relational memory through generalization in the hippocampal formation. *Cell*, *183*(5), 1249-1263.

Wiegand, J. P. L., Gray, D. T., Schimanski, L. A., Lipa, P., Barnes, C. A., & Cowen, S. L. (2016). Age is associated with reduced sharp-wave ripple frequency and altered patterns of neuronal variability. *Journal of Neuroscience*, *36*(20), 5650-5660.

Wills, T. J., Cacucci, F., Burgess, N., & O'Keefe, J. (2010). Development of the hippocampal cognitive map in preweanling rats. *Science*, *328*(5985), 1573-1576.

Wilson, D. I., Watanabe, S., Milner, H., & Ainge, J. A. (2013). Lateral entorhinal cortex is necessary for associative but not nonassociative recognition memory. *Hippocampus*, *23*(12), 1280-1290.

Wirth, S., Baraduc, P., Planté, A., Pinède, S., & Duhamel, J. R. (2017). Gaze-informed, task-situated representation of space in primate hippocampus during virtual navigation. *PLoS biology*, *15*(2), e2001045.

Witter, M. P., Naber, P. A., van Haeften, T., Machielsen, W. C., Rombouts, S. A., Barkhof, F., ... & Lopes da Silva, F. H. (2000). Cortico-hippocampal communication by way of parallel parahippocampal-subicular pathways. *Hippocampus*, *10*(4), 398-410.

Woods, N. I., Stefanini, F., Apodaca-Montano, D. L., Tan, I. M., Biane, J. S., & Kheirbek, M. A. (2020). The dentate gyrus classifies cortical representations of learned stimuli. *Neuron*, *107*(1), 173-184.

Wu, C. T., Haggerty, D., Kemere, C., & Ji, D. (2017). Hippocampal awake replay in fear memory retrieval. *Nature neuroscience*, *20*(4), 571-580.

Yamamoto, J., & Tonegawa, S. (2017). Direct medial entorhinal cortex input to hippocampal CA1 is crucial for extended quiet awake replay. *Neuron*, *96*(1), 217-227.

Yap, E. L., & Greenberg, M. E. (2018). Activity-regulated transcription: bridging the gap between neural activity and behavior. *Neuron*, *100*(2), 330-348.

Yartsev, M. M., & Ulanovsky, N. (2013). Representation of three-dimensional space in the hippocampus of flying bats. *Science*, *340*(6130), 367-372.

Yeganegi, H., Luksch, H., & Ondracek, J. M. (2019). Hippocampal-like network dynamics underlie avian sharp wave-ripples. *bioRxiv*. https://doi.org/10.1101/825075

Yeshurun, Y., Nguyen, M., & Hasson, U. (2021). The default mode network: where the idiosyncratic self meets the shared social world. *Nature reviews Neuroscience*, *22*(3), 181–192.

Ylinen, A., Bragin, A., Nádasdy, Z., Jandó, G., Szabo, I., Sik, A., & Buzsáki, G. (1995). Sharp wave associated high-frequency oscillation (200 Hz) in the intact hippocampus: network and intracellular mechanisms. *Journal of Neuroscience*, *15*(1), 30-46.

Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of memory and language*, *46*(3), 441-517.

Yonelinas, A. P., Ranganath, C., Ekstrom, A. D., & Wiltgen, B. J. (2019). A contextual binding theory of episodic memory: systems consolidation reconsidered. *Nature Reviews Neuroscience*, *20*(6), 364-375.

Yoo, H. B., Umbach, G., & Lega, B. C. (2021). Neurons in the Human Medial Temporal Lobe Track Multiple Temporal Contexts during Episodic Memory Processing. *NeuroImage*, 245, 118689.

Zacks, J. M. (2020). Event perception and memory. *Annual review of psychology*, *71*, 165-191.

Zacks, J. M., Speer, N. K., Swallow, K. M., Braver, T. S., & Reynolds, J. R. (2007). Event perception: a mind-brain perspective. *Psychological bulletin*, *133*(2), 273.

Zacks, J. M., Speer, N. K., Swallow, K. M., & Maley, C. J. (2010). The brain's cutting-room floor: Segmentation of narrative cinema. *Frontiers in human neuroscience*, *4*, 168.

Zaman, A., & Russell, C. (2021). Does autonoetic consciousness in episodic memory rely on recall from a first-person perspective?. *Journal of Cognitive Psychology*, 1-15.

Zhang, Y., Cao, L., Varga, V., Jing, M., Karadas, M., Li, Y., & Buzsáki, G. (2021). Cholinergic suppression of hippocampal sharp-wave ripples impairs working memory. *Proceedings of the National Academy of Sciences*, *118*(15).

Zheng, J., Schjetnan, A. G. P., Yebra, M., Mosher, C., Kalia, S., Valiante, T. A., ... & Rutishauser, U. (2021). Cognitive boundary signals in the human medial temporal lobe shape episodic memory representation. bioRxiv. https://doi.org/10.1101/2021.01.16.426538

Ziv, N. E., & Brenner, N. (2018). Synaptic tenacity or lack thereof: spontaneous remodeling of synapses. *Trends in neurosciences*, *41*(2), 89-99.

Ziv, Y., Burns, L. D., Cocker, E. D., Hamel, E. O., Ghosh, K. K., Kitch, L. J., ... & Schnitzer, M. J. (2013). Long-term dynamics of CA1 hippocampal place codes. *Nature neuroscience*, *16*(3), 264-266.

Zuo, X., Honey, C. J., Barense, M. D., Crombie, D., Norman, K. A., Hasson, U., & Chen, J. (2020). Temporal integration of narrative information in a hippocampal amnesic patient. *NeuroImage*, *213*, 116658.

Zwaan, R. A. (2016). Situation models, mental simulations, and abstract concepts in discourse comprehension. *Psychonomic bulletin & review*, *23*(4), 1028-1034.

Zwaan, R. A., Langston, M. C., & Graesser, A. C. (1995). The construction of situation models in narrative comprehension: An event-indexing model. *Psychological science*, *6*(5), 292-297.

Table

Table 1

Cell types of the hippocampal formation implicated in event construction.

Cell Type	Region(s)	Description	Species	Refs.
Place	HPC	Firing is localised in one (or more) discrete area(s) of space when an animal moves around in an environment.	Rodents, Bats, Birds, Primates	O'Keefe & Dostrovsky, (1971); Ulanovsky & Moss, (2007); Payne, Lynch & Aronov, (2021); Ekstrom et al., (2003)*
Spatial View	HPC, EC	Firing is localised in a discrete area of space when an animal looks around in an environment.	Primates	Rolls, (1999); Killian, Potter & Buffalo, (2015)
Object Vector	CA1, SUB, MEC	Fire in specific vector relationships to local objects in the environment.	Rodents	Deshmukh & Knierim, (2013); Poulter et al., (2021); Høydal et al., (2019)
Vector Trace	SUB	Fire in specific vector relationships to local objects in the environment and leave a trace field when objects are removed.	Rodents	Poulter et al., (2021)
Time	CA1, CA3	Can fire sequentially in a temporally structured experience.	Rodents, Primates	Eichenbaum, (2014); Salz et al., (2016); Reddy et al., (2021)
Grid	MEC	Fire in spatially organised hexagonal fields, as an animal moves around in an environment.	Rodents, Bats, Primates	Hafting et al., (2005); Yartsev & Ulanovsky, (2013); Jacobs et al., (2013)*

Hippocampus (HPC), Cornu Ammonis (CA), Subiculum (SUB), Entorhinal Cortex (EC; medial, MEC). *Human place/grid-like cells navigating in virtual reality. *Note*: other cell types are not described in this present review (see Poulter et al., 2018; Moser et al., 2017).