Segmentation of experience and episodic memory across species

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Abstract

How continuous ongoing perceptual experience is processed by the brain and mind to form unique episodes in memory is a key scientific question. Recent work in Psychology and Neuroscience has proposed that humans perceptually segment continuous ongoing experience into meaningful units, which allows the successful formation of episodic memories. Despite accumulating work demonstrating that non-human animals also display a capability of episodic-'like' memory, whether non-human animals segment continuous ongoing experience into 'meaningful' episodic units is a question that has not been fully explored. Hence, the main goal of the research in this thesis aims to address whether a comparable segmentation process (or processes) of continuous ongoing experience occurs for non-human animals in their formation of episodic-like memory, as it does for humans in their formation of episodic memory. Chapter 2 argues that, similarly to humans, rats can use top-down like prediction-error processing in segmenting for subsequent memory to guide behaviour in an episodic-like spontaneous object recognition task. Chapter 3 suggests that mice readily incorporate conspecific-contextual information using episodic-like memory processing, indicating that conspecifics can act as a segmentation cue for non-human animals. Chapter 4 highlights that humans and rodents may similarly segment continuous ongoing experience during turns made around spatial boundaries. Chapter 5 argues that individual place cells can represent content of episodic nature, with the theoretical implication of this being discussed in relation to episodic memory. Thus, the results presented in this thesis, as well as re-interpretation of previous literature, would argue in favour of non-humans segmenting their experience for episodic-like memory. Finally, the evidence is evaluated in the context of whether episodic-like memory in non-human animals is simply just episodic memory as experienced in humans.

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Declaration

I, Tyler Wayne Ross, declare that no work in this thesis has been submitted for qualification elsewhere and is my own work unless referenced otherwise.

Published and submitted work

Chapter 1 has been published (literature review):

Ross, T. W., & Easton, A. (2022). The hippocampal horizon: Constructing and segmenting experience for episodic memory. *Neuroscience & Biobehavioral Reviews*, *132*, 181-196.

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"The term "memory" itself has become just an umbrella term covering all the different kinds, and one-time dreams of psychologists of coming up with a comprehensive "theory of memory" have become as irrelevant as psychological theories about umbrellas" (Tulving, 2007).

"…if only we could feel what we remember and not just remember what we felt." (Poindexter, 2015).

1. General introduction

In Jackson's (1986) Mary's room thought experiment Mary is a human in the future who lives her entire life confined to a black and white room, never experiencing colour. However, she educates herself through black and white and non-visual sources, learning everything there is to know about the physical world. This includes all knowledge of the various biological and computational mechanistic processes underlying the human brain. The critical question posed to the reader is that upon her experiencing 'what it is like' to see the redness of a ripe red tomato, does she learn anything new? (Jackson, 1986; Jackson, 1982; Nagel, 1974). Yet, regardless of whether Mary learns anything new or not, one can appreciate that experiencing red for the first time will likely become a memorable moment for Mary.

Episodic memory has been taken to be memory for *personally* experienced events, usually specified in a unique spatiotemporal context (Tulving, 1972; Renoult et al., 2019). Indeed, Klein (2015) has argued that episodic memory is the only cognitive process that can genuinely be considered as memory, emphasising a contingency on its experiential ('re-experiencing', Tulving, 2002) component. Specifically, episodic memory as a mental state must be causally connected to an experience the individual formerly participated, and must not simply be *from* the past, it should be *about* the past (Klein, 2015). In essence, "there is something it is like for a mental state to be experienced as an act of remembering" (Klein, 2015, p. 1).

Returning to Mary, if one now considers the perceptual transition of her experience from a colourless reality to suddenly seeing the red stimulus, naturally, one may ask how such an experience will come to be episodically recollected for Mary? For example, will Mary remember the breakfast she had on that day, the paper and paragraph she was reading before experiencing the red stimulus? Will she remember what she did after seeing the red stimulus? The way she interacted with it, examining its every detail and how she then took to all sorts of books describing red things, to compare them to the red stimulus? Here, the point is that humans subjectively experience a relentless stream of continuous input as they go about their daily waking lives, and only a fraction of that information is subsequently retrieved (Bartlett, 1932; Rubin & Wenzel, 1996). By definition, episodic memory as a

cognitive construct is temporally finite, inherently bound to the confines of an episode (event). What then constitutes an episode?

Converging evidence has outlined that a neurocognitive process bridges ongoing perception and episodic memory, termed event segmentation (Zacks et al., 2007; Radvansky & Zacks, 2014). Event segmentation refers to the partitioning of continuous experience into discrete units, where a breakpoint or 'event boundary' typically describes the end of a meaningful unit of activity and the beginning of another. One may consider this as a related process to that of perceptual cognition. Importantly, this highlights an experimental approach where one can ask participants to segment a given stimulus by pressing a button or computer key when they feel one meaningful unit of activity ends and another begins (e.g., Newtson, 1973; Zacks et al., 2001). Critically, work in humans has shown that firstly, behavioural segmentation can be adjusted where finer-grained segmentation can occur on shorter timescales versus coarser-grained segmentation on longer timescales, with finer-grained events enveloped by coarser-grained events (Radvansky & Zacks, 2014). Secondly, this event structure is also echoed in hierarchal cortical activity where early sensory cortices show activity related to events on shorter timescales and other regions such as the hippocampus and angular gyrus show activity related to events on longer timescales (evidenced via fMRI, Baldassano et al., 2017). Lastly,

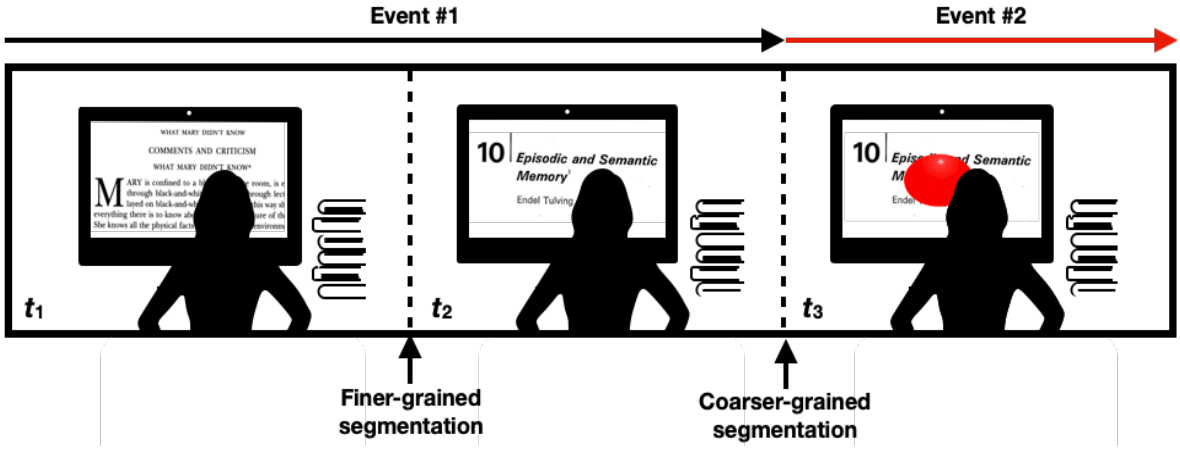

Figure 1. Schematic of event segmentation using the Mary's room thought experiment. Left to right: At t_1 Mary is reading a paper and once she finishes, begins reading another paper at t_2 (middle). At t_3 the red stimulus suddenly appears (right), demarcating the end of a meaningful unit of activity (event) and the beginning of another event accentuated by colour. Notably, the transition from t_1 to t_2 is a finer-grained segmentation (in which t_1 and t_2 may be considered sub-events of event #1) relative to the transition between t_2 and t_3 which is a coarser-grained segmentation.

event boundaries influence memory retrieval and cortical activity especially in the hippocampus (e.g., Ben-Yakov & Henson, 2018; Ezzyat & Davachi, 2011; Zheng et al., 2022). In this way, the moment of seeing the red stimulus likely cues segmentation for Mary, demarcating the ending of a (colourless) event and the beginning of a new event (accentuated by colour; see Fig. 1). Yet, Mary provides an exaggerated example for conceptual clarity. Although event segmentation allows for a theoretical framework to understand that from continuous perceptual experience discrete event units are formed (and hence episodic memory is contingent upon such a process). In truth, the goalposts have just been shifted from asking what constitutes an episode, to instead asking what evokes an event boundary.

1.1. Bounding events by bottom-up and top-down processing

Bottom-up versus top-down processing of external stimuli are considered as two distinct neurocognitive mechanisms relevant to perception and attention. For example, in the context of visual attention, bottom-up processing acts upon input of the raw visual stream where salient visual features in an environment may lead to involuntary shifts in attention (Conner et al., 2004). On the other hand, top-down processing functions on a more strategic level, influenced by knowledge (previous learning and memory), where one's goal can modulate attention such as actively searching for fuel station signage when driving a car very low on fuel. Importantly, bottom-up and top-down processes normally operate in tandem, facilitating an organism's behavioural output (Conner et al., 2004). However, such a dichotomy allows for an organising principle when understanding the potential mechanisms by which event boundaries arise.

Human event segmentation studies using simple 2-D shape animation stimuli have shown that perceiving substantial changes in simple motion features of the shapes were sufficient to drive segmentation behaviour (Zacks, 2004; Hard et al., 2006, accounting for top-down explanations). Indeed, Newtson and colleagues (1987) similarly observed this when using more naturalistic stimuli involving human actors. They argued that "brief bursts of change, or reorganisations of the actor's body, are followed by comparatively low-magnitude, smooth movements", and hence

event boundaries tend to occur around these bursts of perceptual changes (Newtson et al., 1987, p. 202). More recently, it has been reported that image classification network models can perform similarly to humans on a time duration estimation task. Interestingly, this was when the model was trained using scene stimuli and implemented threshold detection of salient perceptual change (Roseboom et al., 2019). For Mary, the perceptual transition from an environment filled of a greyscale spectrum to seeing a red stimulus pop out is a salient perceptual change (Fig. 1), arguably leading to an event boundary occurring via bottom-up processing. However, it can be ambiguous as to how much perceptual change is necessary to cue segmentation in more naturalistic settings. Is the perceptual change threshold variable across individuals or context-dependent? And if one considers that there is no threshold does not continuous experience become infinitely divisible subject to the most minute changes, for example sentences of a book, or words, or letters, or lines (Yates et al., 2023). To this end, alternative theories taking more of a top-down processing perspective have been developed.

Event segmentation theory is one such dominant theory reliant on top-down predictive processing (Zacks et al., 2007). A prerequisite for such a theory is that humans have previous structured knowledge (schema, Bartlett, 1932) of how things in the world usually operate based on previous learning and memory. For example, one knows that in order to make a sandwich, two pieces of bread are required with some sort of filling. Event segmentation theory holds that an observer watching someone going to make a sandwich one is constantly predicting the actions that will unfold. Buttering the bread, slicing the tomato, placing the tomato, sprinkling the grated cheese etc. Once the sandwich is made, the person begins to rinse the knife, soaks the chopping board, pours some washing-up liquid, opens up the dishwasher and so on. These actions are not consistent with the schema of ‘making a sandwich’ and hence due to an accumulation of prediction-errors an event boundary occurs according to the theory, where the event of ‘making a sandwich’ ends and a new event of ‘washing-up the dishes’ occurs (Zacks et al., 2007).

Consider another example where one has ordered a taxi to the airport from the company they have always used. Based on previous experiences one should predict a car to arrive, however on this occasion a horse and carriage turns up

instead, announcing “taxi!”. In this singular moment a ‘hard’ prediction-error occurs cueing segmentation. Empirical support for a top-down view is reported in the aforementioned segmentation experiment using 2-D shape stimuli. It was also shown that when participants were told that movements were intentional as opposed to random, it modulated the relationship between segmentation and movement of the stimuli (Zacks, 2004; e.g., the acceleration of the shape became less predictive of segmentation in intentional group vs. the random group, and the distance between shapes became more predictive vs. the random group). Granted, in the former and latter examples and the Zacks (2004) study perceptual changes accompany such top-down influences. Yet, in one segmentation study experimenters had different groups of participants watch and segment actors doing the same activities (e.g., laundry), but these actions were filmed from a first versus third person perspective. It was found that segmentation was largely viewpoint invariant, that is despite the respective stimuli differing in the amount of perceptual change segmentation was comparable (Swallow et al., 2018). This would argue that segmentation can be driven by top-down processing occurring on a more conceptual level.

In summary, bottom-up and top-down processing of external stimuli both contribute to segmentation of experience into event units. Perhaps in contrast to other cognitive phenomena, bottom-up and top-down mechanisms may converge to produce robust segmentation. Again, in the Mary example of the moments leading up to the red stimulus, while it could be interpreted solely from a bottom-up perspective, one can imagine that she would also not have predicted the stimulus to appear (resulting in a prediction-error). Hence, a combinatory effect of bottom-up and top-down processing is an equally plausible interpretation for the segmentation.

The narrative has predominately taken a human-centric view of event cognition up until this point. This is because many authors have argued that episodic memory is a uniquely human cognitive function (e.g., Tulving, 2002; Crystal & Suddendorf, 2019; Keven, 2016; Mahr & Csibra, 2018). Thus, models such as event segmentation theory have been oriented towards humans (Zacks et al., 2007). However, an important line of questioning considers episodic memory from an evolutionary standpoint where some have argued that episodic memory is not a uniquely human cognitive function (e.g., Allen & Fortin, 2013; Eichenbaum et al.,

2012), these non-human animal models of episodic memory will be discussed in the next section.

1.2. Episodic-like memory in non-human animals

In Tulving's (1972) account there was a self-referential aspect in episodic memory processing, but this was merely an attribution that a person's episodic memory was of their own previous experience, e.g., "episodic memory is a more or less faithful record of a person's experiences" (Tulving, 1972, p. 387). Yet the role of the 'self' became elaborated upon, for example "when we do travel back in time [remember] our conscious awareness of our experience is different from our ordinary "online" awareness of our environment. We seldom confuse the feeling that we are remembering a past event with the feeling that we are looking at the world" (Tulving, 2002, p. 2). This is captured by the notion of autonoetic awareness (or autonoesis), the feeling of 're-experiencing' the past as an experience in itself and is argued to be a quintessential quality of human episodic memory (Tulving, 2002; Klein, 2015). In this way, all the current methods used to directly assess the experiential aspect of episodic memory in humans rely on introspection (e.g., interviews, Palombo et al., 2018) and are not without their challenges (c.f. Zaman & Russell, 2022).

An arguably core component of the scientific method is that a theory needs to be falsifiable (Popper, 1959). One cannot use the same introspective methods in non-human animals (and to some extent in human children; c.f. Mullally & Maguire, 2014) as in most humans beyond a certain age. However, Clayton and colleagues (1998) ingeniously operationalised Tulving's (1972) original view of episodic memory into a content-based behaviourally defined approach. They argue that an animal's egocentrically ('personally') experienced, simultaneous integration of content (what) in specific spatial arrangement (where) and temporal context (when) could constitute as episodic-like memory (Clayton & Dickinson, 1998; Clayton et al., 2003).

Notably 'when' is not the only way to specify what happened and where in memory. One can be uncertain about 'when' per se in chronological time but use other contextual information to specify what happened and where (whilst still realising a personally experienced unique event), and this contextual information

similarly acts to mitigate interference of other similar events in memory (Friedman, 1993; Roberts et al., 2008; Eacott & Easton, 2010). In other words, temporal (when) information can just be seen as part of being 'contextual information' used to specify a particular episode in memory (Eacott & Easton, 2010). Under this more encompassing view, numerous species show successful behavioural indication of episodic-like memory (Clayton & Dickinson, 1998; Eacott & Norman, 2004; Dere et al., 2005; Jozet-Alves et al., 2013; Davies et al., 2022). For example, Eacott and Norman (2004) utilised laboratory rats' spontaneous recognition and exploration for novelty (Berlyne, 1950; Ennanceur & Delacour, 1988; Dix & Aggleton, 1999) and formulated an object-place-context episodic-like task.

In the object-place-context task, visuo-tactile cues of the global environment usually act as 'context' to specify certain occasions in memory. There are two exposure phases followed by the test, constituting a single trial. The first exposure phase is comprised of two different objects that are placed in two distinct locations in one context. After a delay, in the second exposure phase a different context is used and the objects switch locations. After another delay, a particular context is presented again at test and a pair of the same objects are used (duplicates of the objects experienced in the exposure phases). As the test object has been experienced in both locations but only one location in a specific context, an integrated object-place-context memory can be guiding exploration behaviour (Eacott & Norman, 2004).

A common criticism of these integrated what-where-when approaches is that humans can personally retrieve purely semantic knowledge (encyclopaedic-like knowledge about the world; Renoult et al., 2019), in an integrated what-where-when manner (c.f., Klein, 2015; Crystal & Suddendorf, 2019; e.g., Charles Darwin was born in Shrewsbury, England on the 12th of February, 1809). To this end, Fortin and colleagues (2004) developed a way to implement comparable implicit receiver operating characteristics curves in rats to that used human verbal learning. Critically, they demonstrate behaviourally that rats display both recollective and familiarity-based mnemonic components, i.e., reliant on episodic-(like) memory and non-episodic memory, respectively, with lesions of the hippocampus only impairing the episodic-like memory component (Fortin et al., 2004). Moreover, similarly to the

object-place-context task devoid of an explicit reward element as used in the Fortin et al., (2004) study, Eacott and colleagues (2005) showed that rats made more relative turns toward a non-habituated hidden object relative to a previously habituated object, in their specific locations, again being contextually specified via distinct visuo-tactile cues of the environment. Indeed, rats with lesions of the fornix show no such behavioural preference for integrated object-place-context novelty in this task when objects were hidden, but fornix-lesioned rats did display preference to explore the non-habituated object when visible. This suggests impaired episodic-like memory but intact familiarity-based processing (Easton et al., 2009). Taken together, accumulating evidence has shown that non-human animals behaviourally demonstrate a capability of episodic-like memory processing.

1.3. Event segmentation in non-human animals? Formalisation of the thesis program of research

Beyond a cross-species comparative view by assessing the content of the memory, the cognitive process of event segmentation offers novel insights to further assess to what extent episodic memory is shared across species (Templer & Hampton, 2013). As such theory has been initially proposed in a human-centric view (Newtson, 1973; Zacks et al., 2007), this formulates the overarching question of the present thesis: does comparable segmentation of continuous experience occur for episodic-(like) memory in non-human animals?

Chapter 1 provides an extended introduction by reviewing the available literature (at the time of writing). The main formulations can be summarised as fourfold:

I) The hippocampal formation is critically associated with episodic memory in humans and is well evolutionarily conserved in mammalian species being also associated with episodic-like memory (e.g., Vargha-Khadem et al., 1997; Ferguson et al., 2019; Insausti, 1993; Allen & Fortin, 2013).

II) There are similar neurobiological mechanisms in humans and non-human animals to allow the perceptual construction of events particularly in the aforementioned regions.

III) Transitions in spatial context is one good way to make cross-species comparisons in event segmentation.

IV) As well as event segmentation being driven by external changes, it may also be driven by internally generated changes (with hippocampal sharp-wave ripples hypothesised as being a potential psychophysiological correlate, Bilkey & Jenson, 2021).

Chapter 2 addressed whether rats use top-down like processing in the form of prediction-errors to potentially segment their experience. This was realised using a variation of the object-place-context behavioural task (Eacott & Norman, 2004). Chapter 3 builds upon the methodology used in chapter 2. In this chapter, a series of experiments were used to argue that mice readily incorporate social information into episodic-like memory.

Chapter 4 presents a series of experiments using an event segmentation task in human participants. This was inspired by experiments in rodents showing that physical boundaries influence the activity of spatially-modulated cells in hippocampal formation, potentially facilitating discrete representations for sub-spaces (Derdikman et al., 2009). To this end, these experiments were used to argue that turns around spatial boundaries similarly cue event segmentation in humans and non-human animals.

Chapter 5 consists of preliminary electrophysiology experiments in mice asking whether single place cells can integrate spatial context and object specificity to form simultaneously integrated episodic (i.e., object-place-context) representations. Preliminary results argue in favour of the view that place cells (putatively of the hippocampal cornu ammonis 1 region) do form integrated episodic representations, which is discussed in the context of hippocampal indexing theory and episodic memory.

The general discussion will examine if the evidence supports that comparable event segmentation processes occurs in non-human animals and will further explore whether this strengthens the view that episodic-like memory is episodic memory.

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2. Chapter 1 (literature review): The hippocampal horizon: constructing and segmenting experience for episodic memory

2.1. 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.

2.2. 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; Radvansky & Zacks, 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).

2.3. 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).

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).

2.3.1. 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 & Recce, 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).

2.3.2. 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; Nitzan 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).

2.3.3. Cellular representation of time

Hippocampal damage in rodent models indicates that it is necessary for elapsed time discrimination beyond 10 seconds (Sabariego et al., 2021; Kesner, Hunsaker & Gilbert, 2005), and memory for high resolution elapsed time discriminations on short (1 vs 1.5 min.) and longer timescales (8 vs 12 min.; Jacobs, Allen, Nguyen & Fortin, 2013). Additionally, remembering the sequential order of items in events was seen to be hippocampal dependent, yet recognising a task item versus a novel stimulus was intact in these same hippocampal lesioned animals (Fortin, Agster & Eichenbaum, 2002; Kesner, Gilbert & Barua, 2002).

These earlier lesion studies alluded 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.

2.4. 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 would suggest 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, 2020; Richmond & Zacks, 2017; Baldassano et al., 2017).

2.4.1. Long timescales

An emerging body of research in humans has made use of more 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., 2021b;Lee & Chen, 2021; Clewett et al., 2019; Song, Finn & Rosenberg, 2021).

2.4.2. 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).

2.4.3. 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 non-human animals. Finally, given the aforementioned evidence of dynamic hippocampal processing on shorter timescales (sections 2.3, 2.4.2), 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.

2.5. 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, 2021), 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.

2.5.1. 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, 2019; 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).

2.5.2. 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; Dragoi & Tonegawa, 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 2.3), (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.

2.6. 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 the EHM, a given event model is updated (Radvansky & Zacks, 2014; Radvansky & Zacks, 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).

2.6.1. 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 separately encoded 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., 2021b). 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).

2.6.2. 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 2.3) and event segmentation (sections 2.4 & 2.5) 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; Eichenbaum 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 was 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 2.3.1. and 2.4.2) 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).

2.6.3. 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.

2.7. 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.

2.8. References

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2.9. Bridging of chapter 1 and 2

As discussed in section 1.1. of the general introduction, event segmentation in humans can be cued by error in one's predictions (top-down processing). The experiments in chapter 2 explore this possibility in rats using the object-place-context (episodic-like) task. This task, like other spontaneous recognition paradigms, allows the animal to (potentially) learn associations between the cues provided and form predictions in an incidental manner. That is, without the experimenter explicitly shaping the associations for the animal via external reinforcement. In this way, one can subsequently manipulate the cue associations that the animal has previously experienced thereby creating potential prediction-error situations and assess how the animals behaviourally respond.

3. Chapter 2: Rats use strategies to make object choices in spontaneous object recognition tasks

3.1. Introduction

Spontaneous object recognition tasks are critical for allowing cross-species comparisons of complex recognition memory to enhance our mechanistic understanding[1-6]. In the standard version of novel object recognition, a single trial consists of an exposure phase and test phase[7] (Fig. 1A). Rodents typically display successful object recognition memory via novelty preference in this version (i.e., exploring the novel object more than the familiar object, and to a greater extent than chance)[7-9]. However, successful memory expression can also be shown via preference for the familiar object in these tasks[10-12]. Memory is simply determined by preference of one object over another on the basis of past experience. The direction of that preference (for the novel or familiar object) can be driven by external factors, such as anxiety[1,12].

The underlying presumption of SOR tasks is that they are training-free paradigms[13], where the exploration behaviour at the test phase is an unconditioned preference[1] and hence the exploratory preference for an object is spontaneous. In other words, as there is no explicit reinforcement used by experimenters, a strategy should not be learnt in these paradigms compared to other training-based (reinforced) tasks[13]. However, the neural mechanisms that give rise to novelty detection and novelty-seeking motivation[14-16] allows for learning through the identification of novelty (which is inherent in SOR tasks) and this in itself can be behaviourally reinforcing[17].

The mammalian brain also segments experience into discrete events[18,19], and animals can formulate predictions of what to expect in certain situations based on prior knowledge learnt from their memory of experiences in past events[19-21]. This aims to minimise surprise and so when error of predictions is experienced, animals can flexibly update and guide their future behaviour[18,22]. Therefore, such evidence

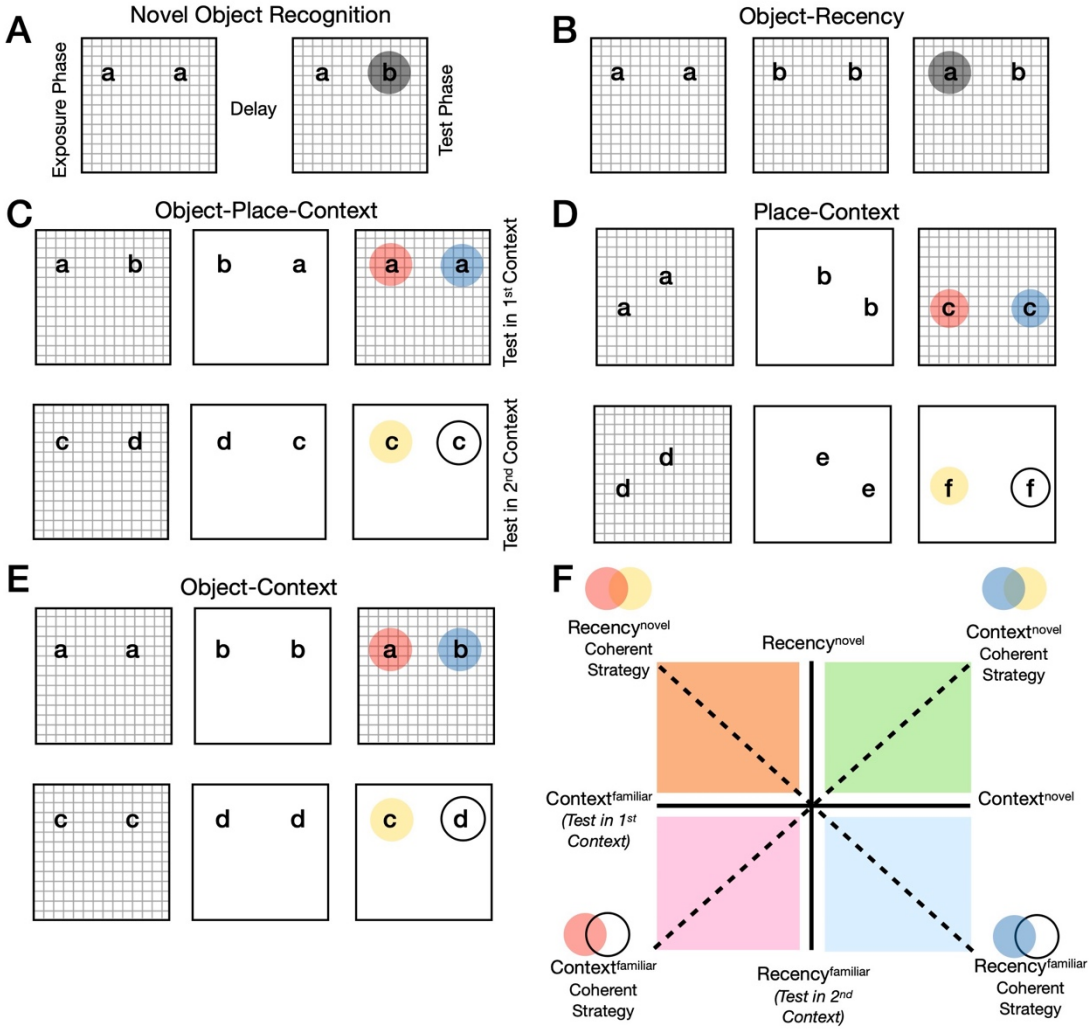

Figure 1. Schematics of various object recognition tasks with 2 objects. **(A)** Standard novel object recognition in the same environment with 1 exposure phase (left), a delay and a novel object present at the test phase (right). The highlighted grey circle denotes expected novelty-based discrimination. Lower case letters denote objects. **(B)** Object-recency task in the same environment with 2 exposure phases (left and middle) and the test phase (right). The highlighted grey circle denotes expected novelty-based discrimination on the object least recently seen**. (C)** Object-place-context task in two different environments (i.e., contexts) with 2 exposure phases (left and middle). Test phase can be made in the 1st context (upper right) or test can be made in the 2nd context (lower right). In test in the 1st context trials, the highlighted blue circle can denote novelty discrimination of integrated object-place-context association or the highlighted red circle can denote novelty discrimination of object in place recency (note that discrimination is ignorant to context, see B). In test in the 2nd context trials, the highlighted yellow circle can denote novelty discrimination of integrated object-place-context or novelty discrimination of object-place recency (they are overlapping). **(D,E)** Other 2 objects/ exposure/ contexts tasks which are susceptible to a context-based versus recency-based strategy where F is applicable. **(F)** Strategy scatterplot for 2 object/context/exposure object recognition tasks. Based on C–E one can average discrimination ratio scores separately for both for test in the 1st context trials and test in the 2nd context trials and plot them for each animal. The average context D2 for trials when test was made in the 1st context on the x-axis, and for trials when test was made in the 2nd context on the y-axis. Thus, one can form angular data and use directional statistics, which can enhance interpretive power if animals are behaving differently to chance. Context^{novel}/ Recency^{novel} denote exploration on the basis of object related novelty preference. Context^{familiar}/ Recency^{familiar} denote exploration on the basis of object related familiarity preference.

provides a strong basis for the possibility that rodents may be making strategic choices in SOR tasks.

Recent development of a continual trials approach to SOR tasks[3,9,23-25] (i.e., running multiple trials within a single session, opposed to one trial a day), means that we can begin to obtain consistent behavioural choices from a single animal over several trials. This aims to reduce the number of total animals, whilst maintaining sufficient statistical power[23] and has offered a novel opportunity to explore whether rodents are behaving coherently using a certain strategy over another.

The object-recency or temporal order recognition task[26,27] (see Fig. 1B) uses two exposure phases before test in a single environment, which constitutes one trial. At test, rodents preferentially explore the novelty of the object seen least recently in this task[26-29]. On the other hand, context-based SOR tasks[30-32] (Fig. 1C-E), which usually use distinct environments as contextual information, also use two exposure phases and a test as a single trial. Rodents can preferentially explore novel objects in context or novel objects in place and context more so than chance at the test phases[30-32].

Recognition of simultaneous object-place-context (OPC) integrations fulfils the requirement of a behavioural definition of episodic memory[4,33]. Thus, if animals were using a novelty driven episodic strategy (based on context) in the OPC recognition task[30], we can expect them to explore the novel object in place and context integration when test is made in the 1st context (the blue circle in Fig. 1C). However in the same OPC task, animals could also be exploring the novelty of the object least recently seen when test is made in the 1st context and this choice would be ignorant to contextual information (the red circle in Fig. 1C). Moreover, it is ambiguous whether animals are using a context-based or recency-based strategy in test in the 2nd context trials, as both predict the same object choice (the yellow circle in Fig. 1C). Therefore, when test phases of trials are made in the 1st context, object-recency memory and object-context memory are in opposition, whereas when test is made in the 2nd context they are overlapping[34]. Firstly, this suggests that it is important to use both types of trials to determine coherent behaviour (see Fig. 1F) and secondly it is possible that different recognition strategies can exist in the same task.

Here, we use a novel unexpected OPC task with a continual trials approach,

and find that rats robustly change their recognition guided behaviour to a recency-based strategy expressed via familiarity preference, after experiencing unexpected ambiguous events. Yet, they could also exhibit a novelty driven episodic strategy in the same task, suggesting that strategy implementation was dependent on task conditions and hence not spontaneous.

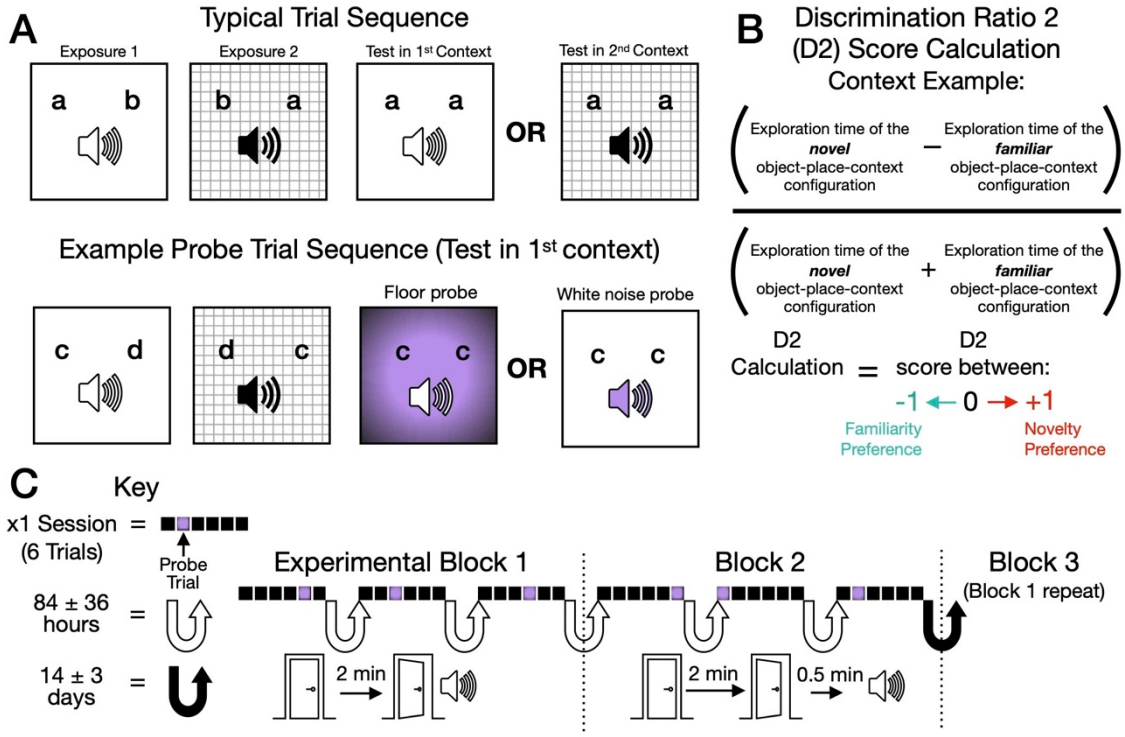

Figure 2. Methodology of trial types and experimental timeline. **(A)** Unexpected object-place-context task. Upper: 'Contexts' were comprised of tone-floor pairings. Typical trials: 2 exposure phases (far and middle left; letters denote objects). The test can be made in the 1st context (right-middle) or in the 2nd context (far-right). Exposure and test phases were 2 min, as were the interval between them and the next trial starting in a session. Lower: Example probe trial (test in the 1st context): Floors are replaced (right-middle; tones remain stable) or tones are replaced (far-right; floors remain stable). **(B)** Discrimination ratio 2 (D2) calculation (context example). For each animal, the context D2 score, recency D2 score and side bias was calculated individually for each trial and then averaged across all trials (in a given session/block) and finally across animals to give an average D2 score. We also separated trials occurring before/after probe trials for a given session, and averaged them across a block, creating a before/after probes context and recency average D2 score. This was sometimes separated further by considering the trials only when test was made in the 1st context or only when test was made 2nd context. **(C)** Timeline of the main experimental blocks. Upper: Each block had 3 sessions composed of 6 trials (1 probe per session; the location of which is indicated by the purple square). There were 3 blocks and finally one session where all 6 trials were probe trials (not shown in C). We included 1 control probe within each block, where at test there were 2 novel objects present (not previously seen during exposure phases). Block 3 was a within-subject counterbalanced repeat of block 1. Lower: In block 1 and 3 the tonal cue played immediately to the onset of the door opening starting a given exposure/test phase. However, in block 2 we delayed the onset of the tone by 0.5 min, this was relative to the door opening and rats shuttling into the open field chamber of only exposure phases of typical trials.

3.2. Results

3.2.1. Rats change their behaviour to a familiarity driven recency-based recognition strategy after probe trials

We used an OPC task where a given context was comprised of both a distinct floor and a unique auditory tone. Importantly, each testing session contained typical trials and a probe trial (Fig. 2; see methods), where at the test phase for the probe we manipulated the previously stable floor-tone context by replacing either the floor, or tone with an unexpected floor or white noise. This created an unexpected ambiguous event as only one of the two contextual elements remained the same. Each experimental block consisted of 3 testing sessions composed of 6 trials (1 probe trial per session). There was a total of 3 experimental blocks and finally one session where all 6 trials were probe trials.

Rats (n = 8) autonomously shuttled through a door separating the holding chamber and open field chamber (where object exploration occurred) until the end of a given session, thus entirely without experimenter handling. Recognition memory performance was evaluated via the discrimination ratio 2 (D2) score[8], calculated separately for an integrated OPC recognition memory (a context-based strategy; Fig. 2B) or an object-place recency strategy. Both a context and recency D2 score gives a value between -1 and +1, where 0 reflects no preference (i.e., chance-level performance, e.g., two-tailed one sample t test). Positive 1 reflects exploration of novelty preference and -1 reflects exploration of familiarity preference. Side bias calculations controls for if animals were consistently exploring left (+1) or right (-1) objects at test phases.

In experimental block 1, we first asked whether rats were recognising objects using any strategy more so than chance and initially found that a recency-based strategy exhibited via familiarly preference best explained average recognition performance, across all trials excluding probes (Fig. 3A).

We next asked whether it was the experience of probes that was affecting the strategy that rats used to recognise objects. We observed that before probes neither the average recency D2 score (M = -0.11, SD = 0.24) nor context D2 (M = -0.03, SD = 0.39) differed from chance performance ($t_{(7)}$ = -1.35, p = 0.22, d = -0.48; $t_{(7)}$ = -0.22,

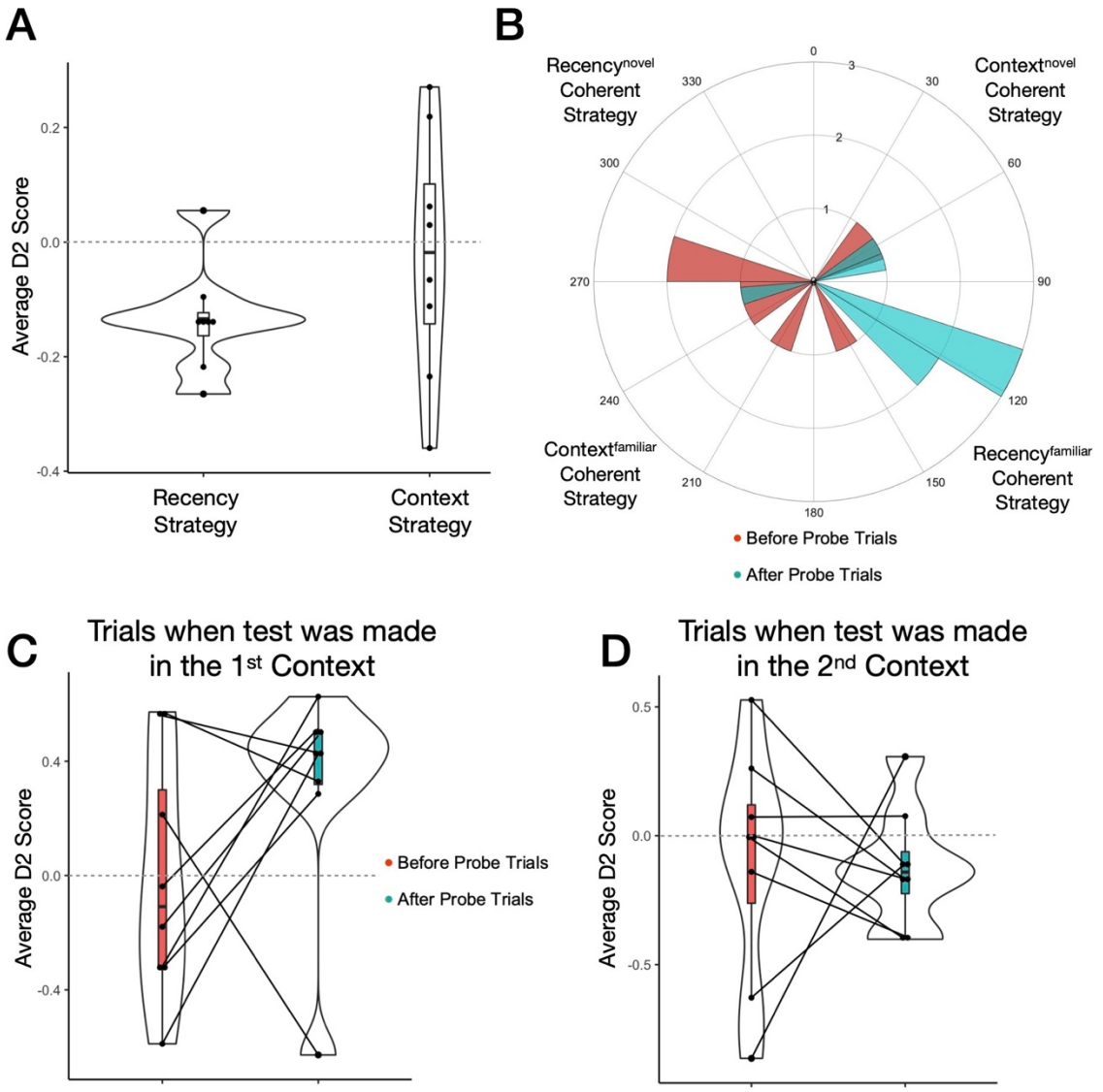

Figure 3. Rats change their behaviour to a familiarity driven recency-based strategy after probe trials. **(A)** Block 1 (probes excluded): The recency D2 (M = -0.13, SD = 0.09) significantly differed from zero ($t_{(7)}$ = -4.03, p = 0.005, d = -1.42, CI 95% -2.41, -0.39). The context D2 score (M= -0.02, SD = 0.22) and side bias (M = -0.04, SD = 0.17) did not differ from zero ($t_{(7)}$ = -0.31, p = 0.76, d = -0.11; $t_{(7)}$ = -0.72, p = 0.50, d = -0.25; respectively). **(B)** Angular histogram before probe angles (M = -109.4°, SD = 85.4°, n = 8), after probe angles (M = 106.0°, SD = 50.2°, n = 8), 20 bins of 18°. The before probe angles were uniformly distributed around the circle (Rayleigh-test: Z = 0.87, p = 0.43), but the after probe angles were not (Rayleigh-test: Z = 3.71, p = 0.02). This implies that there was significant directionality to the data after probe trials, in the theoretical direction for a coherent Recency^{familiar} strategy (see Fig. 1F). Also, the before and after probe angles did not have a common mean direction (Watson–Williams F test: $F_{1,14}$ = 10.40, p = 0.006), suggesting a change in behaviour after experiencing probes in block 1. **(C)** Average before/after probes context D2 score from trials only when the test was made in the 1st context (before: M = -0.01, SD = 0.43; after: M = 0.44, SD = 0.12). The before probes context D2 did not differ from chance ($t_{(7)}$ = -0.09, p = 0.93, d = -0.03), however the after probes context D2 score did ($t_{(6)}$ = 10.23, p < 0.001, d = 3.87, CI 95% 1.61, 6.11) and from the before D2 score ($t_{(6)}$ = -2.63, p = 0.04, d = -0.99, CI 95% -1.89, -0.05). **(D)** Average before/after probes context D2 scores from trials only when test was made in the 2nd context (before: M = -0.10, SD = 0.45; after: M = -0.12, SD = 0.23). Both did not differ from zero ($t_{(7)}$ = -0.61, p = 0.56, d = -0.22; $t_{(7)}$ = -1.48, p = 0.18, d = -0.52; respectively) nor from each other ($t_{(7)}$ = 0.11, p = 0.92, d = 0.04).

$p = 0.83$, $d = -0.08$; respectively). In addition, the after probe context D2 also did not differ from chance (M = 0.13, SD = 0.24; $t_{(7)} = 1.56$, $p = 0.16$, $d = 0.55$). However, the recency D2 score after probe trials (M = -0.27, SD = 0.20) was negative, and significantly differed from chance ($t_{(7)} = -3.96$, $p = 0.005$, $d = 1.40$, CI 95% = -2.38, -0.38), with performance being particularly driven from trials when test was made in the 1st context (Fig 3C). A difference in total exploration did not contribute in explaining the change in behaviour that we observed, as the average total exploration before probes (M = 67.9 s, SD = 38.4 s) did not differ to that after probes (M = 61.6 s, SD = 41.4 s; $t_{(7)} = 0.48$, $p = 0.65$, $d = 0.17$). Therefore, considering these results overall (Fig. 3), there was notable individual variability in performance before probes, whereas after probes, rats seemed to have robustly changed their behaviour to a familiarity driven object in place recency-based strategy on average.

3.2.2. Rats are capable of a novelty driven context-based recognition strategy in the same task

Unlike experimental blocks 1 and 3, we delayed the onset of the auditory contextual cue by 0.5 minutes in block 2 testing (Fig. 2C). We hypothesised that this would enhance the salience of contextual cues[18,19] during these exposure phases and potentially impact strategy implementation.

We initially found no evidence of a coherent strategy when considering all trials together excluding probes (Fig. 4A). However, when analysing before versus after probe trials separately, we found that the average context before probe D2 score was positive and significantly differed from chance (M = 0.26, SD = 0.19; $t_{(7)} = 3.98$, $p = 0.005$, $d = 1.41$ CI 95% = 0.39, 2.39). The recency before probe D2 also differed significantly although notably to a lesser extent (M = 0.19, SD = 0.17; $t_{(6)} = 2.91$, $p = 0.027$, $d = 1.10$, CI 95% = 0.12, 2. 04). Moreover, both the after probe average context D2 (M = 0.17, SD = 0.54, n = 8) and recency D2 score (M = -0.17, SD = 0.68) did not differ from chance ($Z = 0.34$, $p = 0.74$, r = 0.12; $t_{(7)} = -0.73$, $p = 0.49$, $d = -0.26$; respectively). The finding that both the before probe context and recency D2 scores were positive and differed from chance, suggested that performance was being driven mainly from trials when test was made in the 2nd

context. Indeed, the before probe context D2 from test in the 2nd context trials (M = 0.35, SD = 0.27) was positive, and significantly differed from chance on average ($t_{(6)}$ = 3.40, p = 0.014, d =, 1.30, CI 95% = 0.24, 2.31), whereas when only considering trials when test was made in the 1st context, the context D2 before probes did not (M = 0.08, SD = 0.39; $t_{(6)}$ = 0.56, p = 0.59, d = 0.21). Similarly to block 1, the average total time spent exploring before probes (M = 44.3 s, SD = 31.6 s, n = 8) did not

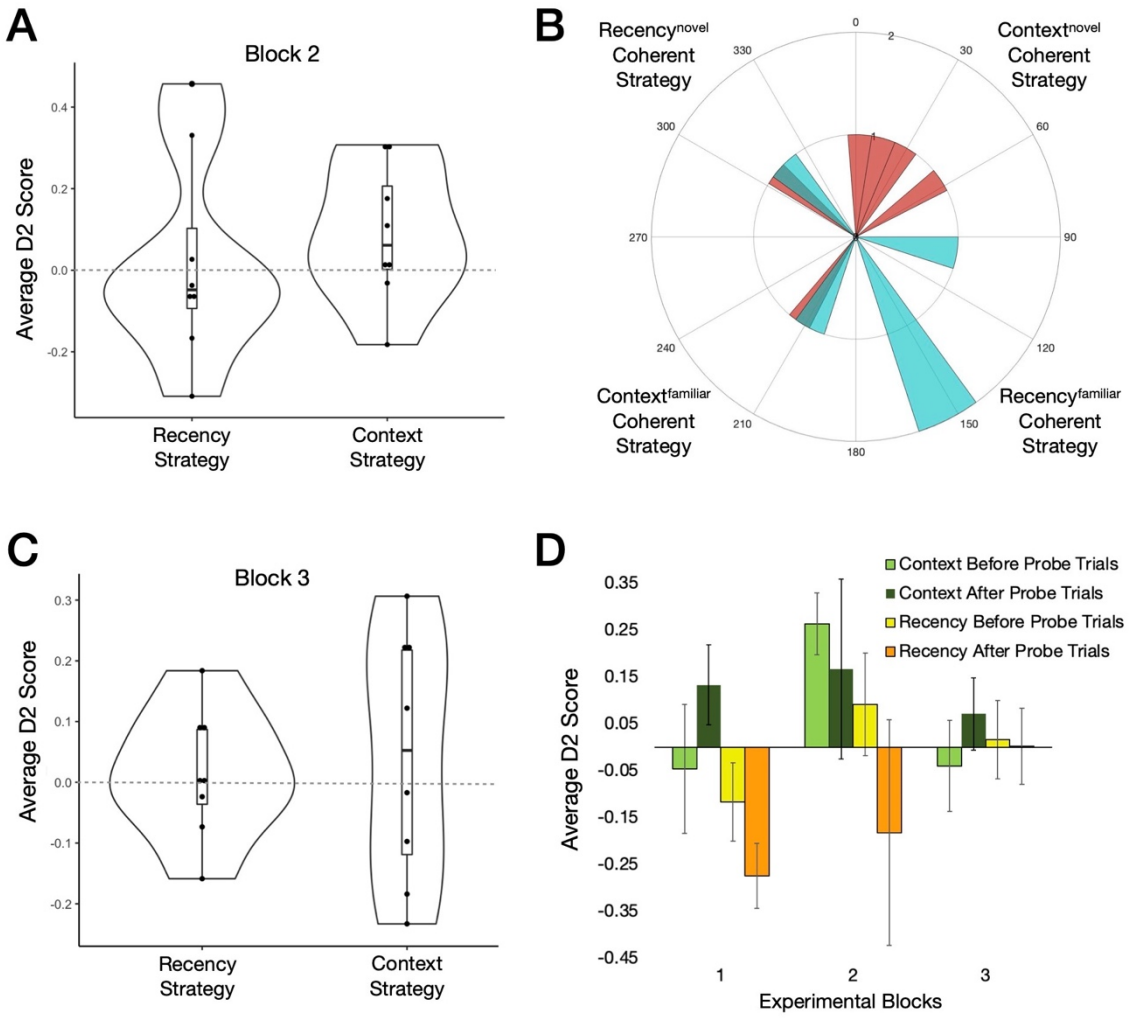

Figure 4. Experimental blocks 2 and 3 and performance across blocks. **(A)** Block 2 (probes excluded): The overall average context D2 score (M = 0.09, SD = 0.17) and the average recency D2 score (M = 0.02, SD = 0.25) did not differ from zero ($t_{(7)}$ = 1.47, p = 0.18, d = 0.52; $t_{(7)}$ = 0.24, p = 0.82, d = 0.09; respectively). There was no side bias present (M = 0.09, SD = 0.24; $t_{(7)}$ = 1.01, p = 0.35, d = 0.36). **(B)** Angular histogram before probe angles (red), after probe angles (blue) for block 2; 20 bins of 18°. Both the before probe trial (M = -0.2°, SD = 64.8°, n = 6) and the after probe trial angles (M = 159.0°, SD = 74.7°, n = 5) were uniformly distributed around the circle (Rayleigh test: Z = 1.67, p = 0.19; Z = 0.92, p = 0.42; respectively). **(C)** Block 3 (probes excluded): The average context D2 score (M = 0.04, SD = 0.20) did not differ from zero ($t_{(7)}$ = 0.59, p = 0.57, d = 0.21), nor did the recency D2 score (M = 0.01, SD = 0.11; $t_{(7)}$ = 0.38, p = 0.72, d = 0.13). Additionally, there was no side bias (M = 0.03, SD = 0.12; $t_{(7)}$ = 0.60, p = 0.57, d = 0.21). (**D**) Average before probe context D2 scores, after probe context D2 scores, before probe recency D2 and after probe recency D2 scores across experimental blocks 1 to 3. Error bars denote ± SEM.

differ to that after probes (M = 37.8 s, SD = 49.7 s, n = 8; Z = -0.56, p = 0.58, r = -0.20).

We next asked how the block 2 context and recency D2 scores compared to blocks 1 and 3 before probe trials (Fig. 4D). For the recency D2 score before probe trials, a repeated measures ANOVA revealed a non-significant result with no observed trends ($F_{2,14}$ = 0.98, p = 0.40, η^2 = 0.12). On the other hand, the before probes context D2 initially revealed a non-significant result ($F_{2,14}$ = 2.32, p = 0.14, η^2 = 0.25), although there was a significant quadratic trend to the data ($F_{1,7}$ = 9.26, p = 0.02, η^2 = 0.57), thus we interpreted post-hoc tests. Fisher's least significant difference post hoc tests revealed no difference between block 1 and block 2 (p = 0.10, d = 0.67), no difference between block 1 and 3 (p = 0.94, d = 0.03), but a significant difference between block 2 and block 3 (p = 0.041, d = 0.88). In consideration of these results overall from block 2 testing (Fig. 4), recognition guided behaviour before probe trials is best explained by a context-based strategy expressed via novelty preference (particularly driven by performance in test in the 2nd context trials). Yet, there was no coherent strategy on average after probe trials in experimental block 2.

3.2.3. The familiarity driven recency-based recognition strategy after probe trials diminishes over time

Experimental block 3 was a repeat of block 1 conducted 14±3 days after block 2 testing. We found that there was no detectable strategy on average in block 3 trials, when analysing all trials together excluding probes (Fig. 4C). Additionally, there were no strategies present before or after probe trials. Neither the average context D2 score before probes (M = -0.05, SD = 0.27) and after probes (M = 0.07, SD = 0.22) differed from chance ($t_{(7)}$ = -0.47, p = 0.65; $t_{(7)}$ = 0.93, p = 0.39; respectively), nor did the recency D2 before probes (M = 0.02, SD = 0.24) and after probes (M = 0.003, SD = 0.23; $t_{(7)}$ = 0.20, p = 0.85; $t_{(7)}$ = 0.03, p = 0.97; respectively). There was also no difference in the average total time spent exploring before probes (M = 65.3 s, SD = 37.4 s) versus after probes (M = 75.4 s, SD = 47.2 s; $t_{(6)}$ = -0.57, p = 0.59, d = -0.22).

Given that there was a strong after probe trial change in behaviour to a familiarity driven recency-based strategy in block 1 (Fig. 3), we asked how the after probes average recency D2 score compared across blocks (Fig. 4C). A repeated measures ANOVA initially revealed a non-significant result ($F_{2,14} = 0.73$, $p = 0.50$, $\eta^2 = 0.09$), yet there was a significant linear trend to the data ($F_{1,7} = 6.31$, $p = 0.04$, $\eta^2 = 0.47$), so we thus interpreted post-hoc tests. Fisher's least significant difference post hoc tests revealed no difference between block 1 and block 2 ($p = 0.73$, $d = 0.13$), no difference between block 2 and 3 ($p = 0.53$, $d = 0.23$), but a significant difference between block 1 and block 3 ($p = 0.04$, $d = 0.89$). Thus, there was evidence that the behavioural change of expressing a familiarity driven recency-based strategy, after experiencing probe trials, diminished from block 1 compared to block 3.

3.2.4. No coherent strategy in probe trials across blocks and in the all probe trial session

There was no clear strategy on average in probe trials averaged across blocks 1 to 3 nor in the all probe session (Fig. 5). Control probe trials during experimental blocks 1 to 3, where novel objects were introduced in the test phase

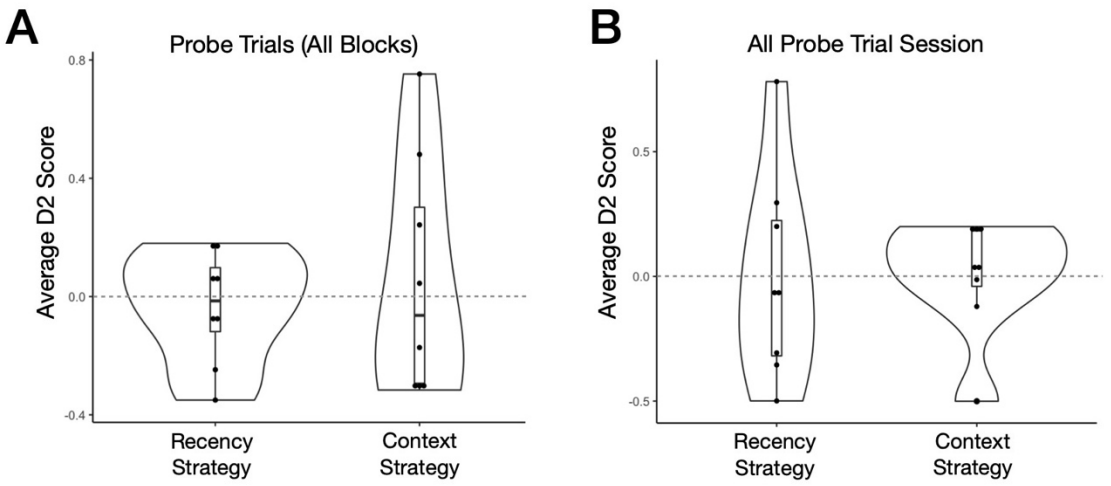

Figure 5. Probe trials across block 1–3 and the all probe trial session. **(A)** Probe trials (averaged across blocks 1–3): The average context D2 score (M = 0.05, SD = 0.40) and recency D2 score (M = -0.04, SD = 0.20) did not differ from zero ($t_{(7)} = 0.38$, $p = 0.72$, $d = 0.13$; $t_{(7)} = -0.53$, $p = 0.61$, $d = -0.19$; respectively). **(B)** All probe trials session: The average context D2 score (M = 0.001, SD = 0.23) and recency D2 score (M = -0.002, SD = 0.42) did not differ from chance ($t_{(7)} = 0.01$, $p = 0.99$; $t_{(7)} = -0.01$, $p = 0.99$; respectively). Also, there was no side bias present (M = -0.02, SD = 0.22; $t_{(7)} = -0.21$, $p = 0.84$).

not previously seen in exposure phases (one per block), yielded no particular side bias (M = 0.03, SD = 0.40; $t_{(7)} = 0.19$, $p = 0.86$, $d = 0.07$). Moreover, repeated measures ANOVAs revealed no differences or trends between average context probe D2 scores and average recency probe D2 scores across blocks ($F_{2,14} = 0.73$, $p = 0.50$, $\eta^2 = 0.10$; $F_{2,14} = 0.68$, $p = 0.52$, $\eta^2 = 0.09$; respectively). Overall, this suggested that there was great individual variability in recognition behaviour across probe trials, leading to no coherent strategy by rats on average.

3.3. Discussion

For the first time we show that rats change their response in an SOR task based on predictability of the task conditions (Fig 3). Importantly, no explicit external reinforcement shaped the behaviour. In all cases behaviour was driven by memory of previous events, but the nature of the memory driving the behaviour (recency or episodic) was determined by the predictability of the task conditions.

By manipulating contextual information in unexpected ambiguous events, we posit that this violated the rats' predictions of the previously stable floor-tone context associations[18-22], devaluing mnemonic associations reliant on contextual information[34,35]. Thus, the behavioural change after probes to an object in place recency-based recognition strategy (free from a context-based association), allows for maximising mnemonic confidence of past experience[36], whilst minimising future prediction error[22] and still behaviourally identifying novelty[1]. Moreover, the familiarity preference of the recency-based strategy that we observed is in accordance with evidence that non-human laboratory animals can express a more conservative approach in their exploratory behaviour[10-12,31,37]. For example, young rats exhibited a developmental switch from familiarity to novelty preference in the novel object in place task[11].

In the same cohort of rats, we show that they could still exhibit a novelty driven episodic (context-based) strategy on average in the same task (Fig. 4). This is supported by previous findings in other OPC tasks in a continual trials apparatus[24] and in one trial a day testing[30,38,39]. We postulate that delaying the onset of the tone enhanced the salience of the contextual cues[18,19], likely recruiting associative

mnemonic hippocampal processing[40-47], as good episodic recognition performance in the OPC task has been seen to be dependent on the hippocampus[38] and fornix[30].

As rats progressively experienced a greater number of probe trials, the unexpected nature of them should have lessened (intuitively, becoming more expected over time). There was evidence to support this, as the recency D2 score after probes decreased linearly from block 1 to block 3 (Fig 4D), suggesting increased variability in their recognition guided behaviour after probes over time. Indeed, in a hippocampal-dependent episodic-like task explicitly using valence, rats could remember episodic integrations over long retentions (>24 days), but this was similarly accompanied by a notable degree of individual differences in behavioural performance[48,49]. Furthermore, we speculate that the lack of any coherent strategy on average seen during experiential blocks, as well as probe trials themselves, was in part due to individual differences in hippocampal-mediated learning over time[21,43-47], and especially in block 3, it is possible that rats had retained varying degrees of schematic memory[e.g.50,51] that 'probe trials can occur' in the task. However, future context-SOR work may use probe trials to further explore this possibility.

The reporting of novelty object preference in the literature outweighs that of familiarity preference, notably in relation to context-SOR in rodents[31]. Therefore, there remains many unknowns regarding expression of familiarity preference. For example, in the same group of animals, does the age[11] and anxiety[12] factors that influence expression of familiarity preference in one SOR task type (e.g., novel OR) equally influence expression in the novel object-in-place task or a context-SOR task, (despite these various SOR tasks recruiting and relying upon differing neuronal structures[3-6,13-15])? Moreover, we have used a relatively short time for exposure/test phases and inter-phase-intervals (IPI; 2 min). This may have contributed to the change of recognition behaviour we observed in block 1 and the lack of coherent recognition behaviour at times, as longer exposure phases and IPIs (especially the IPI between exposure 2 and test) have been seen to help stabilise episodic-like memory expressed via novelty preference in one trial a day designs[52,53]. That being said, like in a previous rat continual trials OPC task[24], which also used short timings (2 min), we similarly observed the emergence of episodic-like memory being expressed via novelty preference. Thus, future work using a continual trials approach

to context-SOR may seek to optimise the timings of exposure/test phases and IPIs, depending on the nature of the experiment and practical limitations.

Recognition memory can be modelled as a dual process, where recollective retrieval is a distinct neuro-cognitive process to familiarity-based retrieval[5,54], (not to be confused with familiarity preference in SOR tasks). There is strong evidence that non-human animals have recollective retrieval capabilities[33,55-57], which requires mnemonic access to the contextual detail (source information) of the recalled content[4,57]. Interestingly, in an analogous human OPC task, it was found that when using temporal order (recency-based) information to accurately recognise event content, participants could use familiarity or recollection[58]. However, when using source (context-based) information, participants could only rely upon recollection[58]. Our novel analytic approach provides better detection of context and recency-based strategies in relevant SOR tasks (Fig. 1), which allows us to draw greater cross-species parallels to source versus temporal-based in human event memory and perhaps recollective versus familiarity-based retrieval. It also enhances explanatory power of the context-SOR data, where a given manipulation may not be globally impairing recognition memory, but instead could be driving a switch in strategy, which is a necessary issue that future research should consider. Finally, for context-SOR tasks we argue that it should at least become standard practice for experimenters to report discrimination ratio scores both averaged together and separately for trials when test is made in the 1st context, and for trials when test is made in the 2nd context[e.g.34].

In conclusion, if behaviour is truly spontaneous and implicit in all object recognition paradigms, it becomes very challenging to interpret why certain strategies do seem to emerge over others, and why behaviour changes after experiencing certain events during these tasks. Based on our findings from these experiments we argue against the spontaneous presumption of behavioural manifestation. We propose that, like any other training-based task, rats are continually learning and are seeking out for information which can ultimately influence their volitional mnemonic-dependant exploratory behaviour. However, in context-SOR tasks these strategies are more easily observed using multiple trials within a session for a single animal (to allow consistent behaviour to be seen) and

adopting novel analytic tools which allow the investigation of all possible solutions to the task, not simply experimenter defined novelty.

3.4. Methods

3.4.1. Subjects

Nine male Lister hooded rats (supplied from Charles River, U.K.) were housed in groups of 3 (aged 5-6 weeks upon arrival; 150±10 g), in a room maintained on a 12-hour light-dark cycle (07:00-19:00 h), with daily monitoring of temperature and humidity (20±1°C; 55±10%; respectively). Each home cage measured 56×38×22 cm (l×w×h; RC2F, NKP isotec., U.K.) and were equipped with a rat tunnel and a guinea pig shelter (Datesand Limited., U.K.). All stages occurred during the light phase and rats had free availability of food and water ad libitum throughout. Animals were not euthanised as part of the experiments. All experiments were conducted in accordance with the U.K. Animals Scientific Procedures Act (1986) and approved by Durham University AWERB and the Home Office (procedure licence number: PP8877096). Reporting follows the recommendations in the ARRIVE guidelines.

3.4.2. Apparatus and objects

Rats were tested in an apparatus designed for continual trials rat SOR (Model CI.80514R-1, Campden Instruments., U.K.). The open field was ~50×50×30.5 cm (l×w×h), the holding area was ~25.5×35×30 cm and they were connected via a single doorway ~7×8×9. A pellet dispenser and port (~4.5×3.5 cm) was present in the holding chamber. Walls and the door were metallic, with red Perspex covering the open field and a transparent Perspex covering the holding area. A speaker and camera were positioned centrally over the open field (~50 cm high). The auditory cues were played from a sound generator and were pure tones 1-5 kHz or white noise (62±8.5 dB SPL). In the unexpected object-place-context (OPC) task, 4 ‘contexts’ were comprised of removable, sensorily distinct floors (~53×50 cm) paired with pure tones, they were as follows: 1kHz with a cream translucent smooth floor, 2kHz with a stainless-steel hatched floor, 3kHz with a red sandpaper floor and 5kHz with a cream translucent floor with a grid of small holes. For probe trials, a rubber

black floor or white noise were used both of which were habituated.

The objects varied in material, shape, size, texture and visual complexion, each object had a minimum of three duplicates and were paired quasi-randomly. Objects were positioned to the far corners of the open field opposite the door (i.e., rats egocentrically had objects left and right to them, as they entered the open field). At the end of testing sessions, objects, floors and the apparatus were cleaned using disinfectant wipes (Clinell® universal wipes, GAMA Healthcare Ltd., U.K.). The scheduling of the camera, door, tones and dispenser operations were controlled automatically by programming (ABET II software; Campden Instruments, U.K).

3.4.3. Habituation and pretraining

Rats acclimatised to their home room for 10 days before handling. Experimenter handling begun with tunnels first taking place in the home room (~10 min per group). Then in cage groups they were transported and handled in the laboratory (dim, diffuse white light from a lamp; 100 W and white noise being played) for ~10 min for a further 5 days. The laboratory was where all testing took place.

Briefly, the initial habituation and pretraining were as follows: 1) cage group habituation (30 min), 2) single animal habituation (20 min), 3) shuttle training between the holding area and open field (where animals had to consistently anticipate and or shuttle within the ~2 min abort window) and 4) object habituation in the open field, with pilot OPC trials using only tonal cues as contexts.

Four weeks had elapsed between the last pilot trials and the start of habituation for the unexpected OPC task. Animals were first habituated individually to the stable floor-tone contexts with the door open (~15 min), 1 context per day, then 2 contexts per day. During this time, the dispenser delivered a chow pellet (45 mg LabTab™ MLab., Indiana, U.S.) each minute into the port. Next, the shuttle and object habituations occurred together with object exploration in the open field, intervals in the holding area and the abort timer all being 2 min. The dispenser delivered a pellet upon entry to the holding chamber and the experimenter placed a pellet between the objects (equidistant from each object) before object exploration in the open field, motivating shuttling and exploration (i.e., baiting). These pellets were

not used as rewards, as they remained consistent throughout exposure/test phases regardless of rats' object exploration or lack of object exploration (i.e., even when no object exploration occurred). At this stage, all contexts were experienced once (~20 min) or twice (~40 min), with a different pair of the same objects experienced in each context. This occurred in a single habitation session and it was over 3 consecutive days. Gate errors could occur by an animal not shuttling all the way through the door (e.g., turning back once the door was closing) or not shuttling before the abort timer expired. If 3 gate errors were made within a habituation session, the session was aborted for that day. All objects used during habituation were not used during testing.

3.4.4. Testing protocol

Eight rats were used in the OPC task, with a continual trials approach[23] (1 did not learn to shuttle efficiently). Each testing session contained 5 typical OPC trials and 1 probe trial (Fig. 2). Sessions begun by the rat being placed into the holding area and nose poking the pellet port, initiating automatic scheduling. For all trials, each exposure and test phase were timed for 2 min after the animal entered the open field and the door closed. After these 2 min, the animal would then return to the holding area initiating a 2 min interval timer once the door closed and could obtain a pellet dispensed into the port. A 2 min interval remained for the start of the next trial within a given session. This allowed sufficient time for the experimenter to change objects, contexts and bait.

Three testing sessions comprised 1 experimental block and there were 3 main experimental blocks (Fig. 2C). This was followed by an all probe trial session (where each of the 6 trials were probes). The time between each session within a block was 84±36 hours. In block 1 and 3, the tonal context played immediately as the door opened to exposure and test phases. However, in block 2, there was 0.5 min delayed onset between the door opening, the animal entering the open field and the tone being played for exposure phases of typical trials (probe trials remained the same as in block 1 and 3). Block 2 testing started 72±24 hours after block 1. Block 3 was a within-subject counterbalanced repeat of block 1 and started 14±3 days after block 2. The experiencing of the trial order sequence, context and object order, and

placement of the novel OPC integrations were counterbalanced throughout all experiments. Additionally, the position of probe trials were counterbalanced across blocks. Finally, objects were not repeated during blocks 1 and block 2, but were for block 3 as it was a repeat of block 1 and were for the all probe trial session (taken from session 1 of block 2).

3.4.5. Behavioural analyses

Behaviour was measured off-line via the recorded footage of experimental trials. Object exploratory behaviour was determined as when rats were within ~2 cm of the object and actively exploring (i.e., visibly whisking, sniffing or touching it). Actions such as sitting upon the object or using it to support rearing were not considered as exploratory behaviour. The duration of exploration behaviour (s) of each object for a given test phase was manually scored via the ChamberView software (Campden Instruments, U.K.) and were not performed blindly by the experimenter. If animals made gate errors (see habituation and pretraining) within a trial, it was excluded from analyses, and if less than half of all the trials for that session were not completed (i.e., the animal made 3 errors and the session was aborted) the other trials of the session were excluded. However, trial completion rate across the main experimental blocks were comparable with no observed trends (block 1: M = 83.3%, block 2: M = 78.5% and block 3: M = 94.4%; $F_{2,14} = 2.28$, $p = 0.14$, $\eta^2 = 0.25$). Recognition memory performance was evaluated through the discrimination ratio 2 (D2) score[8] (Fig. 2B). For integrated OPC recognition memory (a context-based strategy), the context D2 score was calculated as follows: (exploration time of the novel integrated OPC configuration – exploration time of the familiar configuration) / (total exploration time of the novel + familiar configurations). Moreover, an object-place-recency D2 score was also calculated: (exploration time of novel object in place recency – exploration time of the familiar configuration) / (total exploration time of the novel + familiar configurations). Finally, the side bias calculation: (exploration of the left object at test – exploration of the right object at test) / (total exploration of the left and right object). For each animal, the context D2 score, recency D2 score and side bias was calculated individually for each trial and then averaged across all trials (in a given session or block) and finally across

animals to give an average D2 score. We also separated trials occurring before/after probe trials for a given session, and averaged them across a block, creating a before/after probes context and recency average D2 score. The D2 score data were tested for normality and a non-parametric alternative was used if p was ≤ 0.05, using SPSS (2021, IBM Corp). Outlier cases were identified based on quartiles (where k = 2.07)[59] and were excluded from statistical tests.

One can plot individuals' test in the 1st context trial average context D2 scores against test in the 2nd context trial average context D2 scores and calculate the angle of given data points (0±180°). If animals are indeed performing differently from chance, angular data allows the use of circular (directional) statistics which can enhance explanatory power[60-62], in terms of strategy (Fig. 1C-F). We used the MATLAB (2020b, The MathWorks, Inc) circular statistics toolbox[62], to compute circular descriptive and inferential statistics. Thus, all statistical analyses were performed on the average D2 score or angle across animals and all measures reported were two-tailed tests.

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3.6. Bridging of chapter 2 and 3

In naturalistic settings many animals are innately social species and live in groups. Indeed, some authors have argued that episodic memory supports more complex sociality when living in larger group sizes. To this end, building upon the methodology of the previous chapter, novel variants of existing spontaneous recognition tasks were developed in chapter 3 to probe social episodic-like memory processing in mice. Similarly to chapter 2, manipulating conspecific-cue associations in test phases which were previously perceived (and potentially incidentally learned) can create prediction-error situations for the mice and one can interpret potential episodic-like memory processing by assessing how the mice behave via exploratory behaviours.

One of the outcomes of chapter 2 was that a novel way to analyse context-based spontaneous recognition task data was realised. Specifically, animals are able to use a context-based or recency-based strategy in the same task design. This shaped the methodology used in chapter 3, leading to one of the key motivations in chapter 3 experiments being to further understand which strategies are more salient for mice under spontaneous recognition conditions. Especially, when different potential contextual episode specifiers are available to the mice and when context-based and recency-based strategies are pitted against each other by experimental design. Thus, this following chapter aims to further bridge episodic-like memory processing in non-human animals to event segmentation and episodic memory processing in humans.

4. Chapter 3: Mice remember experiences via conspecific-context: models of social episodic-like memory

4.1. Introduction

Many animals are innately social species and live in groups[1,2]. The demand (upon individuals) of maintaining complex social dynamics within group living, is thought to have contributed to evolutionary shaping of the brain[1,2]. Recognition memory is a necessary cognitive capacity to enable successful complex social living and networking[3-6]. It can be modelled as a dual process where familiarity (knowing) is distinct from recollection (remembering)[7,8]. You may recognise that a conspecific is familiar, but you may not remember any experiences of how you may know them. This remembering, a core feature of episodic memory, one's memory for unique past events[9], allows for the basis of more complex sociality[3,4]. For example, being vigilant of a once trustworthy conspecific that you deem is no longer trustworthy, because you remember the occasion that they stole your family's share of food (see[3,10]).

When considering the evolutionary trajectory of episodic memory, some argue that in its essence it is a human specific ability[4,11]. Alternatively, some argue that a form of episodic memory exists in many species, evidenced behaviourally[12-14] and by evolutionarily conserved neural mechanisms[15,16]. Hence, a more nuanced approach seeks to understand what elements of episodic memory are shared between species[17]. In this way, episodic-like memory has been behaviourally characterised as memory for a simultaneous integration of content (what) in its specific spatial arrangement (where) and temporal context (when)[12]. However, 'when' is not the only way to specify episodes in memory. Animals may struggle to remember episodes via an absolute moment in time and may instead rely upon 'how long ago'[18,19] (recency-based memory - susceptible to familiarity processing[14,20,21]). Thus, integrated what-where stimuli can also be remembered via contextual specifiers, including the physical environment, acting as an 'occasion setter'[14]. This is a more holistic interpretation which includes (but is not limited to) 'when' being used as the episode

specifier. In this work, we further explore temporal cues and the role of contextual specifiers beyond the physical environment.

Rodents have been seen to display episodic-like memory in spontaneous object recognition (SOR) paradigms using both temporal context and other contextual markers to specify and remember episodes[24-26]. Interestingly, however, where recency-based 'when' and context-based recognition strategies are available in the same tasks[27], it seems to be context-based strategies that more commonly shape behaviour overall[28-30]. This raises the question of what kinds of information can readily be used as contextual specifiers, enough to motivationally drive behavioural output during retrieval (over recency-based strategies or randomness), especially in such 'spontaneous' tasks where there are minimal explicit external reinforcers being used by experimenters[31].

In nearly all context-SOR rodent studies, changes in context are operationalised as discrete manipulations of the global environment, typically involving changes in visuo-tactile and or geometric cue information (of walls, floors, and the extra-maze)[24,28,30,32]. It is well-established that these kinds of changes can evoke profound changes in ensembles of hippocampal neurons (see[33,34]), and such ensemble coding changes are thought to contribute to contextual episodic-like memory processing[16,35-38]. Yet, even in an experimental setting rodents can naturally form complex social networks[39], can learn and retrieve hierarchal social status information[40] and display pro-social behaviour dependent on nurture factors[41]. Thus, such work suggests that rodents may flexibly incorporate social information into episodic-like memory (c.f.[42]).

Here, we use two new variants of the object-in-context SOR paradigm. In the first object-in-context SOR experiment (Experiment 1), we asked if 'context' could be specified via the presence/absence of a freely roaming conspecific (Fig. 1). In a second object-in-context SOR experiment (Experiment 2), we asked if 'context' could be specified via the presence/absence of an additional static local object. In the first experiment, we show that mice readily use conspecific presence and absence as contextual information to separate and distinguish particular events, and this episodic-like strategy was over an object recency-based strategy that was also possible in the SOR. In the second object-in-context SOR experiment, the presence

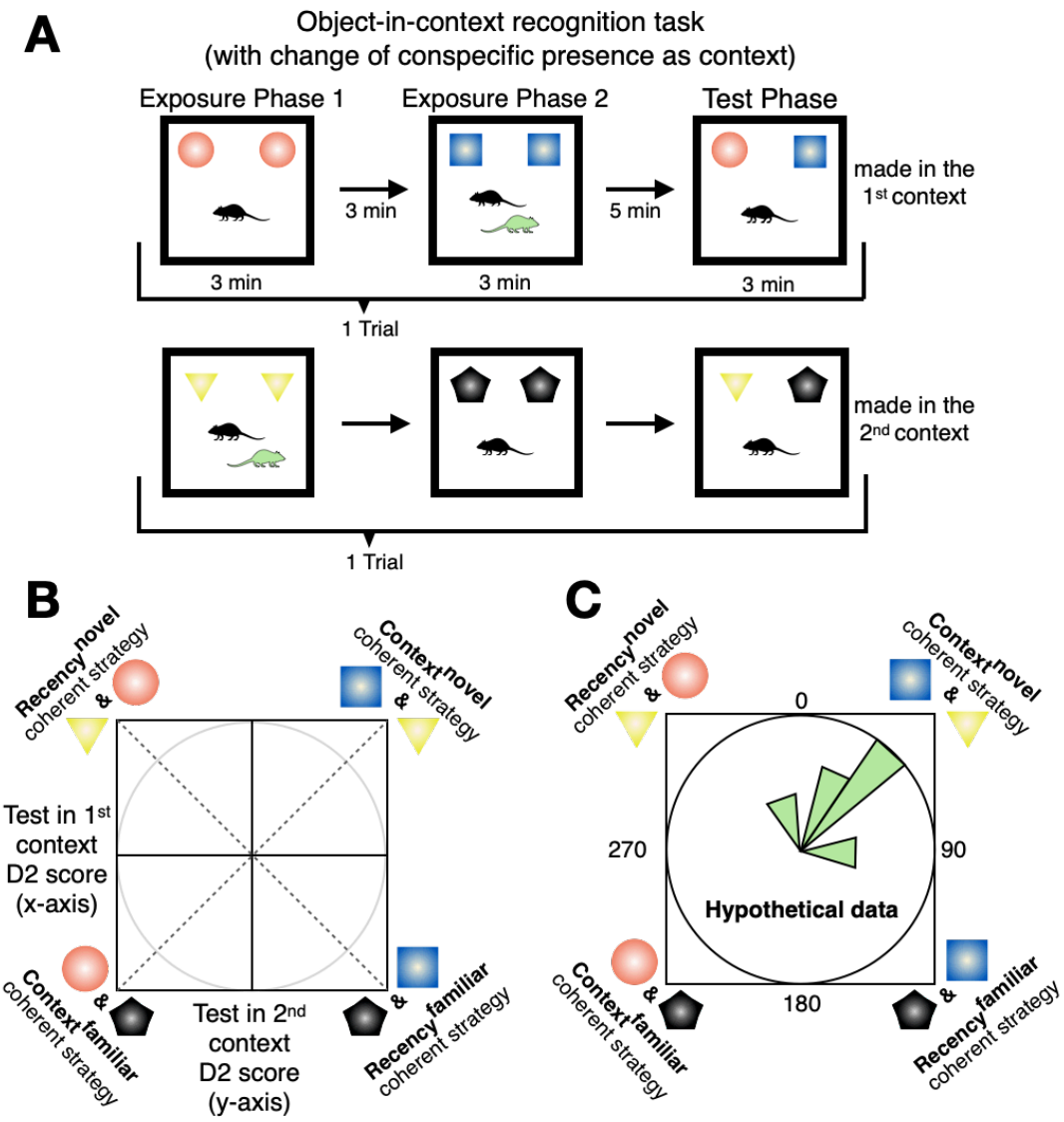

Figure 1. Schematics of the object-in-context recognition task with a conspecific partner as context example. **(A)** In the object-in-context task mice are presented with 2 exposure phases, both containing the same objects. 'Context' was specified as presence/absence of a freely roaming conspecific (experiment 1; green mouse in A; same-sex cage and litter mates). The test phase contained a copy of each object experienced from the exposure phases and was only made when the experimental subject was alone (black mouse in A; see main text for reasoning). The test phase could be made in the 1st context (upper), or it could be made in the 2nd context (lower). Thus, two exposure phases and a test phase constituted a single trial (4 trials in each experimental session per animal). **(B)** The D2 ratio scores from test in the 1st context trials can be plotted against test in the 2nd context trial D2 scores and expressed as circular data (via an arctangent function) to test for potentially coherent behavioural strategies across the two types of trials (see[27] and methods). Context^{novel} and recency^{novel} denote exploration based on object novelty preference, whereas context^{familiar} and recency^{familiar} denote familiarity-based exploratory preference. **(C)** Depicts hypothetical circular data plotted in an angular histogram. In this hypothetical example, the circular mean is ~45°, suggesting common context^{novel} strategy. One can conduct inferential circular statistics asking whether the data is uniformly distributed around the circle or not. In this hypothetical example, if the data is not uniformly distributed around the circle, and thus significantly clustered around the mean of ~45°, this is indicative of a coherent context^{novel} strategy. Such circular analyses are contingent upon evidence of behavioural recognition preference differing to chance level performance and can enhance explanatory power of the spontaneous recognition task data in terms of strategy.

and absence of an additional local object (kept the same throughout the testing session) did not elicit a coherent recognition strategy.

We also developed a new conspecific-in-context SR task (Experiment 3, Fig. 2), based broadly on the model of the standard object-in-context SR task, but employing conspecifics instead of objects. Thus: a) as per the usual convention, context was specified via environment-based change of the floor and wall visuo-tactile cues; b) conspecifics were kept in stable locations (like objects) within wire cups. Here, just as with the standard object-in-context SR task, we asked if mice could detect, and thus preferentially explore, a novel conspecific-in-context configuration (mismatch) over a previously presented conspecific-in-context configuration. To directly pit contextual mismatch against recency-based exploration, we introduced a third conspecific in the second exposure phase, so that in the test phase the conspecific who was not part of the contextual mismatch was seen longer ago (Fig 2). In this way, two novelty-oriented discriminatory strategies were available: 1) explore the conspecific more in the novel conspecific-in-context configuration (context mismatch strategy); 2) explore the conspecific more who was seen longer ago (recency strategy). As we shall see, the results favoured a conspecific-in-context episodic-like memory account.

4.2. Results

4.2.1. Experiment 1: conspecific presence/absence is sufficient to act as a contextual specifier for mice to remember episodes

In this object-in-context task SOR variant (Fig. 1A), context was specified by the presence and absence of a freely roaming conspecific partner for experiment 1. This partner was a same-sex littermate and cagemate of the subject. We tested 10 subjects. Subject-partner dyads were kept the same throughout the testing session (a session consisted of 4 trials) and so was the experimental environment. We have recently shown that in object-in-context SOR tasks, animals can either use a recency-based strategy (ignorant of contextual information) or a context-dependent strategy, where the novelty stems from the contextual mismatch at test[27]. The test phase can be situated in the 1st context or in the 2nd context. We ran tests in both

contexts for each mouse, and it was imperative to analyse both types of trials separately to assess overall coherent recognition behavioural strategy[27,43] (Fig. 1).

It was important to impose a restriction upon the test phase; namely, that the experimental subject should be alone. This was done for two reasons. 1) This enables more straightforward comparisons to other object-in-context SOR variants, where no conspecific is present. 2) The conspecific partner's behaviour could bias the experimental subject. As the conspecific partner will have only been present in one out of two of the exposure phases, one of the objects would be unfamiliar for that partner (hence novel) if they were to be present in the test phase. This is crucially different to what the experimental subject has experienced, interacting with both objects during the exposure phases (i.e., both objects should be familiar at test for the experimental subject). Indeed, even though conspecific presence has been

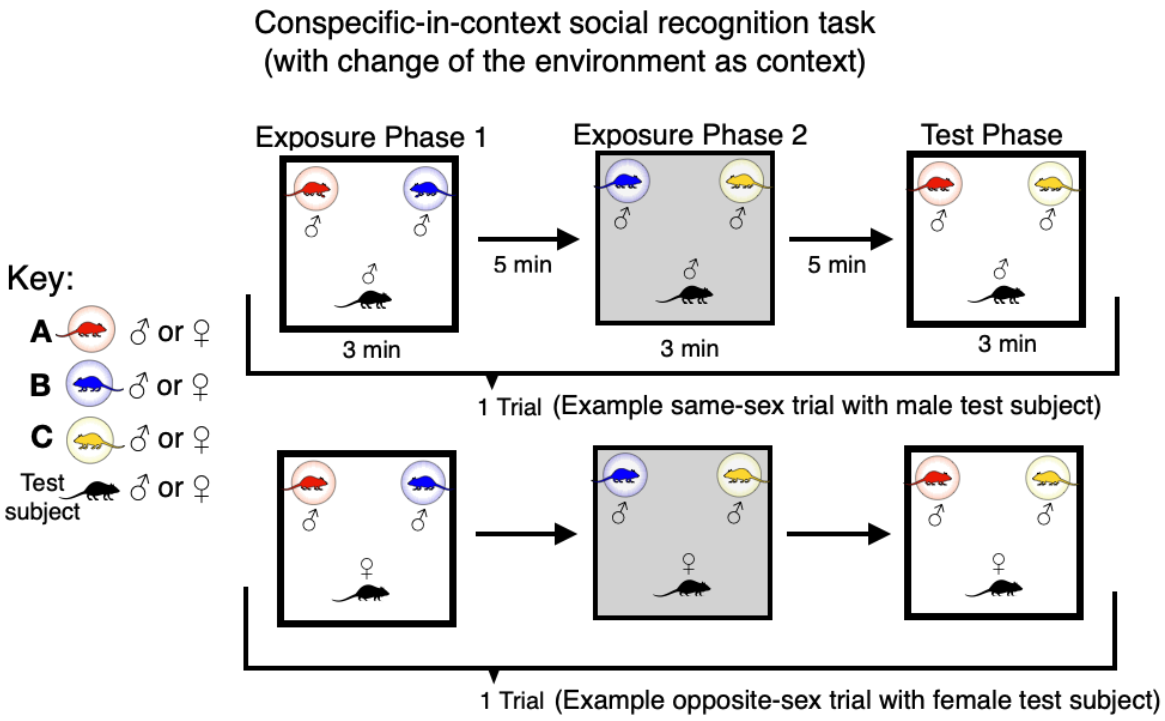

Figure 2. Schematics of the social conspecific-in-context recognition task variant with environment-based change as the context specifier. The conspecific-in-context task was constituted by 3 phases forming a single trial (2 exposure phases, left and middle, and a test phase, right). Here, context was specified via change of the physical environment. In the test phase, both conspecifics should be familiar (based on experience from the exposure phases), but one was seen less recently presented in the same context and place (A; red) and the other was more recently seen, yet now presented in a contextual mismatch (C; yellow). Conspecifics were same-sex cage and littermates in two separate sessions of a single trial per animal (an example male same-sex trial is shown; upper). However, in a final session we also tested opposite-sex littermates (an example opposite-sex trial with a female test subject is shown; lower).

previously seen to enhance behavioural expression of learning and memory in rodents[44,45], our SOR protocol differs to these where all animals had had the same experience in SOR exposure and or test phases[44,45]. Moreover, a subordinate's behaviour could be constrained by a dominant conspecific's scent-marking or

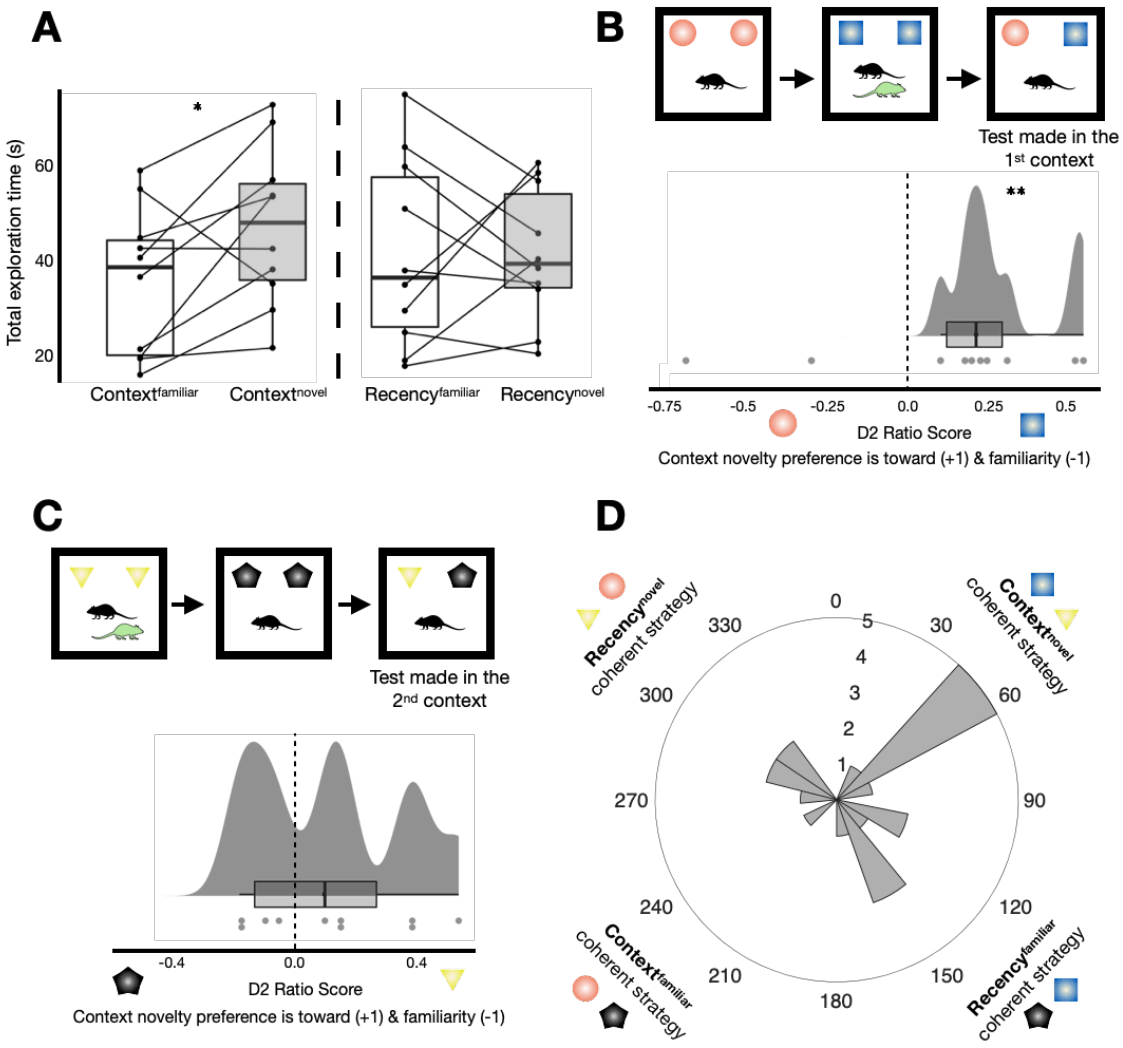

Figure 3. Experiment 1: conspecific presence and absence are sufficient to act as a contextual cue for mice to remember episodes. **(A)** Total exploration time (s) summed across all test phases. Mice explored the context^{novel} configuration (M = 46.97s, SD = 16.77s) significantly more on average than the context^{familiar} configuration (M = 35.14s, SD = 15.62s; $t_{(9)}$ = -2.43, p = 0.038, d = -0.77, CI 95% 0.04 to -1.46). There was no difference between the recency configurations (recency^{novel}: M = 41.02, SD = 14.13s; recency^{familiar}: 41.09s, SD = 19.93s; $t_{(9)}$ = 0.01, p = 0.99, d = 0.004). **(B)** Overall performance was particularly driven by tests situated in the 1st context. The average context discrimination 2 (D2) score was positive (M = 0.29, SD = 0.16) and differed significantly from zero ($t_{(7)}$ = 5.05, p = 0.001, d = 1.79, CI 95% 0.62 to 2.91). **(C)** The average context D2 score for trials when the test made in the 2nd context was also positive (M = 0.12, SD = 0.25) but did not differ from zero ($t_{(9)}$ = 1.51, p = 0.17, d = 0.48). **(D)** Angular histogram depicting the circular data; n = 20. D2 ratio scores were taken from consecutive trials to form circular data points and thus represents animal-trial data; see methods). Plotted in 16 bins of 22.5°, circular descriptive and inferential statistics are reported in the main text. *Denotes $p < 0.05$. **Denotes $p = 0.001$.

aggression at test[46], and this in combination with the exposure phase difference could mask the experimental subject's own strategic preference (or lack thereof).

Mice spent significantly more time exploring the novel object-in-context (context^{novel}) configuration (M = 46.97s, SD = 16.77s) than the context^{familiar} configuration (M = 35.14s, SD = 15.62s; $t_{(9)}$ = -2.43, p = 0.038, d = -0.77, CI 95% -0.04 to -1.46; Fig. 3A, left). In contrast, there was no difference between the recency^{novel} (M = 41.02s, SD = 14.13s) and the recency^{familiar} configurations (M = 41.09s, SD 19.93s; $t_{(9)}$ = 0.01, p =0.99, d = 0.004, Fig. 3A, right). The discrimination ratio 2 (D2) score data yielded a similar picture (context D2: M= 0.13, SD = 0.22; $t_{(9)}$ = 1.83, p = 0.10, d = 0.58; recency D2: M = -0.005, SD = 0.23; $t_{(9)}$ = -0.065, p = 0.95, d = -0.02). In fact, however, closer inspection showed that when tested in the 1st context, the average context D2 score was positive and strongly different from zero (Fig. 3B; M = 0.29, SD = 0.16; $t_{(7)}$ = 5.05, p = 0.001, d = 1.79, CI 95% 0.62 to 2.91), whereas this was not the case for testing in the 2nd context (Fig. 3C; M = 0.12, SD = 0.25; $t_{(9)}$ = 1.51, p = 0.17). One possible explanation for this is relative recency of the contextually specifying cue[28,43], which in this case the conspecific was more recently seen in test in the 1st context trials compared to test in the 2nd context trials, potentially making their absence at test more salient in such trials. Yet, this emphasises the importance of context-based SOR research in reporting trial types separately to better understand the possible differences in recognition behaviour between them[27,28,43].

We next asked whether the circular data was uniformly distributed around the circle or whether there was indication of directionality (Fig. 1). There was evidence that the circular data was not uniformly distributed around the circle with some biasing towards the context^{novel} quadrant (Fig 3D; n = 20, $\bar{\theta}$ = 79.9°, v = 70.0°, $\bar{R}$ = 0.25, Rao's spacing test: U = 165.31, $p < 0.05$).

These results overall suggested that mice used a context-based recognition strategy expressed via novelty preference. This was with performance being mainly driven from test in the 1st context trials, although there was some evidence of coherent context^{novel} object exploration across consecutive trials (that is, also across different trial types; Fig. 3B-D). Thus, mice are able to use conspecific presence and their absence as contextual information to separate and identify unique episodes in

memory.

4.2.2. Experiment 2: no coherent strategy emerges when context is specified via an additional local object

This object-in-context task variant used presence and absence of an additional local object as contextual information. Similarly to the dyads of mice, the object acting as a potential context specifier was kept the same throughout the experimental session, as was the physical environment. And mice were only tested in the absence of the object that potentially acted as a context-specifier, in order to be comparable to the conspecific-context variant (experiment 1). Also, this experiment was conducted at the end of the experimental timeline (SFig. 1), as this aimed to minimise tedium and possible behavioural carryover affects from the previous object-in-context SOR task[47].

There was no difference between the total time spent exploring the context^{novel} configuration (Fig. 4A, left; M = 42.83s, SD = 21.63s) and the context^{familiar} configuration (M = 62.23s, SD = 29.09s; $t_{(8)} = 1.47$, $p = 0.18$, $d = 0.49$). In addition, there was no difference between the recency^{novel} (Fig. 4A, right; M = 61.72s, SD = 39.96s) and the recency^{familiar} configurations (M = 52.70s, SD = 17.87s; $t_{(9)} = -0.64$, $p = 0.54$, $d = -0.20$). The D2 ratio data conveyed a similar picture (context D2: M = -0.03, SD = 0.30; $t_{(9)} = -0.32$, $p = 0.76$, $d = -0.10$; recency D2: M = -0.0003, SD = 0.20; $t_{(9)} = -0.005$, $p = 1.00$, $d = -0.001$). When analysing the different trial types separately, the average context D2 scores for both when the test was situated in the 1st context (Fig. 4B; M = -0.03, SD = 0.25), and when situated in the 2nd context (Fig. 4C; M = - 0.03, SD = 0.44) were clearly not different from zero ($t_{(9)} = -0.38$, $p = 0.72$, $d = -0.12$; $t_{(9)} = -0.22$, $p = 0.83$, $d = -0.07$; respectively). Lastly, the circular data (Fig. 4D; n = 20, $\bar{\theta} = 172.5°$, $v = 74.2°$, $\bar{R} = 0.16$) was uniformly distributed around the circle (Rao's spacing test: $U = 138.84$, $p > 0.50$). Therefore, these results suggested that there was no coherent strategy used in the 'additional local object as context' variant.

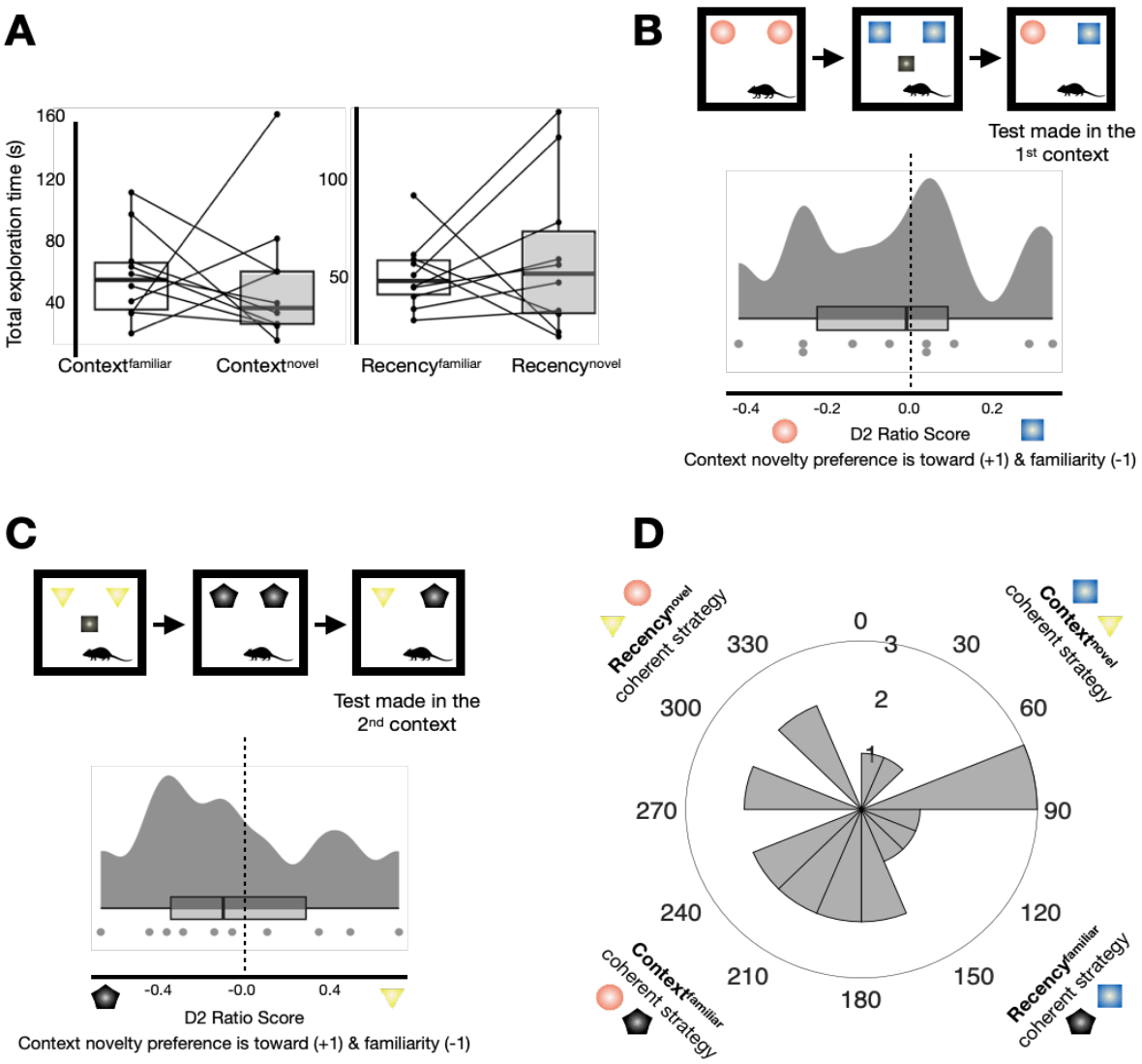

Figure 4. Experiment 2: no coherent strategy emerges when context is specified via an additional local object. **(A)** Total exploration time (s) summed across all test phases. There were no differences between exploration of any particular configurations (context^{novel}: M = 42.83s, SD = 21.63s; context^{familiar}: M = 62.23s, SD = 29.09s; $t_{(8)} = 1.47$, $p = 0.18$, $d = 0.49$; recency^{novel}: M = 61.72s, SD = 39.96s; recency^{familiar}: M = 52.70s, SD = 17.87s; $t_{(9)} = -0.64$, p = 0.54, $d = -0.20$). **(B)** The average test in the 1st context D2 score did not significantly from zero (M = -0.03, SD = 0.25; $t_{(9)} = -0.38$, $p = 0.72$, $d = -0.12$). **(C)** The average test in the 2nd context D2 score did not significantly from zero (M = -0.03, SD = 0.44; $t_{(9)} = -0.22$, $p = 0.83$, $d = -0.07$). **(D)** Angular histogram depicting the circular data (n = 20), plotted in 16 bins of 22.5°, circular descriptive and inferential statistics are reported in the main text. Of note, the objects used in this task variant were not the same as used in the conspecific as context task variant (i.e., the schematics are kept the same for clarity purposes).

4.2.3. Comparison of the context specifiers: conspecific partner (experiment 1) and the additional local object (experiment 2)

Due to our protocol of testing the subject when they were only alone, another possibility that could explain recognition behaviour (during test phases of these object-in-context variants), is a simple object recognition strategy based upon novelty-detection with ignorance of the contextual information. For example, this could occur if there was little acquisition of objects when exposed in the presence of the conspecific relative to when the subject was alone. Hence, mice would explore the same object as predicted via a context^{novel} strategy but due to this object simply being more unfamiliar (and thus novel) at test. We thus conducted control analyses concerning the object exploration in exposure phases of experiment 1 and experiment 2 (SFig. 2).

A mixed repeated measures ANOVA comparing summed total exploration in exposure phases relative to test phases, revealed that for both experiment 1 and experiment 2 there was more exploration in exposure phases vs. test phases (SFig. 2; exploration of exposure phases was scaled to match that of test phases; Fisher's least significant difference, LSD, post-hoc tests: $p = 0.01$, $p < 0.001$, experiment 1 and 2; respectively). This suggested successful acquisition of objects did occur during exposure phases; in other words, objects at the test phases were likely familiar to mice in both experiments 1 and 2. Interestingly, we also found significantly more total exploration on average in experiment 2 (M = 143.71) relative to experiment 1 (M = 101.72; $F_{(1,9)} = 14.04$, $p = 0.005$, $\eta_p^2 = 0.61$), indicating that there was minimal decline in task motivation across experiments 1 and 2.

We next sought to compare exposure phases of the 'context' specifiers (i.e., conspecific partners in experiment 1 vs. an additional local object in experiment 2), and 'presence' of the context specifier (that is, the context specifier's presence vs. its absence). A mixed repeated measures ANOVA yielded a significant interaction between 'context' and 'presence' ($F_{(1,9)} = 9.11$, $p = 0.02$, $\eta_p^2 = 0.50$). Fisher's LSD post-hoc analyses indicated that within experiment 1, there was significantly more object exploration in exposure phases when the conspecific was present (SFig. 2; M = 34.59) versus when mice were alone (M = 26.08; $p = 0.017$), which is in

accordance with previous reports[44,45]. Contrastingly, within experiment 2, levels of exploration in the presence of the additional local object (M = 40.69) were similar to when it was absent (M = 45.82; $p = 0.32$).

In summary, the control analyses further support the notion that in experiment 1 mice were using a mnemonic strategy reliant on the contextual information (the conspecific partner; Fig 3). However, in experiment 2, despite some indication of successful object acquisition from exposure phases (similarly to that seen in experiment 1; SFig. 2) we found no evidence of a coherent recency-based or context-based strategy when an additional local object could have been used as a potential context specifier (Fig. 4).

4.2.4. Experiment 3: mice preferentially explore contextual mismatch information associated with familiar conspecifics over a recency-based mnemonic strategy

Inspired by the object-in-context SOR paradigm, for experiment 3, we adapted the standard social discrimination task[22,23] to construct a conspecific-in-context variant (see Introduction, Fig. 2, SFig. 3). The aim of the design was to make two novelty-oriented discriminatory strategies available, and to pit them against each other. Figure 2 pictorially illustrates the two potential strategies. In the test phase, the mice could preferentially explore either: 1) the conspecific in the novel conspecific-in-context configuration, seen more recently and presented in the same place, but where there was now a contextual mismatch (conspecific C, yellow, in Fig. 2); or 2) the conspecific who was seen longer ago, presented in the same place and context (conspecific A, red, in Fig. 2, recency strategy). In this way, we could investigate the question of whether mice show a spontaneous exploratory preference for a context-based or recency-based mnemonic strategy when both are available, as in the context SOR tasks but now with respect to conspecifics.

Experiment 3 comprised three sessions of this conspecific-in-context design, with a single trial per session. Two sessions were with conspecifics of the same sex, and one of the opposite-sex (SFig. 1). Having a second same-sex session allowed for examination of recognition behaviour once subjects had had further habituation of

the task conditions, whilst also allowing for within-subject counterbalancing of context order and conspecific placement to enhance within-subject reliability. Moreover, previous work in rodents has suggested that social interaction behaviour and neuromodulatory mechanisms can be dependent on conspecific-sex, with increased salience associated with members of the opposite sex[48-50]. Thus, the idea of the final opposite-sex session was to examine whether recognition behaviour would differ because of using opposite-sex conspecifics which should be more socially salient stimuli. In this way, the to-be-recognised opposite-sex conspecifics may hinder or boost preferential exploratory behaviour (of a particular recognition strategy) relative to same-sex conspecific stimuli.

A mixed repeated measures ANOVA was conducted on the exploration behaviour in the test phases across sessions (Fig. 5A). There was an overall significant main effect of 'session' (same-sex sessions 1 and 2, and the opposite-sex session 3; $F_{(1.24,11.13)} = 26.73$, $p < 0.001$, $\eta_p^2 = 0.75$). Bonferroni corrected post-hoc tests showed that there were comparable levels of exploration across same-sex session 1 (M = 4.97s) and same-sex session 2 (M = 4.13s, $p = 1.00$). Whereas there was significantly more exploration in the opposite-sex session 3 (M = 18.08s) relative to session 1 and 2 ($p = 0.003$, $p < 0.001$; respectively). There was also an overall significant main effect of 'conspecific' (that is, conspecific A, red, vs. conspecific C, yellow, see Fig. 2 and 5, $F_{(1,9)} = 5.67$, $p = 0.04$, $\eta_p^2 = 0.39$). Post-hoc tests showed that across sessions there was more exploration of the contextually mismatched conspecific C (M = 10.34s; Fig. 5B) relative to the least recently seen conspecific A (M = 7.78s, $p = 0.04$) who was presented in the same context and place at test. This is consistent with forming an episodic-like conspecific-in-context memory.

There was no overall interaction between session and conspecific ($F_{(2,18)} = 1.32$, $p = 0.29$, $\eta_p^2 = 0.13$). Yet, similarly to the overall significant main effect of session, post-hoc tests showed that regardless of conspecific (A or C) more exploration was made session in 3 relative to session 1 and 2 (all $p \leq 0.006$; comparable exploration levels across session 1 and 2, all $p \geq 0.60$. This very clear result suggests the enhanced salience of members of the opposite-sex. Given these marked differences in exploratory expenditure across same-sex sessions versus the opposite-sex session, we next sought to check using the D2 ratio score (Fig. 5C;

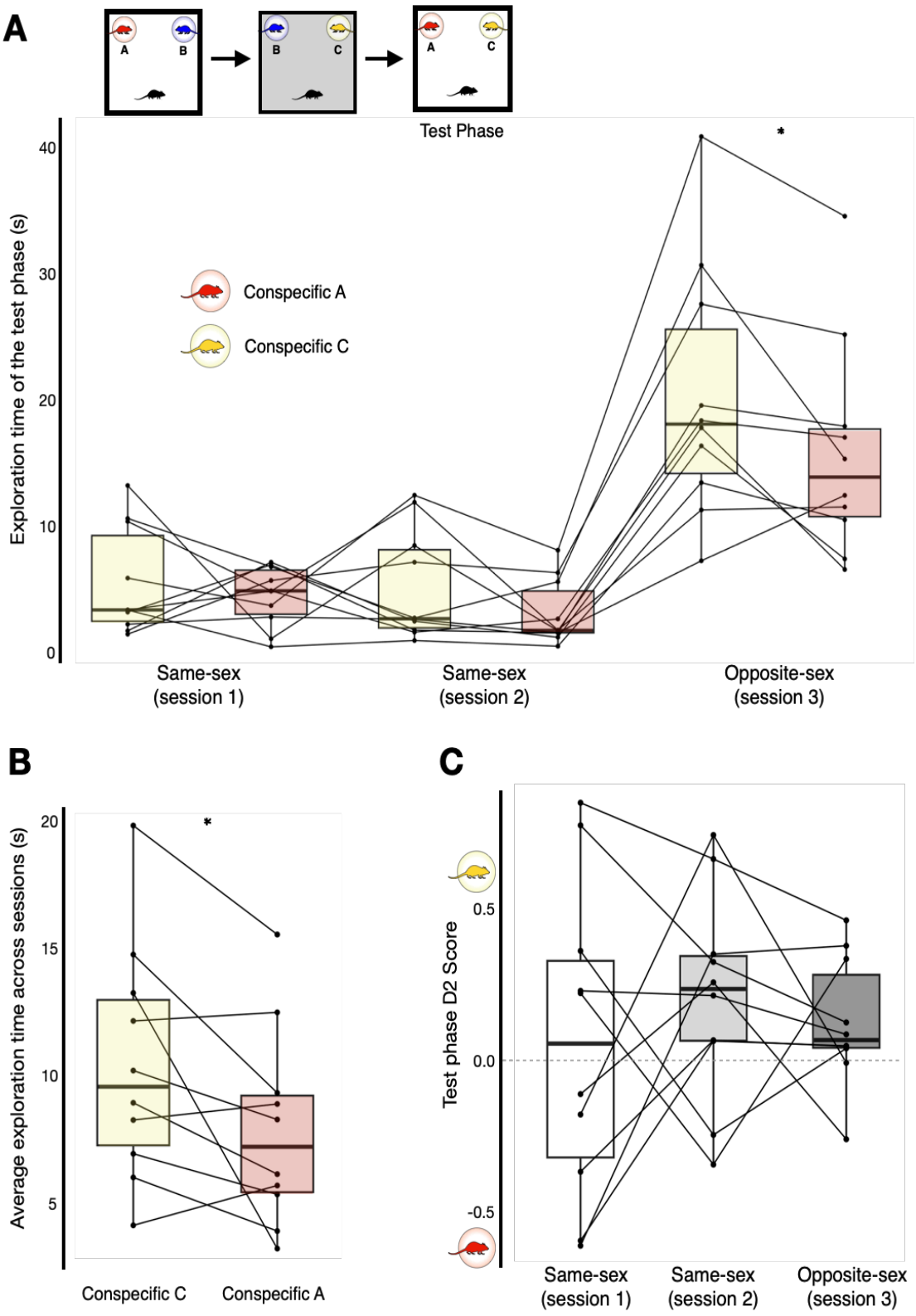

Figure 5. Experiment 3: mice preferentially explore contextual mismatch information associated with familiar conspecifics over a recency-based mnemonic strategy. **(A)** Upper left: reminder schematic of the conspecific-in-context task (see also Fig. 2). Lower: exploration times of conspecific A and C in the test phase by session. **(B)** Average exploration time of conspecific A (M = 7.78s) and C (M = 10.34s) across all sessions. **(C)** D2 ratio score of the test phase by session. (A-C) Descriptive and inferential statistics reported in the main text. *Denotes p <0.05.

which accounts for individual differences in exploration levels), whether preferential exploration towards certain conspecifics differed across sessions. A repeated measures ANOVA yielded no sign at all of differences in recognition performance across sessions ($F_{(2, 18)}$, $p = 0.64$, $\eta_p^2 = 0.05$, Bonferroni post-hoc tests all $p = 1.00$). This suggested that exploratory preference on average was similar across these sessions, validating our finding of overall exploratory preference towards conspecific C (Fig. 5B). Finally, post-hoc tests within sessions, revealed that there was comparable levels of exploration towards conspecific A and C in session 1 (Conspecific C: M = 5.52s, Conspecific A: M = 4.42s, $p = 0.53$; D2 score: M = 0.06, SD = 0.52, $t_{(9)} = 0.34$, $p = 0.75$, $d = 0.11$), and in session 2 (Conspecific C: M = 5.19s, Conspecific A: M = 3.08s, $p = 0.12$; D2 score: M = 0.21, SD = 0.35, $t_{(9)} = 1.89$, $p = 0.09$, $d = 0.60$, CI 95% -0.09 to 1.26). However, in the opposite-sex session, there was significantly more exploration of conspecific C (M = 20.32) versus conspecific A (M = 15.84, $p = 0.044$; D2 score: M = 0.12, SD = 0.21, $t_{(9)} = 1.82$, $p = 0.10$, $d = 0.58$, CI 95% -0.11 to 1.24). This suggested that the overall exploratory preference toward the contextually-mismatched conspecific C (Fig. 5B) was particularly driven by recognition behaviour in the opposite-sex session, possibly due to the enhanced salience in the nature of the social stimuli[48-50].

4.3. Discussion

Being able to flexibly remember episodes via social-context is of evolutionary importance[1-4]. Our experiments suggest that the same cohort of mice not only preferentially explored conspecifics associated with environment-based contextual mismatch information (experiment 3; Fig. 5), but used conspecific presence and absence as a means to remember unique episodes in memory (experiment 1; Fig. 3). These findings echo the substantial evidence reported using SOR paradigms, that when there is availability of both context-based novelty and recency-based novelty, rodent exploratory behaviour is more directed to the unexpected contextual change[28-30].

Interestingly, no overall strategy emerged when context was specified by an additional local object (experiment 2; Fig. 4), and this was seemingly not due to

reduced motivation nor lack of object acquisition during exposure phases (SFig. 2). There are undeniable differences between conspecifics and a static local object, in terms of the sensory cues that emanate from them and their biological relavance[1,48-50]. Yet, it would of course be premature to conclude from this experiment alone that objects cannot be used by mice as contextual information in defining unique episodes (especially when learnt via explicit reinforcing[14,31]). What does seem reasonable to conclude is that, the presence/absence of a conspecific has sufficient ethological salience under incidental spontaneous conditions to be incorporated into episodic-like memory, and this salience is clearly greater than that for a man-made object, (especially when that object becomes increasingly habituated to over time, as was the case in experiment 2).

A previous study suggested that when rats were exposed to an unfamiliar context (a change in the physical environment), there was a reduction of investigation and mild aggression towards a juvenile conspecific, who was increasingly familiarised to from three previous sessions in a different, familiarised context[51]. The experimenters argued that although rats still recognised the conspecific, the behavioural change could be interpreted as increased habituation to the conspecific[51], that is, not only due to contextual novelty but perhaps a novel association of the conspecific-in-context. We extend such work by showing in experiment 3, that when mice are given a free choice to explore a more recently-seen familiar conspecific associated with environment-based contextual mismatch and a less recently seen familiar conspecific presented in the same place and context, they preferentially explore the former.

Converging evidence demonstrates that successful social mnemonic processing can strongly rely upon the hippocampal formation[52-56]. Hippocampal principal cells can show place-dependent activity as rodents traverse their environment, hence termed place cells[33-35]. But strikingly, hippocampal principal cells may also flexibly integrate information about conspecifics in their responsivity[56-61], for example place-like activity of these cells can also relate to positional information of conspecifics (i.e., social place cells[58-60]). Notably, such social place cells were not reported when rats' behaviour was dependent upon observationally tracking a robot's movement[62].

When substantial changes are made to the environment, place cells exhibit a phenomenon known as 'remapping', whereby some cells fire in one environment, but not another, or fire in different locations in each environment[33-36,63-65]. Thus, at the population-level, two sufficiently-different environments are represented distinctly, via 'global remapping'[35,63], in a manner that may specify two different contexts. Indeed, the argument has been explicitly made, potentially finessing long-running issues with defining 'context', that "electrophysiology opens the door to a measurement-based approach with a clear definition: a new context is one that is sufficient to evoke global remapping"[66].

It seems reasonable to infer that hippocampal place cell remapping occurs in the majority of context-SOR studies, since these studies typically employ marked changes in the physical environment to specify context. Moreover, increases in rearing on hind legs typically accompanies place cell remapping in novel, physically different, contexts[67-69] implying a link between place cell remapping and context-sensitive exploratory behaviour in rodents. How strong place cell remapping needs to be, and in which hippocampal sub-regions, to act as a universal context-differentiation readout signal remains unclear. Our behavioural observations here suggest that conspecific presence/absence can define 'context' and thus distinguish otherwise-similar episodes in the same physical environment. Taken together with evidence of partial place cell remapping in sub-regions CA2 and ventral CA1 across scenarios that differ only socially[54,70,71] it seems reasonable to suggest that: 1) social as well as physical-environmental cues can define behaviourally-relevant context shifts in rodents as well as other species, especially humans; 2) remapping in hippocampal place cells, even in rodents, may not need to be driven by changes in physical-environmental cues, nor to be 'complete/global', in order to serve as a context-shift signal.

In conclusion, we have implemented new spontaneous recognition task variants to show that mice readily use social episodic-like memory to drive their exploration. The tasks offer a novel way to tease apart the mechanisms of social recognition memory in a crucially different way to the current, frequently used social discrimination protocols. This is especially relevant in modelling atypical, disease and neuropsychological disorders with rodent models, as in response to given

manipulations animals may display chance level performance or be using recency-based or context-based (episodic-like) mnemonic strategies to guide their behaviour.

4.4. Methods

4.4.1. Subjects

Ten B6FVBF1 mice (5 male) were bred inhouse at the life science support unit (Durham University, U.K.). They were ~10 weeks of age when habituation begun (Females weight: M = 24.1g, SD = 1.0g; Males weight: M = 30.4g, SD = 1.8g) and were housed in two cages in same-sex groups of 5. Each home cage measured 45 × 28 × 13 cm (l × w × h; Model: MB1, NKP isotec., U.K.) and were equipped with 2 mouse tunnels and 2 igloos (Datesand Limited., U.K.). The home room was maintained on a 12-h light-dark cycle (07:00-19:00h), with daily monitoring of temperature and humidity (20 ± 1°C; 55 ± 10%; respectively). All stages occurred during the light phase and mice had free availability of food and water ad libitum throughout (i.e., were not food or water deprived). Animals were not euthanised as part of the experiments. All experiments were conducted in accordance with the U.K. Animals Scientific Procedures Act (1986), approved by Durham University AWERB and in accordance with the Home Office (procedure licence number: P7B7D2E4B). Reporting follows the recommendations in the ARRIVE guidelines.

4.4.2. Apparatus and objects

All reported experiments took place in an apparatus designed for spontaneous recognition (Model CI.80514R-1, Campden Instruments., U.K.). The specifications of which are previously reported[27]. Only the open field area was used presently, white noise played continuously from above the open area (62 ± 8.5 dB SPL) and an additional camera was also used for behavioural recording (Model: MWC72ZD/A, iPhone 11 Pro). Environmental contexts were comprised of sensorily distinct floors and were sometimes paired with a wall cue (see SFig. 3A-C). The objects varied in material, shape, size, texture and visual complexion, each object had a minimum of 3 duplicates and were paired quasi-randomly (example pair shown in SFig. 3D). In experiment 2, the additional local object that could act as context is shown in SFig. 3E. For experiment 3 the social conspecific-in-context recognition experiments, conspecifics were placed within a wire cup, and all were weighed down with the same object (see SFig. 3F). For all experiments, objects and conspecifics

were positioned towards the far corners of the open field opposite the door (i.e., mice egocentrically had objects/conspecifics left and right to them, as they were placed into the open field, always in the same direction, north towards the objects/conspecifics). At the end of testing sessions for the experiments 1 and 2, objects, floors and the apparatus were cleaned using disinfectant wipes (Clinell universal wipes, GAMA Healthcare Ltd., U.K.). For experiment 3, the wire cups and floors were cleaned and dried between each phase and at the end, this was to minimise the crossing of scent-marking cues of conspecifics between phases.

4.4.3. Habituation

Mice were first handled in their home room for a minimum of 3 consecutive days, before being transported (in cage groups) to the experimental room where all reported testing took place (white noise played and the room was lit by diffuse white light from 2 lamps, 60 W & 100 W). The first-time mice were habituated to the open field was in context X (see SFig. 3A) and they did so in cage groups (30 minutes). Following this, they were habituated once in the same dyads as used for the experimental session, but objects were now present (two of the same and they were not used in any experiments; 30 minutes). Prior to experiment 3, context Y and Z (SFig. 3B-C) were habituated to on the same day in cage groups (30 minutes each, ~1.5 hours between; the wire cups were present). Lastly, prior to experiment 2, context X was re-habituated twice on separate days, once without objects and once with the same habituation objects as used previously. Both habituations occurred in cage groups and lasted for 20 minutes.

4.4.4. Procedure: object-in-context experiments (experiments 1 and 2)

A given trial was composed of 3 phases (Fig 1A; 2 exposure phases and a test phase). The same pair of objects are placed in exposure 1, where mice explored them for ~3 minutes before being returned to a separate holding cage (for ~3 minutes, the same design as the home cage and kept within the experimental room). A different pair of objects are presented in exposure 2 and again mice explored them for ~3 minutes. Approximately 5 minutes elapsed before experiencing of the test phase, which contained a copy of an object from exposure 1 and a copy of an object from exposure 2 and lasted for ~3 minutes (example object pair shown in SFig. 3D). There was a ~3 minute interval before the next trial begun. For experiment 1, a given dyad of mice were composed randomly of same-sex cage

(and litter) mates. The test subject was always placed into the context first and removed last, being returned into the same holding cage as the partner. The partner who was not the test-subject for that session was tested 6 days later (SFig. 1). For experiment 2, the additional local object acting as a potential context specifier (see SFig. 3E) was placed in with the other objects but kept the same throughout the session and was never present in the test phase (like in experiment 1). The objects used in experiment 2 were not the same as used in experiment 1. Test phases could be situated in the 1st context or test phases could be situated in the 2nd context (Fig. 1A). Four trials comprised a single experimental session and the trial order, object order and placement of the object-in-context novelty was counterbalanced. Notably, the context specifier could not be counterbalanced as we required the subject to always be alone in the test phase (see main text for reasoning).

4.4.5. Procedure: social conspecific-in-context recognition (experiment 3)

A given trial was composed of 3 phases (2 exposure phases and a test phase; see Fig. 2). In the first exposure phase, the test subject experienced two conspecifics contained within wire cups in a given environment-based context (~3 minutes), before being returned alone into a holding cage. After ~5 minutes, the test subject was placed back into the apparatus but now the context had been changed and they could explore a familiar conspecific or a newly introduced unfamiliar conspecific in the task conditions altogether (~3 minutes). This was considered as a second exposure phase to allow for the scenario that occurs in the test phase. Again after ~5 minutes elapsed, the test subject was returned into the apparatus and the context was changed back to that experienced in the first exposure phase. Subjects in the test phase could then explore a familiar conspecific, more recently-seen in the same place, who now had a contextual mismatch or they could explore an also familiar conspecific who was seen less recently, but presented in the same place and context (lasting ~3 minutes). This experiment was conducted twice using same-sex cage and littermates (the second session was within-subject counterbalanced) and lastly once using opposite-sex littermates (SFig. 1; all randomly assigned as to which conspecifics were to-be-recognised, and all mice experienced containing in the wire cups, within completion of sessions across animals). The context and conspecific order were all counterbalanced and hence so was the placement of the novel conspecific-in-context in test trials.

4.4.6. Behavioural analyses

Behaviour was measured off-line via the recorded footage of experimental trials. Exploratory behaviour was regarded as when mice were within ~2cm of the object (or the wire cup/conspecific) and actively exploring it (i.e., sniffing, touching, biting and visibly whisking). Behaviour such as climbing and sitting upon objects, or the wire cup configurations were not considered as exploration, and neither was using them to support rearing. The duration of exploratory behaviour (s) with respect to objects, wire cups and conspecifics (of all phases) was manually scored unblinded by the main experimenter (#1). All reported statistics are based upon the main experimenter's scoring. Importantly, a random subset (20% of each experiment test phase) was scored blinded by two other trained experimenters (#2 and #3, who had less experience overall in comparison to experimenter #1). Scoring between all experimenters were significantly and positively correlated (#1 vs. #2: $r_{(54)} = 0.75$, $p < 0.001$, CI 95% 0.60 to 0.85; #1 vs. #3: $r_{(54)} = 0.83$, $p < 0.001$, CI 95% 0.72 to 0.90; #2 vs. #3: $r_{(54)} = 0.89$, $p < 0.001$, CI 95% 0.81 to 0.93). Additionally, intraclass correlation coefficient (ICC) analysis suggested good to excellent reliability of scoring[72] (The average measure ICC was 0.91, CI 95% 0.77 to 0.96, $F_{(55,110)} = 19.07$, $p < 0.001$; 2-way random-effects model, absolute-agreement, $k = 3$, mean-rating).

Total exploration time (s) was the summed exploration across trials by animals of a given configuration (e.g., the novel object-in-context) or else specified. In no case did side-bias better explain recognition performance over a context or recency-based strategy (Fig. 3A; Fig. 4A; Fig. 5C; $t_{(9)} = -1.92$, $p = 0.09$; $t_{(8)} = -0.12$, $p = 0.90$; $t_{(9)} = 0.86$, $p = 0.42$; respectively). The classically described discrimination ratio 2 (D2) scores for a context-based or recency-based strategy is previously reported[27], from a context D2 ratio score calculation novelty preference is toward +1 and familiarity preference toward -1, with 0 indicating no preference. For experiment 3 D2 scores, preference to explore the conspecific associated with the contextual mismatch was indicated as values towards +1. For each animal, the D2 score was calculated individually for each trial and then averaged across all trials and finally across animals to give the reported overall mean D2 scores (unless specified by trial/test type). All data was tested for normality (& sphericity where applicable) and a non-parametric alternative (Greenhouse-Geisser correction) was used if $p < 0.05$, using SPSS, v28 (2021, IBM Corp). Outlier cases were identified based on quartiles (where $k = 2.07$)[73] and were excluded from statistical tests. All reported measures were two-tailed tests.

We plotted animals' test in the 1st context D2 scores against test in the 2nd context D2

scores and formulated circular data (via an arctangent function, converted from radians to degrees, 0 ± 180°). Importantly, such circular analyses should be interpreted with dependence upon evidence of exploratory preference differing to chance level performance, but it can enhance explanatory power of the spontaneous recognition task data. Perfectly coherent strategies across trial types (Fig. 1B) would be indicated by circular data points aligning at 45°, 135°, -135° (225°) and -45° (315°). For example, ~45° for a coherent context^{novel} strategy in a context-based SOR task (Fig. 1C). Data points aligning more towards 0°, 90°, 180° and -90° (-270°) would suggest that exploratory preference is exhibited in only 1 out of the 2 trial/test types. We designed the object-in-context experiments (experiments 1 and 2) in such a way where test in the 1st context trials were interleaved with test in the 2nd context trials, allowing 2 consecutive trials (i.e., the first and last 2 trials from experiment 1 and 2)) to form animal-trial circular data points. We used the MATLAB (2020b, The MathWorks, Inc) circular statistics toolbox[74] and package circular[75] in R (2021.09.0, RStudio, PCB) to compute circular descriptive and inferential statistics. To use a single circular test capable of accommodating distributions that were not expected to be unimodal, we employed Rao's spacing test[74].

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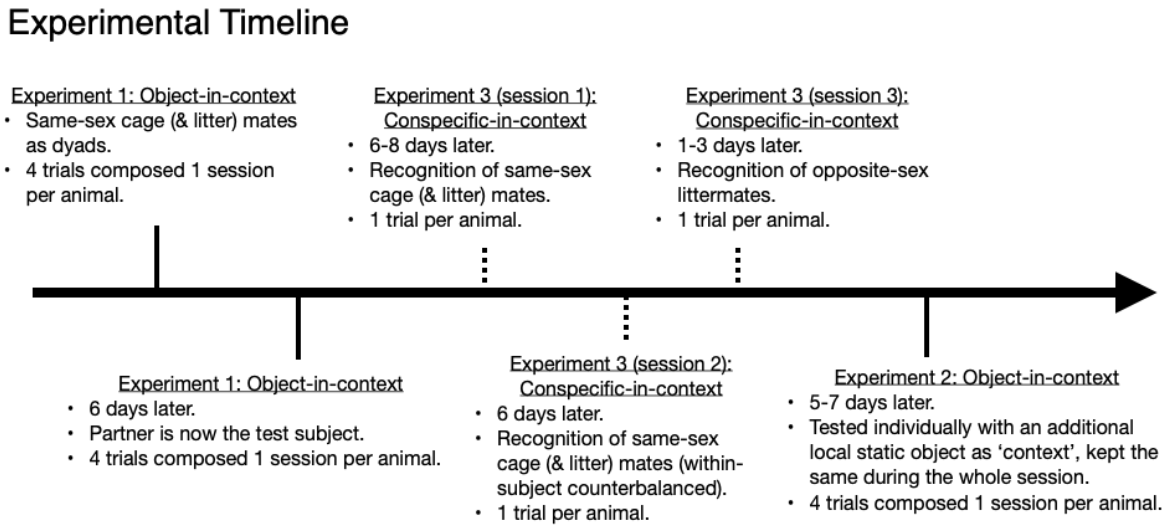
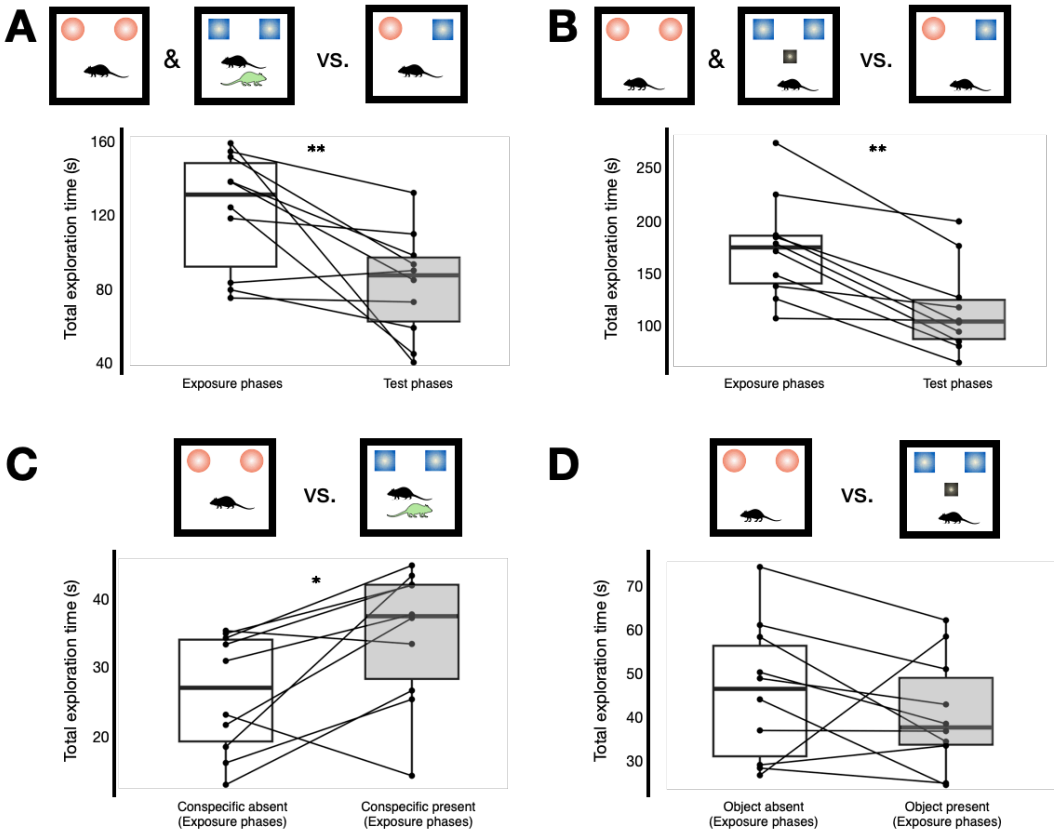
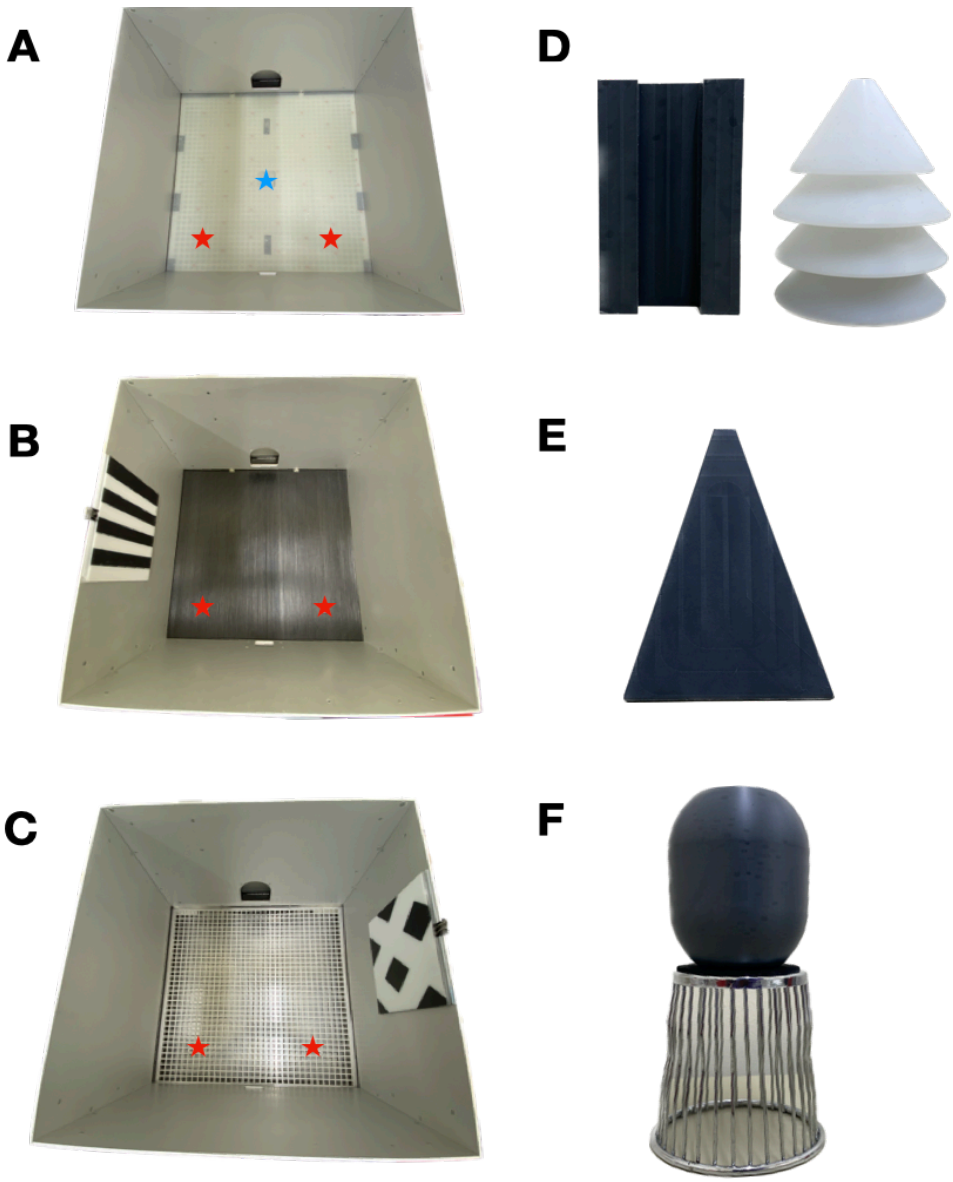
4.6. Chapter 3 supplementary figures



Supplementary Figure 1. The timeline for all the presently described experiments.



Supplementary Figure 2. Analyses of object exploration during the exposure phases of the object-in-context variants. **(A)** Summed total object exploration during exposure phases scaled to compare against summed total exploration in the test phases. A mixed repeated measures ANOVA yielded a significant main effect of 'context' (conspecific, experiment 1, vs. object variant, experiment 2; $F_{(1,9)} = 14.04$, $p = 0.005$, $\eta_p^2 = 0.61$). Fisher's least significant difference post-hoc (LSDph) analyses (for all following comparisons) revealed that there was significantly more exploration in Exp 2 (M = 143.71) vs. Exp 1 (M = 101.72, $p = 0.005$). There was also a significant main effect of 'phase' (exposure vs. test phase; $F_{(1,9)} = 46.70$, $p < 0.001$, $\eta_p^2 = 0.84$. Significantly more exploration in exposure phases (M = 147.17) vs. test phases (M = 98.26, $p < 0.001$). The ANOVA yielded no initial overall interaction between context and phase ($F_{(1,9)} = 1.25$, $p = 0.29$, $\eta_p^2 = 0.12$). However, post-hoc tests revealed that within context, there was significantly more exploration in the exposure phases of Exp 1 (M = 121.33) vs. the test phases (M = 82.11; $p = 0.01$, *shown in A*). **(B)** Post-hoc tests also revealed that there was significantly more exploration in the exposure phases of Exp 2 (M = 173.01) vs. the test phases (M = 114.42; $p < 0.001$). **(C)** A mixed repeated measures ANOVA was conducted for object exploration during only the exposure phases. Similarly to A, there was a significant main effect of context ($F_{(1,9)} = 12.33$, $p = 0.007$, $\eta_p^2 = 0.58$; more exploration in Exp 2, M = 43,25, vs. Exp 1, M = 30.33, $p = 0.007$). There was no main effect of 'presence' (conspecific/object presence vs. absence; $F_{(1,9)} = 0.25$, $p = 0.63$, $\eta_p^2 = 0.03$), nor 'trial-type' (test made in the 1st context vs. test made in the 2nd context trials; $F_{(1,9)} = 1.58$, $p = 0.24$, $\eta_p^2 = 0.15$). There was a significant 2-way interaction between context and presence ($F_{(1,9)} = 9.11$, $p = 0.02$, $\eta_p^2 = 0.50$). Post-hoc tests revealed that within presence, there was more exploration in Exp 2 in absence of the object (M = 45.82) vs. when mice were alone in Exp 1 (M = 26.08, $p = 0.001$). However, there was no difference between the presence exposure phases across Exp 1 and 2 (Exp 2: M = 40.96; Exp 1: M = 34.59, $p = 0.19$). *As shown in C*, within context (of Exp 1), there was significantly more exploration when there was conspecific presence (M = 34.59) vs. their absence (M = 26.08, $p = 0.017$). Finally, the ANOVA revealed no overall 3-way interaction between, context, presence and trial-type ($F_{(1,9)} = 0.11$, $p = 0.75$, $\eta_p^2 = 0.01$; within context & trial-type: test in the 1st context conspecific presence, M = 32.66 vs. alone, M = 24.64, $p = 0.09$. Test in the 2nd context conspecific presence, M = 36.52 vs. alone, M = 27.52, $p = 0.11$). **(D)** There was no difference between the exposure phases of Exp 2 (presence: M = 40.69 vs. absence: M = 45.82; $p = 0.32$). Within context and trial-type: test in the 1st context trials object acting as context present (M = 44.75), vs. absent (M = 53.53, $p = 0.43$). Test in the 2nd context trials object present (M = 36.62), vs. absent (M = 38.11, $p = 0.87$). Of note, schematics of only test in 1st context trials are shown for consistency, both trial types were considered for all reported analyses. *Denotes $p < 0.05$, **Denotes $p \leq 0.01$



Supplementary Figure 3. Environment-based contexts and objects. **(A)** Context X open field, used for the object-in-context spontaneous recognition variants (experiment 1 and 2). It was comprised of no wall cues and a translucent Perspex floor with no holes. For reference, the door was considered south and the objects were placed towards the far corners north indicated via the red stars. The blue star indicates placement of the additional local object (see E) that could act as context. **(B)** Context Y open field, one of the two contexts used for the social conspecific-in-context recognition experiment 3. It was comprised of a striped, textured rubber black floor, paired with a polarised striped cue card on the east wall. Red stars indicated approximate placement of the wire cups (see F) containing conspecifics. **(C)** Context Z open field, the other context used for the conspecific-in-context social recognition experiment 3. It was comprised of steel mesh flooring paired with a polarised diamond patterned cue card on the west wall. **(D)** Example object pair used for the object-in-context experiments. Black object: 5.5 × 5.5 × 9.0cm (l × w × h). White object: 8.0cm diameter, 9.0cm height. **(E)** The additional local object acting as context, kept the same throughout the session. Position indicated via the blue star in A. It measured 5.5 × 5.5 × 7.2cm. **(F)** The chrome steel wire cup (10.2cm diameter, 10.8cm height; Model: 31570, Spectrum Diversified Designs, Inc., Ohio, U.S.A.) used to contain conspecifics, and object used to weigh it down (8.0cm diameter, 9.0cm height). See red stars in B and C for approximate placement in the environment. Of note, the lighting during experimental testing was dimmer than that depicted in A-C.

4.7. Bridging of chapter 3 and 4

The results of chapter 2 and 3 would argue that non-human animals can and do segment their experience for episodic-like memory. However, a limitation of these spontaneous recognition paradigms, when aiming to make a link to event segmentation, is that spatiotemporal shifts between the test area and the holding chamber/cage (where animals are kept during interval between phases) could also be facilitating the bounding of events and are imposed by the experimenter.

In chapter 1, section 2.4.3., one of outcomes in reviewing the literature was that it highlighted that changes in spatial context may be a good way to make cross-species comparisons in event segmentation (especially from rodent models to humans). To this end, the experiments in chapter 4 were largely inspired by a potential neural correlate of event segmentation cued by turns around spatial boundaries, which was originally evidenced in rats. Hence, this following chapter principally explored whether humans also segment more at turns around spatial boundaries in an explicit event segmentation paradigm. One of the benefits of working with human participants is that they can verbally express why they segment. Together, verbal explanation and behavioural assessment can leave little ambiguity as to whether turns around spatial boundaries may similarly cue event segmentation across different species.

5. Chapter 4: Turns around repetitive spatial boundaries facilitate an increase in event segmentation over time

5.1. Introduction

Despite experiencing a continuous stream of ongoing input as we go about our waking daily lives, our memory of such past experience is fragmented into discrete units via episodic neurocognitive processing (Ross & Easton, 2022; Richmond & Zacks, 2017). Indeed, as an individual's experience is perceptually constructed and evolves (updates) over time, neurocognitive theories have proposed that event segmentation occurs, where an 'event boundary' refers to the end of a meaningful unit of activity and the beginning of another (Newtson, 1973; Zacks, et al., 2007; Radvansky & Zacks, 2014). Naturally, these transitional moments in one's experience are inherently important for subsequent successful or unsuccessful memory formation (Zacks et al., 2007; Ezzyat & Davachi, 2011; Horner et al., 2016; Flores et al., 2017; Sargent et al., 2013; Pettijohn et al., 2016; Sinclair et al., 2022). With people being able to adjust the timescale at which they can consider an event boundary (Radvansky & Zacks, 2014); namely, finer-grained segmentation on shorter timescales versus coarser-grained segmentation on longer timescales (also reflected in hierarchal cortical activity; Baldassano et al., 2017). Thus, what influences evocation of event boundaries has become a crucial question in neurocognitive research.

Extensive work based upon literary texts as well as movie stimuli has specifically highlighted that aspects such as: time, space, entity (e.g., characters), causation and motivation (e.g., goals) are key for event representations and segmentation (Zwaan et al., 1995). Such aspects impact long-term memory and related cortical activity (Clewett, et al., 2019; Lee & Chen, 2022; Cohn-Sheehy et al., 2021; Reagh & Ranganath, 2023; Ben-Yakov & Henson, 2018; Milivojevic et al., 2016; Nentwich et al., 2023). For example, the hippocampus which is sensitive to event boundaries and critical for successful episodic recollection, shows enhanced activation to the off-set of short movie stimuli as if to demarcate the ending of the

movie event (Ben-Yakov & Dudai, 2011; Ben-Yakov et al., 2013; Richmond & Zacks, 2017; Vargha-Khadem et al., 1997). A commonality in such text and movie stimuli is the prominent role of narratives usually encompassing several of the aforementioned aspects. Some have argued that comprehension and communication of narratives are not only a crucial component of human episodic memory (Keven, 2016; Mahr & Csibra, 2018; Boyd, 2018) but has been shaped by evolution to promote cooperation within human groups, better achieving shared goals (Smith et al., 2017).

The widespread usage of narrative-based stimuli, especially when presented in a linguistic framework, inherently biases interpretations of event segmentation behaviour towards humans (Boyd, 2018). This is problematic as there is accumulating evidence that many non-human animal species can perceptually construct and retrieve simultaneously integrated event information ('episodic-like' memory; Clayton et al., 2003; Allen & Fortin, 2013; Eacott & Norman, 2004; Dere et al., 2005). This suggests that there are some evolutionarily conserved neurocognitive mechanisms shared across some species, highlighting the need for more comparable approaches to understand links between event perception, segmentation and episodic-(like) memory.

Navigating around boundaries, or transitions between spatial contexts are candidate examples of cues for event segmentation, that are applicable to many animals and agents (Brunec et al., 2018; Lee, 2023; Ross & Easton, 2022). For example, turns due to boundaries may demarcate new events and can distort spatiotemporal cognitive judgements about distance and duration (Brunec et al., 2018; Brunec et al., 2017). Importantly, physical boundaries in environments have been seen to impact the activity of spatially modulated functional cell types in the rodent hippocampal formation (Fig. 1A; Derdikman et al., 2009; Lever et al., 2009; Krupic et al., 2015). This, coupled with observations that such transitions in spatial/geometric context also drastically influences human memory (Fig 1B; Radvansky & Copeland, 2006; Horner et al., 2016; Buckley et al., 2022; Brunec et al., 2020; Marchette et al., 2017; Seel et al., 2019; Bellmund et al., 2020; Segen et al., 2022), would argue that spatial context has an effect on event segmentation and is a good way to make cross-species comparisons.

Prediction-based theories of event segmentation can address the cognitive

process more holistically (Zacks et al., 2007; Franklin et al., 2020; Rouhani et al., 2020). That is, they can explain why segmentation occurs in narratives, spatial context and in other situations, whilst still allowing one to understand such event cognition across animals, agents and in human development. A prerequisite for such predictive models is that animals and agents have previous structured knowledge representations of how certain situations generally work (schema; Bartlett, 1932) and use this as a basis to predict future experiences (Zacks et al., 2007; Friston, 2010). When there is a mismatch between what one expects versus what occurs, a 'prediction error' arises (likely cueing an event boundary) and it is adaptive for one to learn and remember from that experience to minimise future prediction error (Zacks, 2020; Friston, 2010). For example, you are about to pay at the checkout for your weekly food shopping and suddenly the cashier says, "you are free to take your items, someone has already paid", for many this would be unexpected (evoking an event boundary) and may become a memorable moment. However, there are several lines of evidence that predictive-based accounts and their relationship to event cognition is more complex than solely prediction error computations (Avrahami & Kareev, 1994; Schapiro et al., 2013; Logie & Donaldson, 2021; Tauzin, 2015).

Upon repeated viewings to the same movie stimulus, it was recently shown that human cortical activity in some regions increasingly and reliably preceded event boundaries (Lee et al., 2021). Indeed, 'repetition enhanced' activation can manifest behaviourally, with stronger recognition memory performance being seen to relate to increased activation in sub-regions of the hippocampal formation when participants are presented with repeated stimuli (short movies, face-scene pair; Ben-Yakov et al., 2014; Zhan et al., 2018; respectively). Furthermore, if event-level prediction error relies on schema representations, what segmentation occurs in young infants when their knowledge of the world is still developing? Children even at a very young age do form predictions and are surprised when their predictions are wrong (Gopnik, 2010). Yet, learning through repetitive events are equally important, as for example three-year-old children remember novel object-name parings for longer when read the same narrative three times versus when read three different narratives (Horst et al., 2011). And infants may be neurocognitively segmenting events differentially to adults needing longer temporal integration windows, being particularly sensitive to

repeated occurrences (Yates et al., 2022; Gopnik, 2010). Together, such work would suggest that despite some experiences turning out to be entirely predictable event segmentation still occurs for animals and agents when reduced to the salient changes in perceptual content (c.f. Roseboom et al., 2019) and or due to the repetitive nature (Avrahami & Kareev, 1994).

5.2. Experiment 1

Here, we approach event segmentation through the lens of comparative cognition and were inspired by fragmentation of single-cell spatially modulated representations in the rodent hippocampal formation by physical boundaries. Specifically, grid cells typically display hexagonal patterned firing fields as rodents traverse open spaces (Hafting et al., 2005). However, one can create compartmentalised spaces by inserting physical boundaries into the environment, and for example form what we refer to as a corridor arm maze (CAM). It was found that spatially modulated firing of grid cells was reset as rats turned into proceeding corridors in the CAM (Fig. 1A; Derdikman et al., 2009). In this way, discrete spatial representations were formed for each corridor arm. Studies in humans have also shown that the number of turns modulates compression of a route during mental navigation memory (Bonasia et al., 2016). And there is better recollective memory for pre-turn events versus post-turn events and events in the middle of a route (Brunec et al., 2020). Taken together, this would suggest that turns may be natural breakpoints for humans and some non-human animals (Brunec et al., 2018; Ross & Easton, 2022), however to our knowledge this remains to be explicitly tested. Thus, our main hypothesis in experiment 1 was that in a virtual CAM (Fig. 2) turns at the end of the corridor would cue event segmentation as participants passively watched an agent traverse a fixed path from a first-person perspective.

It was important to have good control over the parameters of the video stimulus, as this offers advantages over some movie and narrative text stimuli (c.f., Magliano et al., 2014). For example, cinematic techniques used in movies can facilitate one's segmentation (Cutting & Iricinschi, 2015; Cutting et al., 2012), with text and movie stimuli sometimes containing cuts or 'jumps' in spatiotemporal

context which impacts segmentation (e.g., Ezzyat & Davachi, 2011). Yet, such cuts or jumps do not always reflect the typical continuity of an organism's sensory experience in reality. Hence, it was critical to have the agent in the stimulus continuously traversing around the boundaries whilst participants were segmenting.

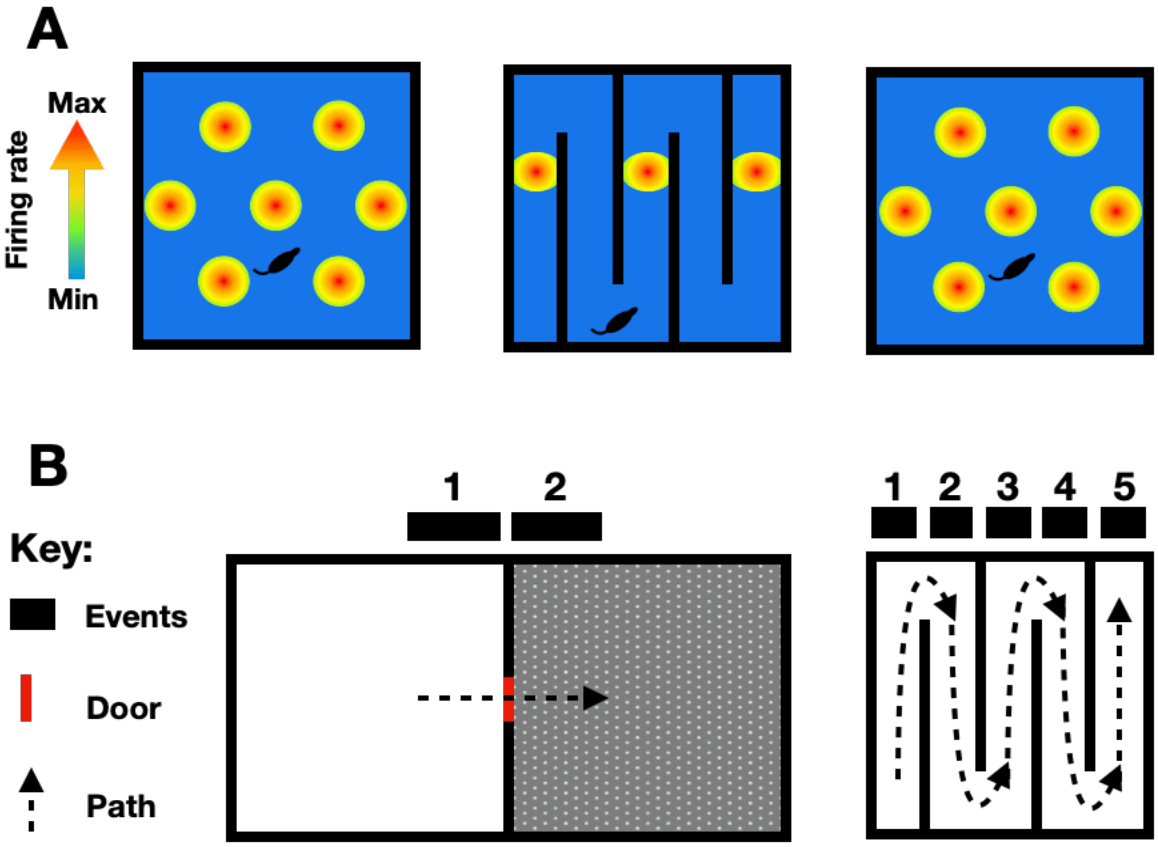


Figure 1. Schematics of how spatial context can influence event segmentation. **(A)** Schematic based upon empirical work of Derdikman et al., (2009), reporting fragmentation of grid cell spatial representations in rats. Left, depicts a schematic example of a single grid cell which typically displays regularly spaced firing fields (forming a hexagonal pattern) as animals traverse their open field environment. Middle, inserted inner boundaries forming corridors (hence, we refer to this spatial layout as the corridor arm maze; CAM) influences grid cell firing, forming discrete spatial representations for corridor arms and were reset by rats' turns into proceeding corridors. Right, the typical grid cell firing field pattern returned when rats were placed into the open field environment with no inner boundaries present. **(B)** Left, human empirical work has shown that transitions between doors to different, distinctly decorated rooms influences memory processing and segmentation (e.g., Radvansky & Copeland, 2006; Horner et al., 2016). Right, together the above work led to our main hypothesis, that people would segment more when they passively watched an agent traverse around turns relative to corridors straights.

5.2.1. Methods

5.2.1.1. Participants

Forty participants were recruited online from the Durham University Psychology participant pool and nearby community, receiving course credits for their participation where applicable. All participants for all experiments provided informed consent, also acknowledging that they had typical or corrected-to-typical eyesight. All experiments were approved by the local ethics subcommittee at Durham University. A power analysis (G*Power 3.1.9.7.) for experiment 1 suggested a minimum sample size of 30 participants (two-tailed paired t-test, $dz = 0.5$, $\alpha = 0.05$, $\beta = 0.75$). We recruited more than this minimum estimate to account for potential outliers and online testing. One outlier case was excluded based on their key press count and quartiles (where $k = 2.07$, Hoaglin et al., 1986), thus for experiment 1 the data from 39 participants were analysed (29 female, 18-30 years, $M_{age} = 19.82$, $SD_{age} = 2.52$).

5.2.1.2. Materials

All virtual environments were constructed in Unity (2021.3.7f1, Unity Technologies). This was done using the 'CineMachine' package and videos were created (60 FPS, 1080p, 16:9 aspect ratio, MP4), displaying a maze comprised of 6-corridors from the first-person perspective along a pre-determined path for experiment 1 (Fig. 2A, the video lasted 60s). All experimental video stimuli can be obtained via the open science framework (https://doi.org/10.17605/OSF.IO/6SWZD). We used PsychoPy (v2021.2.3., PsychoPy®) to create and structure the experimental proceedings, which was then uploaded onto the pavlovia.org server (Pavlovia®) to be completed online independently by participants. A caveat of this approach was that we were not able to control the screen size in which participants experienced the experiment (although during piloting the experiment always loaded as a full window upon a user's screen).

5.2.1.3. Procedure

Once consented participants first filled out their demographic information (sex and age). They were then shown a start screen which stated that the video would begin next, and it included the task instructions: “when you feel one meaningful unit of activity ends and another begins, we ask you to press the ‘SPACEBAR’ key” (Fig. 2B). Participants were required to click the screen to acknowledge that they were ready to begin and were subsequently shown the video stimulus (there were no practice trials). Whilst the video was playing, only presses of the spacebar were recorded. The participant was entirely passive throughout the duration of the stimulus (i.e., they had no control over the speed of the video and could not skip to the next screen before the stimulus had ended). For experiment 1, the same video stimulus was repeated, although importantly, after the end of the first stimulus viewing participants were told another video would begin next and were reminded of the task instructions, again having to click before the following video was shown. After the second stimulus viewing, participants watched another video stimulus and completed a memory tasks before being debriefed and the experiment ending (the methods and results of the memory task are not presently reported).

5.2.1.4. Data analyses

The system recorded the number of spacebar key presses made and the timings of such presses. Whereas the key presses analyses took a within participant approach, the binning approach considered responses across participants using key press timings. We first opted to use coarser-grained binning (5s per bin, centred at every 2.5s) as this roughly corresponded to the amount of time it took for the agent to traverse the length of the corridor and around the turn, ~5s respectively (Fig. 2E). This resulted in ‘bin types’, namely corridor (straight) bins vs. turn bins. Finer-grained binning of 1s per bin (centred at every second) was subsequently used to better understand whether presses were distributed equally around turns. We also sought to understand once participants had made their first key press how long did it take until they made their subsequent press (i.e., the regularity in pressing). To address this, we first took the inter-press-intervals within participants (of those who made ≥2 presses) and computed the probability density estimates using these inter-press-

intervals across all participants by fine binning (ksdensity function, MATLAB). Time interval grouping (0-4, 5-9, 10-14, 15-19, 20-24, 25-29s) of the probability density estimates was constructed based upon the coarser-grained binning, which allowed easier interpretation of pressing regularity in relation to the CAM stimulus.

When assessing how presses were distributed around turns, we used finer-grained binning initially focusing upon turn bins of the coarser-grained binning and ±1 bin. A further positive bin was subsequently added into the analyses to better capture the distribution around the turn. Thus, the middle of the turn was considered as bin 0, with positive bin values denoting the agent transitioning from the turn into the next following corridor and negative bin values denoting the agent transitioning from the preceding corridor into the turn (Fig. 3A-B). The 2 peak bins in pressing count were considered as the 'start' (bin -2) and 'end' (bin 2) of the turn, respectively (having significantly greater counts than bin -3 and bin 4, see results section 5.2.2.3.). We compared start-end bins to the bins in between them (turn 'middle' bins, -1 to 1) to better understand whether pressing in these start-end bins could be driving segmentation behaviour overall at turns (the number of start-end bins were not scaled to match that of turn middle bins). The analyses of these data were performed across all turns and across viewings.

A ratio score was constructed to better assess the magnitude of the relative amount of pressing made in the corridor (straights) vs. the turns. This was done using finer-grained binning where turns and their preceding corridors were paired (turn bins -2 to 3, corridor: all preceding bins). Importantly, the number of corridor bins were scaled to match that of turn bins. Thus, the ratio score was calculated as follows: (summed press count of turn bins) – (summed press count of corridor bins) / (summed press count of turn bins + corridor bins). This produced values ranging from -1 to 1, where values towards 1 indicated greater pressing in turns relative to preceding corridor straights, but vice versa for values toward -1, with 0 indicating equivalent pressing in turns and corridor straights).

To reiterate, all data that supports the present findings can be obtained on the open science framework server (https://doi.org/10.17605/OSF.IO/6SWZD). For all analyses we used SPSS (2021, IBM Corp) and MATLAB (2020b, The MathWorks, Inc). Data were appropriately tested for normality (and sphericity assumptions where

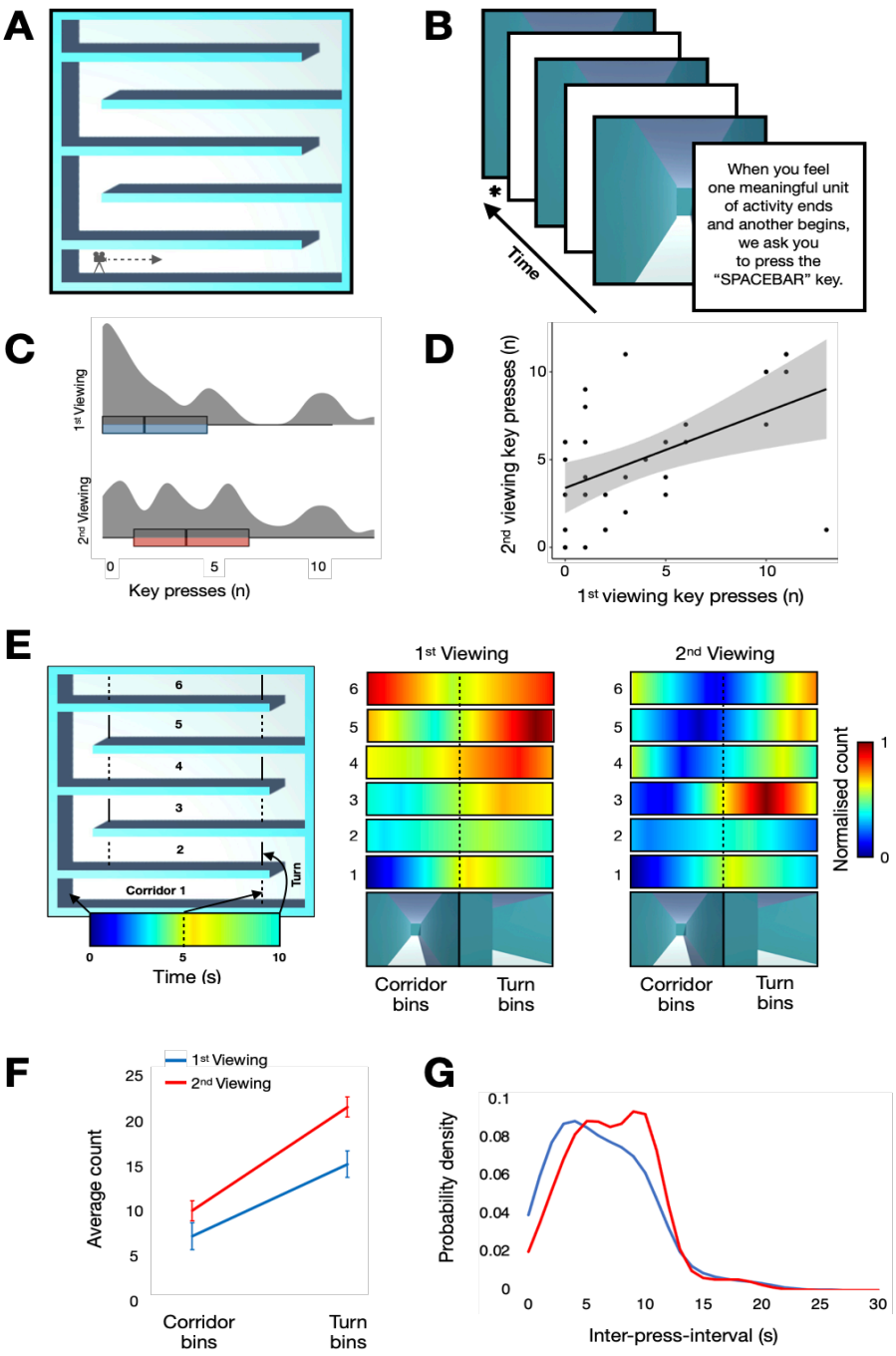


Figure 2. Experiment 1 key presses and coarser-grained event segmentation binning. **(A)** Participants passively viewed the agent traversing a fixed path from a first-person perspective in the corridor arm environment. **(B)** They were instructed "when you feel one meaningful unit of activity ends and another begins, we ask you to press the spacebar key", and viewed the same stimulus twice with a break and repetition of the instructions in between. * Denotes a memory test, the methods and results of which are not presently reported. **(C)** Box plot distributions of the number of key presses made across 1st and 2nd viewings (blue and red, respectively) of the stimulus. **(D)** Correlation between 1st viewing number of key presses against 2nd viewing number of key presses within participants. Linear line of best fit (shared area is CI95%). **(E)** Left: Schematic depicting courser-grained bins of 5s in relation to the corridor arm environment. Middle & right: Heat maps displaying the normalised count (across each viewing, separately) of key presses made across the 6-corridor arms by corridor (straight) bins versus turn bins. **(F)** Average key press count of corridor (straight) bins versus turn bins by viewing. Error bars denote ±1 SEM. **(G)** Probability distribution of the inter-press-interval by viewing.

applicable), and a non-parametric alternative (Greenhouse-Geisser correction for analysis of variance, ANOVA) was used if $p < 0.05$. All reported statistics were two-tailed tests and post-hoc tests were Bonferroni corrected to account for multiple comparisons.

5.2.2. Results

5.2.2.1. Key presses

For experiment 1, we found a significant increase in the number of key presses made by participants from the 1st viewing (Md = 2.00, SD = 3.96) to the 2nd viewing (Md = 4.00, SD = 3.69; $Z = 2.47$, $p = 0.013$, $r = 0.40$; see Fig. 2C). With participant's number of key presses from the 1st viewing positively and significantly correlating with their key presses from the 2nd viewing (Fig. 2D; $r_{(37)} = 0.44$, $p = 0.005$). This initially suggested that 1) there was segmentation occurring in relation to the CAM stimulus and 2) there was a relationship between behavioural responses in the 1st and 2nd viewing. Yet, in order to examine our main hypothesis in experiment 1, that more segmentation should occur at the end of the corridors, we next sought to analyse where/when key presses were being made in the CAM.

5.2.2.2. Event segmentation: coarser-grained

A coarser-grained binning approach to the event segmentation analysis (Fig. 2E; see section 5.2.1.4.) yielded a significant main effect of viewing (i.e., 1st vs. 2nd viewing of the stimulus; mixed-$ANOVA_{rm}$, $F_{(1,5)} = 12.81$, $p = 0.02$, $\eta_p^2 = 0.72$) and a significant main effect of 'bin type' (i.e., corridor bins vs. turn bins, $F_{(1,5)} = 46.85$, $p = 0.001$, $\eta_p^2 = 0.90$). Post hoc tests revealed that, similarly to the aforementioned key presses analysis, there were overall more presses made in the 2nd viewing (M = 15.92) versus the 1st viewing (M = 11.33, $p = 0.02$), and in support of our main hypothesis, we observed across the viewings that more presses were made in turn bins (M = 18.50) relative to corridor bins = (M = 8.75, $p = 0.001$). We were also interested whether and how this effect was impacted by viewing, that is, an interaction between viewing and bin type. Initially, we found no overall interaction

between viewing and bin type ($F_{(1,5)} = 3.42$, $p = 0.12$, $\eta_p^2 = 0.41$). However, post hoc tests showed that within viewing, there was significantly more presses made in turn bins of both the 1st and 2nd viewings (Fig. 2F, M = 15.33, M = 21.67; respectively) versus presses made in corridor bins (M = 7.33, M = 10.17; $p = 0.003$, $p = 0.002$; respectively). Additionally, within bin type, there was more presses made in turn bins of the 2nd viewing versus the 1st viewing, $p = 0.014$. Whereas levels of pressing were comparable in corridor bins across viewings, $p = 0.11$.

To better understand these initial findings, we next sought to understand once participants had made a press how long did it take before they made a subsequent press. To this end, we analysed the inter-press-interval probability density (Fig. 2G, see section 5.2.1.4.). A mixed repeated measures ANOVA yielded no main effect of viewing ($F_{(1,4)} = 0.84$, $p = 0.41$, $\eta_p^2 = 0.17$), but a main effect of 'time interval' (i.e., 0-4, 5-9, 10-14, 15-19, 20-24, 25-29s intervals, $F_{(5,20)} = 24.82$, $p < 0.001$, $\eta_p^2 = 0.86$), and an overall significant interaction between viewing and time interval ($F_{(5,20)} = 10.50$, $p < 0.001$, $\eta_p^2 = 0.72$). Within the 0-4s and 20-24s time interval groups there was a significantly greater probability estimate in the 1st viewing (M = 0.071, M = 0.002, respectively) relative to the 2nd viewing (M = 0.052, M = 0.001; $p = 0.005$, $p = 0.014$; respectively). However, within the 5-9s bin, it was significantly greater in the 2nd viewing (M = 0.089) versus the 1st viewing (M = 0.078, $p = 0.04$). Whereas probability estimates were comparable within the 10-14s, 15-19s and 25-29s bins across viewings (1st viewing: M = 0.035, M = 0.006, M = $1.4E^{-5}$; 2nd viewing: M = 0.048, M = 0.005, M = $1.6E^{-7}$; $p = 0.11$, $p = 0.21$ and $p = 0.27$; respectively. See supplementary table 1 for within viewing post-hoc tests).

5.2.2.3. Event segmentation: finer-grained

Despite our initial evidence suggesting more segmentation occurring in turn bins (Fig. 2E-G), we next sought to use finer-grained bins to better understand if segmentation was distributed equally around the turn (see section 5.2.1.4.).

There was a significantly positive correlation between counts by the fine binning across viewings ($r_{(58)} = 0.60$, $p < 0.001$), a relationship similarly observed in the number of key presses made within participants across viewings, together suggesting that segmentation was overall similar across viewings. Indeed, a simple linear regression revealed that counts by bin from the 1st viewing significantly

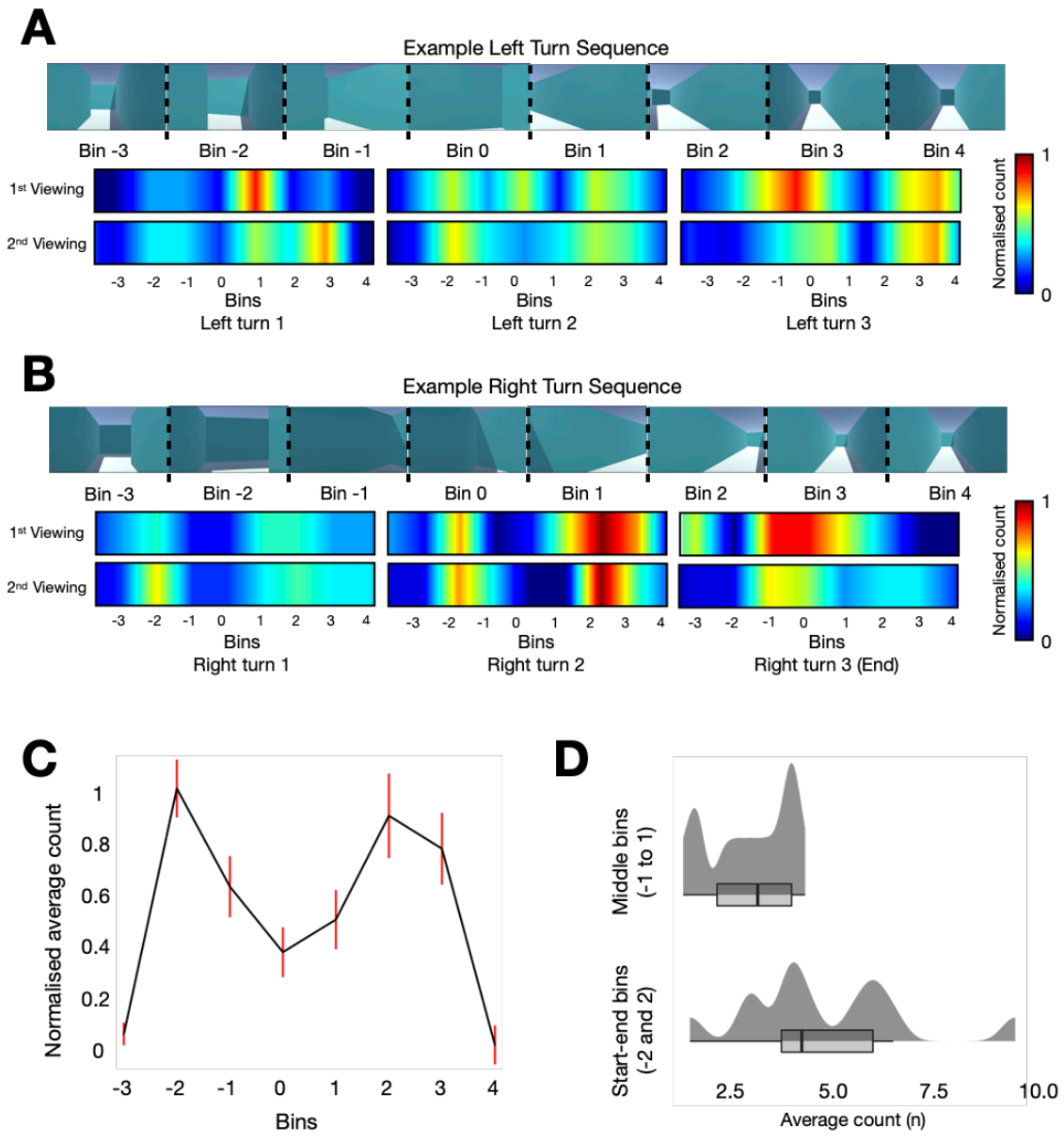


Figure 3. Experiment 1 finer-grained event segmentation binning focused around turns. **(A)** Upper: schematic representing the frame by frame left turn sequence of the agent's traversal (from bins -3 to 4; 1s finer-grained bins, see section 5.2.1.4.). Lower: heat maps displaying the normalised count (across each viewing, separately) of key presses made across the left turn bins by viewing. **(B)** Same as for A but for right turns. **(C)** Normalised average count of key presses made by turn sequence bins (averaged across all turns and viewings). Error bars denote ±1 SEM. **(D)** Box plot distributions of the average count by turn 'start-end' bins (-2 & 2, respectively) versus turn 'middle' bins (-1 to 1).

predicted counts by bin in the 2nd viewing, accounting for 45% of the variance ($F_{(1,58)}$ = 47.28, $p < 0.001$, $R^2 = 0.45$, $\beta = 0.92$, $t = 6.88$, $p < 0.001$). Moreover, there were discrete moments that segmentation was occurring as participants watched the agent traverse around turns in the CAM (Fig. 3). A repeated measures ANOVA yielded a significant overall effect ($F_{(3.82, 42.00)} = 6.74$, $p < 0.001$, $\eta_p^2 = 0.38$), best fitted by a quartic function ($F_{(1,11)} = 27.09$, $p < 0.001$, $\eta_p^2 = 0.71$). There were significantly more presses as the agent approached the end of the corridor to make its turn (Fig. 3A-B, Bin -3, M = 1.25 vs. Bin -2, M = 5.00, $p = 0.001$) and significantly less presses as it exited the turn and approached towards the middle of the corridor (Fig. 3A-B, Bin 4, M = 1.08, vs. Bin 2 and Bin 3, M = 4.58, M = 4.08, $p = 0.029$, $p = 0.09$; respectively. See also supplementary table 2). When considering bin -2 and bin 2 as 'start' and 'end' bins of the turn event, respectively, we observed that there were significantly more presses made in these start-end bins (M = 4.79, SD = 2.08) relative to the bins in between them (i.e., turn 'middle' bins, -1 to 1. M = 3.00, SD = 1.05, $t_{(11)} = 2.36$, $p = 0.04$, $d = 0.68$, CI95% 0.04 to 1.30; Fig. 3C). Lastly, we constructed a ratio score based upon the finer-grained segmentation analyses (see section 5.2.1.4.), finding that the ratio scores were comparable across the 1st and 2nd viewing (M = 0.49, SD = 0.27, M = 0.63, SD = 0.11, respectively, $t_{(5)} = 1.11$, $p = 0.32$, $d = 0.45$)

5.2.3. Discussion

Together these results from the first experiment suggested evidence of 1) more event segmentation occurring in turns bins (already from the 1st viewing), in accordance with our main hypothesis. 2) There was some indication of behavioural change across viewings, with an increased number of presses being made from the 1st to 2nd viewing. The inter-press-interval data also reflected this change, showing an increased likelihood to press more regularly with a 5-9s interval in the 2nd viewing compared to the 1st viewing. Conversely, there was an increased likelihood to press more regularly with a 0-4s and 20-24s interval in the 1st viewing compared to the 2nd viewing. However, when the total number of segmentations were accounted for (via the ratio score analysis) the magnitude of pressing more in turns relative to corridor

straights was comparable across viewings. Lastly, 3) across viewings there were discrete moments of segmentation in the CAM around turns which demarcated the start and end of turn events, largely driving segmentation behaviour overall at turns.

5.3. Experiment 2

Given the initial findings in the CAM from experiment 1, especially concerning the change in behaviour across viewings (Fig. 2), we next wanted to further examine what potential role a break had on segmentation behaviour in the context of the entire experimental procedure. As previously mentioned, activity of the human hippocampus shows enhanced activation to the off-set of short movie stimuli, with one interpretation being that the ending of a movie event cues segmentation (Ben-Yakov & Dudai, 2011; Richmond & Zacks, 2017). In this way, if movie off-sets to break transitions are event boundaries in themselves, breaks may provide opportune moments for reflection of the stimulus and one's segmentation (c.f., Faber & Gennari, 2015), solidify predictions for fore-coming segmentation (Zacks et al., 2007). To address this question, we implemented a between-group design for experiment 2 where one group experienced a single viewing of the agent continuously traversing an 18-CAM without breaks (simply, group *continuous*). Whereas the other group also experienced viewing of 18-corridors but with breaks in between at the end of the 6th and 12th corridor (simply, group *breaks*). Notably, a reminder of the instructions was shown during these breaks.

5.3.1. Methods

5.3.1.1. Participants

A total of 72 participants were recruited for experiment 2 across the Durham University Psychology participant pool, Newcastle University Psychology participant pool and nearby community (separate ethical approval was achieved by the Newcastle University Psychology ethics committee). Unlike experiment 1, after the segmentation task we asked participants an open-ended question as to why they did or did not make presses during the task. Two participants were thus initially excluded

as 1) they made no presses across the experiment and 2) they failed to provide a typed answer as to why they did not press, suggesting that they either were not attending to the task or had technical difficulty. For group *continuous*, the data from 25 participants were analysed (18 female, 1 other, 18-28 years, M_{age} = 19.96, SD_{age} = 2.44). For group *breaks*, one participant was further excluded based upon their key press count and quartiles (where k = 2.07, Hoaglin et al., 1986). This resulted in the data of 44 participants being considered for the analyses (31 female, 18-30 years, M_{age} = 21.09, SD_{age} = 3.70).

5.3.1.2. Materials

Virtual environments were constructed in Unity (2021.3.7f1, Unity Technologies) as stated earlier (see experiment 1 methods, section 5.2.1.2.). Group *breaks* experienced the same 6-corridor maze as in experiment 1. In comparison, group *continuous* experienced an extended 18-corridor maze (lasting 180s), where after the 6th corridor straight the agent's path would have ended in the 6-CAM, but instead continued for a further 12-corridors.

5.3.1.3. Procedure

Both groups experienced the same experimental proceedings as in experiment 1 up until the video stimulus played (see experiment 1 methods, section 5.2.1.3.). After the first stimulus viewing, group *breaks* were shown the same stimulus another two times with a break showing the reminder of the instructions in between them (like in experiment 1; group *continuous* experienced no breaks; Fig 4A). Participants of both groups were then asked to complete a short, typed answer in response to: "in your own words, could you briefly describe why you pressed the space key (or why you did not press the space key)". They were given ~60s to provide the worded response before being debriefed and the experiment ending.

5.3.1.4. Data analysis

For some analyses the 18-corridors were divided into thirds of 6-corridors,

aiming to better reflect the experimental difference between the groups in the analyses. To reiterate, the *breaks* group experienced a break at the end of the 6th and 12th corridors, whereas the *continuous* group experienced no breaks, yet both groups perceived the agent traversing a total of 18 corridors. In regard to the word cloud, the majority of words were reduced to their root form and superfluous words were removed (pronouns and determiners, e.g., 'I', 'the', respectively).

5.3.2. Results

5.3.2.1. Key presses and event segmentation

The findings of experiment 1 that more segmentation was made around turns were replicated in experiment 2 across both groups (see supplementary Fig. 1). Regarding key presses data, the *continuous* group (Fig. 4B; M = 12.72, SD = 11.90) made significantly fewer presses relative to the *breaks* group (M = 20.73, SD = 11.23, summed across the 18-corridors within participants; $t_{(67)} = 2.79$, $p = 0.007$, $d = 0.70$, CI95% 0.20 to 1.2). Moreover, within the *continuous* group, presses across CAM thirds were positively and significantly correlated (1st vs. 2nd third, $r_{(23)} = 0.95$, $p < 0.001$, 1st vs. 3rd third, $r_{(23)} = 0.92$, $p < 0.001$, 2nd vs. 3rd third, $r_{(23)} = 0.92$, $p < 0.001$). And similarly, within the *breaks* group presses across viewings were positively and significantly correlated (1st vs. 2nd viewing, $r_{(42)} = 0.68$, $p < 0.001$, 1st vs. 3rd viewing, $r_{(42)} = 0.63$, $p < 0.001$, 2nd vs. 3rd viewing, $r_{(42)} = 0.87$, $p < 0.001$).

Analyses of the inter-press-interval yielded a significant main effect of time interval (Fig. 4C; $ANOVA_{rm}$, $F_{(1.11, 8.88)} = 32.51$, $p < 0.001$, $\eta_p^2 = 0.80$), but not group (i.e., *continuous* vs. *breaks* group, $F_{(1,8)} = 0.67$, $p = 0.44$, $\eta_p^2 = 0.08$) nor an overall interaction between time interval and group ($F_{(1.11,8.88)} = 0.62$, $p = 0.47$, $\eta_p^2 = 0.07$). Post hoc tests revealed that the probability estimate was greater in the *continuous*

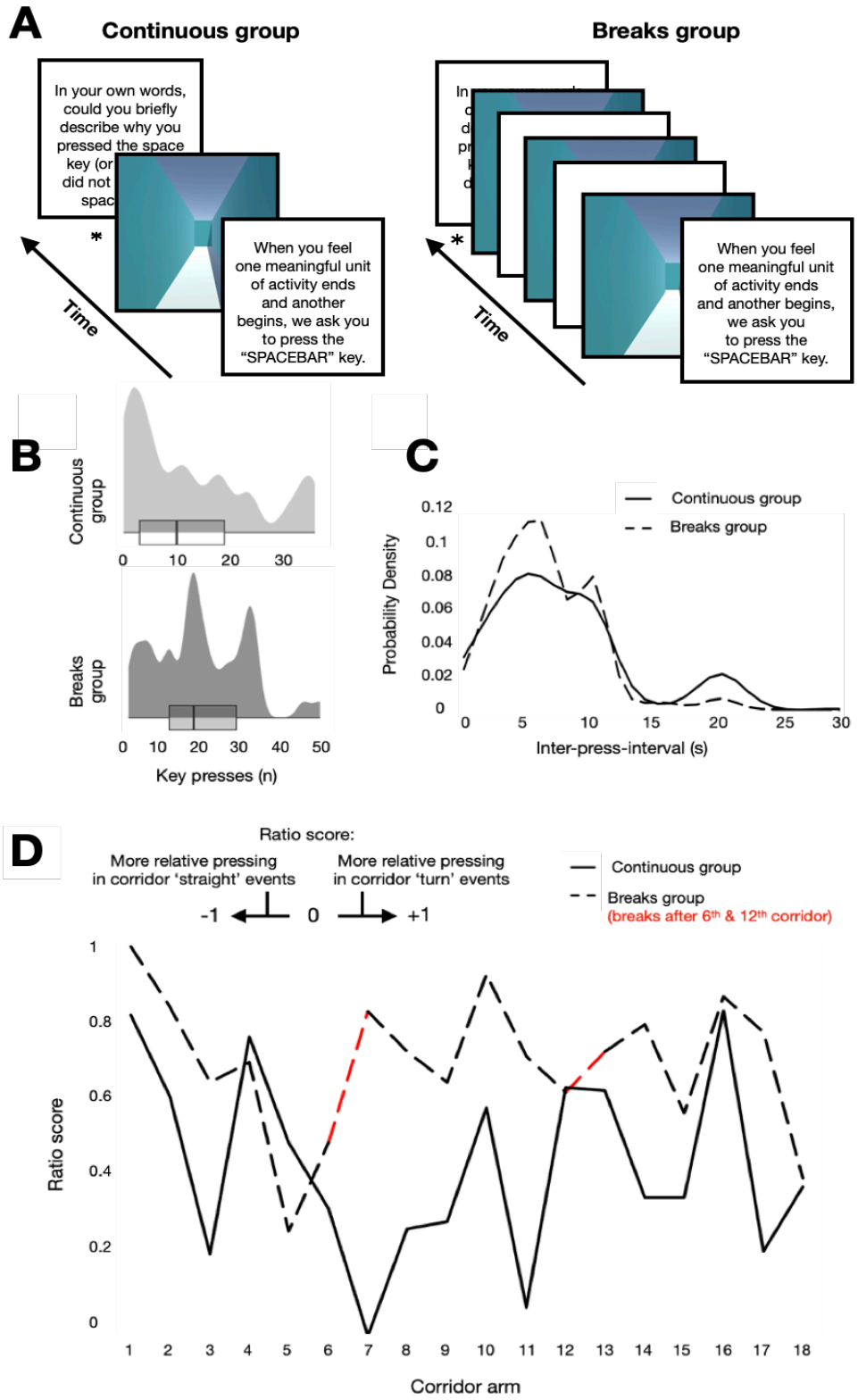


Figure 4. Experiment 2 key presses and event segmentation. **(A)** Experimental procedure for the *continuous* group (left) and *breaks* group (right). See also Fig. 2A-B. * Denotes the end of the segmentation task and start of question as to why participants pressed. **(B)** Box plot distributions of the number of key presses made by group (upper: *continuous* viewing of 18-corridors; lower: viewing of 18-corridors with *breaks*). **(C)** Probability distribution of the inter-press-interval by group. **(D)** Line graph of the ratio score (see upper C) across the 18-corridors by group. Red denotes breaks after the 6th and 12th corridor for the *breaks* group.

group for intervals of 25-29s (M = 0.0007) versus that of the *breaks* group (M = 0.0001, $p < 0.001$). Whereas for all the 0-4s, 5-9s,10-14s and 15-19s, 20-24s intervals the probability estimates were comparable ($p = 0.56$, $p = 0.16$, $p = 1.00$, $p = 0.11$, $p = 0.06$; respectively. See also supplementary table 3).

We next utilised the ratio score based upon the finer-grained segmentation analyses (see section 5.2.1.4.). To reiterate, this was where values towards 1 indicated greater pressing in turns relative to preceding corridor straights, but vice versa for values toward -1, with 0 indicating equivalent pressing in turns and corridor straights (Fig. 4D). There was no main effect of 'thirds' (that is, the 18-corridors divided into thirds of 6-corridors; $ANOVA_{rm}$, $F_{(2,20)} = 0.51$, $p = 0.61$, $\eta_p^2 = 0.05$), but a significant main effect of group ($F_{(1,10)} = 10.09$, $p = 0.01$, $\eta_p^2 = 0.50$), with a greater overall ratio in the *breaks* group (M = 0.72) relative to the *continuous* group (M = 0.42, $p = 0.01$). There was no overall interaction between thirds and group ($F_{(2,20)} = 2.48$, $p = 0.11$, $\eta_p^2 = 0.20$). However, post hoc tests revealed that while there were no differences within groups (all $p \geq 0.33$), both within the 2nd and 3rd thirds the ratio score for the *breaks* group (M = 0.77, M = 0.70, respectively) was greater than that of the *continuous* group (M = 0.29, M = 0.44, $p = 0.003$, $p = 0.05$; respectively). In contrast, within the 1st third, the ratio scores were comparable (*continuous*: M = 0.52, *breaks*: M = 0.65, $p = 0.29$).

5.3.2.2. Why people segmented: participant's worded responses

A word cloud was constructed to give an overall sense of the most frequent words used in explanations (Fig. 5; see section 5.3.1.4.). 'Turn' and 'corner' (8.3% and 5%, respectively) were amongst the most frequently used words and have clear connotations to space. For example, "pressed spacebar when turning around corners" [participant 4659]. "When it turned around the corner, it's meaningful. Then turned left, go straight, right, then left again" [participant 8632]. "Travelling straight vs turning. This was the reasons I pressed it…" [participant 4091]. Such explanations are thus seemingly consistent with the segmentation behavioural findings in experiments 1 and 2, being that turns around the boundaries were cueing segmentation (Fig. 3 and SFig. 1).

5.3.3. Discussion

These results suggested that breaks between stimulus viewings had an impact on the event segmentation in the CAM. There were more presses made across 18-corridors when participants experienced breaks compared to when they watched continuously (Fig. 5A). While there were no differences between groups in the likelihood that they repeatedly pressed at shorter intervals (0-24s), the *continuous* group showed a greater likelihood to repeatedly press at longer intervals (25-29s), which hinted that this group may have been overall less consistent in their pressing (Fig. 4B). This was supported by the ratio analyses, where there was an overall greater magnitude towards more relative pressing in turn events relative to corridor events in the *breaks* group. Yet, importantly, ratio scores were comparable across groups within the 1st third of their respective stimuli (i.e., prior to the 1st break

Figure 5. Word cloud from experiment 2. Participants were asked to give a short, worded answer as to why they pressed the spacebar key (i.e., why they segmented).

of the *breaks* group). Whereas after breaks, that is within the 2nd third and final third (after the 6th and 12th corridor, respectively) the ratio scores were greater in favour of the *breaks* group (Fig. 4C). Given these behavioural findings and that the hippocampus displays enhanced activation to the off-set of short movie stimuli which influences memory performance (Ben-Yakov & Dudai, 2011; Ben-Yakov et al., 2013), it strengthens the view that transitions from stimuli ending to breaks commencing can be considered as event boundaries. Therefore, this is an important factor to consider in the context of an entire experimental procedure for segmentation experiments. However, we note that in this present experiment we did not control whether the repetition of the task instructions mediated the behavioural change across groups, hence future studies will need to establish how essential this is in facilitating segmentation behavioural change. Lastly, participant's worded responses were largely consistent with their segmentation behaviour. Thus, from experiment 2 the evidence suggests that breaks with repetition of the task instruction may facilitate behavioural change in event segmentation studies especially across viewings of the same stimulus.

5.4. Experiment 3

Passive viewing of an agent traversing in a virtual CAM produced reliable event segmentation in turns around the boundaries (Fig. 2-4). However, previous segmentation studies have shown that perceptual detection of movement related change of actors and agents is sufficient to drive segmentation (Newtson et al., 1987; Zacks, 2004; Hard et al., 2006). This led us to question how essential were inner boundaries in influencing segmentation behaviour. To this end, we used an open field maze (OFM; Fig. 6A), where the agent traversed the same fixed path as in the CAM but there were no inner boundaries present. Additionally, in a separate maze we had the agent traverse in a continuous manner along a single corridor (i.e., making no turns; SFig. 2). Thus, these two spatial layout could act as controls to address how the inner boundaries of the CAM potentially influenced event segmentation behaviour.

5.4.1. Methods

5.4.1.1. Participants

A total of 44 participants were recruited for experiment 3 across the Durham University Psychology participant pool and nearby community. For the OFM analyses two outlier case was excluded based on their key press count and quartiles (where $k = 2.07$, Hoaglin et al., 1986), resulting in the data from 42 participants (32 female, 18-32 years, $M_{age} = 20.81$, $SD_{age} = 3.10$) being considered for the analyses (including analyses made between the OFM and single corridor maze). For analyses within the single corridor maze, a further 5 participants were excluded based upon the same criteria, resulting in the data of 37 participants being analysed (27 female, 18-32 years, $M_{age} = 20.89$, $SD_{age} = 3.27$).

5.4.1.2. Materials

Virtual environments were constructed in Unity (2021.3.7f1, Unity Technologies) as stated earlier (see experiment 1 methods, section 5.2.1.2.). The OFM was the same dimensions as the CAM however no inner boundaries were present and the agent traversed the same path as in the CAM experiment (Fig. 6A). The single corridor maze was an elongated version of one corridor of the CAM, where the agent continuously traversed until the end boundary (lasting 60s).

5.4.1.3. Procedure

The experimental procedure similarly followed that of experiment 1 (see experiment 1 methods, section 5.2.1.3.). However, after the second stimulus viewing (the same stimulus as the first) participants completed the task in relation to the other maze, again viewing that stimulus twice. Thus, for experiment 3 participants viewed a total of 4 videos with breaks in between them. Notably, the order of which maze type was viewed first was equally counterbalanced across participants.

5.4.1.4. Data analyses

When analysing the OFM separately we implemented the approaches previously used as specified (see experiment 1 methods, section 5.2.1.4.). However, for the single corridor maze we split the maze into halves based upon finer-grained binning (where the 1st 30 bins constituted the 1st half, and the latter 30 bins constituted the 2nd half). In making comparisons across the spatial layouts of experiment 3 to that of the CAM, we pooled participant data from experiment 1 and the *breaks* group from experiment 2 (data from the 1st and 2nd viewing). This was because *break* group participants had had the same experimental experience up until the end of the 2nd stimulus viewing. In contrast, participants from the *continuous* group in experiment 2 experienced no break which impacted segmentation (see experiment 2 results, section 5.3.2.). Thus, data from 83 participants (60 female, 18-30 years, M_{age} = 20.50, SD_{age} = 3.26) were considered for analyses from the CAM group (for the OFM group, see experiment 3 methods, section 5.4.3.1.). To assess whether and how segmentation changed over time across the pooled CAM data and the OFM data, we divided these mazes into thirds using coarser-grained binning. This differed to previous approaches, as now a given third was constituted by press counts from a left turn bin and right turn bin and their preceding corridor (straights). Thus, this allowed examination of how segmentation behaviour evolved within viewings (within group), across viewings (within groups) and between groups.

5.4.2. Results

5.4.2.1. Open field maze and single corridor maze: key presses and event segmentation

There was an overall effect regarding the key presses data across mazes and viewings ($\chi^2_{(3)}$ = 41.22, $p < 0.001$). Post hoc analyses showed that in the OFM there was no difference in the amount of presses made from the 1st viewing (Fig. 6B; M = 6.19, SD = 4.39) to the 2nd viewing (M = 6.48, SD = 3.92; Z = -1.14, p = 1.00). Similarly, within the single corridor maze there were no differences across viewings (SFig. 2; 1st viewing: M = 2.38, SD = 5.33; 2nd viewing: 3.48, SD = 6.05; Z = -0.38, p

= 1.00). However, across mazes there were more presses made in both the 1st and 2nd viewings of the OFM compared to that of the single corridor maze ($Z = 4.65$, $p < 0.001$, $Z = 3.89$, $p = 0.001$; respectively). In the OFM, participant's number of presses from the 1st viewing were positively and significantly correlated with their presses in the 2nd viewing (Fig 6C; $r_{(40)} = 0.83$, $p < 0.001$, similarly observed between counts by fine binning, $r_{(58)} = 0.74$, $p < 0.001$, with counts by bin in the 1st viewing significantly predicting counts by bin in the 2nd viewing accounting for 62% of the variance, $F_{(1,58)} = 93.80$, $p < 0.001$, $R^2 = 0.62$, $\beta = 0.95$, $t = 9.69$, $p < 0.001$, simple linear regression). Yet, there were no such relationships across viewings in the single corridor maze (within participant's number of key presses made, SFig. 2, $r_{(35)}$

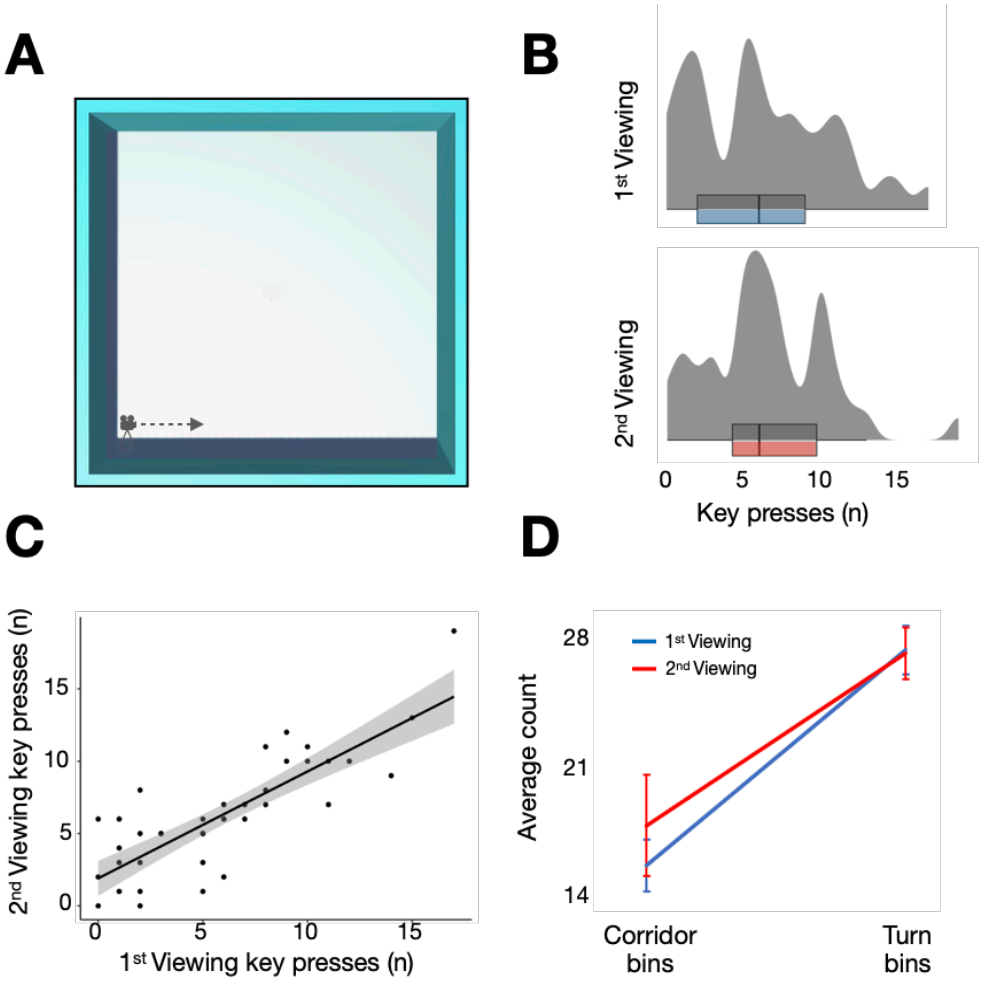


Figure 6. Experiment 3 key presses and event segmentation for the open field maze. **(A)** Schematic of the open field maze (OFM) where there were no inner walls (see Fig. 2). The path traversal of the agent was the same as that of experiments 1 and 2 in the corridor arm environment. **(B)** Box plot distributions of the number of key presses made across 1st and 2nd viewings (blue and red, respectively) of the OFM stimulus. **(C)** Correlation between 1st viewing number of key presses against 2nd viewing number of key presses within participant. Linear line of best fit (shared area is CI95%). **(D)** Average key press count of corridor (straight) bins versus turn bins by viewing. Error bars denote ±1 SEM.

= 0.16, $p = 0.35$; counts by bin, $r_{(58)} = -0.12$, $p = 0.38$).

When splitting the single corridor maze into halves (see section 5.4.1.4) there was initially a significant overall effect considering viewings and halves ($\chi^2_{(3)} = 9.01$, $p = 0.03$). However, post hoc analysed yielded no significant differences (SFig. 2 and 3; all $p \geq 0.13$). Moreover, implementing the same courser-grained approach to the OFM as the previous experiments, we observed no significant main effect of viewing ($ANOVA_{rm}$, $F_{(1,5)} = 0.36$, $p = 0.57$, $\eta_p^2 = 0.07$), but a significant main effect of bin type ($F_{(1,5)} = 22.73$, $p = 0.005$, $\eta_p^2 = 0.82$). There was no indication of an overall interaction ($F_{(1,5)} = 1.00$, $p = 0.36$, $\eta_p^2 = 0.17$). Post hoc analyses showed that significantly more presses that were made overall in turn bins (Fig. 6D and SFig. 3 M = 27.42) relative to straight (corridor) bins in the OFM (M = 16.92, $p = 0.005$). Indeed, within viewings more presses were made in turn bins of both the 1st and 2nd viewings (M = 27.50, M = 27.33; respectively) versus straight bins (M = 15.83, M = 18.00, $p = 0.004$, $p = 0.02$; respectively). However, in accordance with the key presses data there were a comparable number of presses made across viewings in turn bins and straight bins ($p = 0.94$, $p = 0.30$; respectively).

5.4.2.2. Overall comparison of experiments 1 and 2 to experiment 3: key presses and event segmentation

In the previous experiments we observed some indication that segmentation behaviour changed across viewings in the CAM. Given that there is a key difference between the CAM and OFM, that is the inner spatial boundaries of the CAM. The next set of analyses asked whether and how behaviour changed across groups (especially over time, within and across viewings; see section data analysis 5.4.1.4.).

There were a comparable number of presses made averaged across viewings in the CAM with inner boundaries present (M = 5.54, SD = 3.85) relative to the OFM with no inner boundaries present (Fig. 7A; M = 6.33, SD = 3.97; $Z = -1.02$, $p = 0.31$). However, significantly more presses were made averaged across viewings in the CAM versus the single corridor maze (M = 2.93, SD = 4.43, $Z = -4.47$, $p < 0.001$).

Similarly to previous experiments we observed that there were discrete moments of segmentation occurring around turns (Fig. 7B). There was no significant

main effect of group (i.e., CAM vs. OFM; $ANOVA_{rm}$, $F_{(1,34)} = 2.12$, $p = 0.15$ $\eta_p^2 = 0.22$), but a significant main effect of bin, and a significant interaction of bin and group ($F_{(3.78, 128.60)} = 28.47$, $p < 0.001$, $\eta_p^2 = 0.46$; $F_{(3.78, 128.60)} = 9.33$, $p < 0.001$, $\eta_p^2 = 0.22$; respectively). And both were best explained via a quartic function ($F_{(1,34)} = 156.96$, $p < 0.001$, $\eta_p^2 = 0.82$; $F_{(1,34)} = 28.66$, $p < 0.001$, $\eta_p^2 = 0.46$; respectively). Post hoc analyses showed that, within bins -2 to 0 and bin 4, there were significantly more presses made in favour of the OFM group (M = 10.67, 7.33, 4.42 and 6.67; respectively) relative to the CAM group (M = 7.79, 5.00, 2.46 and 1.67; $p = 0.03$, $p = 0.04$, $p = 0.006$ and $p < 0.001$; respectively). Contrastingly, within bin 2, there were

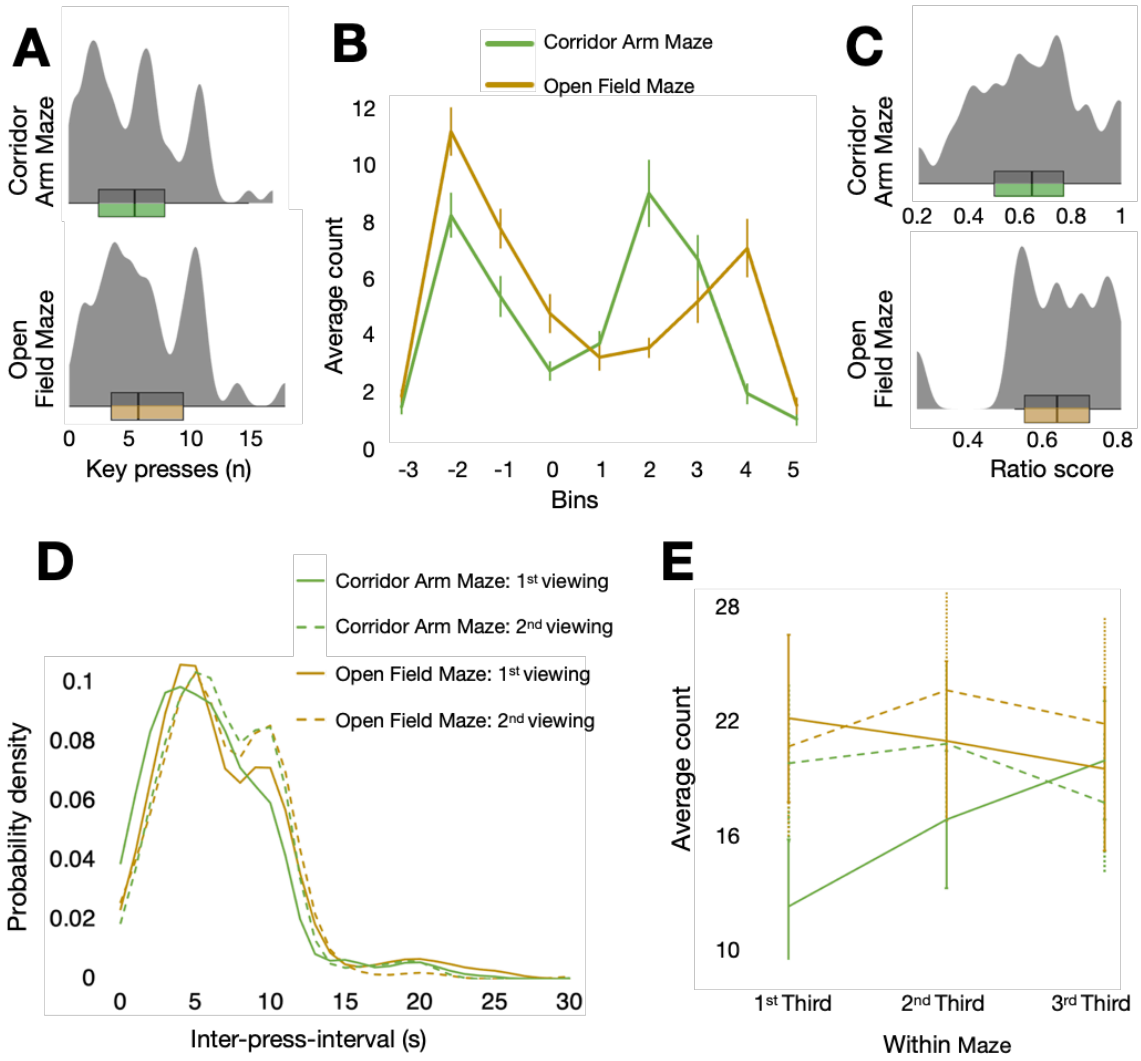


Figure 7. Comparison of event segmentation in the corridor arm maze versus the open field maze. **(A)** Box plot distributions of the number of key presses made by group (corridor arm environment, green, versus open field environment, gold). **(B)** Average count of key presses made by turn sequence bins (averaged across all turns and viewings) by group. Error bars denote ±1 SEM. **(C)** Box plot distributions of the ratio score across viewings by group. **(D)** Probability distributions of the inter-press-interval by group and viewing. **(E)** Average count of key presses made across within maze thirds by group and viewing. Error bars denote ±1 SEM.

significantly more presses made in favour of the CAM (M = 8.54) versus the OFM group (M = 3.25, $p = 0.003$). Finally, there were comparable amount of presses made in bins -3, 1 and 5 (CAM group: M = 1.21, 3.38 and 0.79, respectively; OFM group: M = 1.58, 2.92 and 1.25, $p = 0.34$, $p = 0.52$ and $p = 0.24$, respectively).

Formulating and comparing turn event start-end bins versus turn middle bins (see Fig. 3 and experiment 1 methods, section 5.2.1.4), we found a significant main effect of bin type (that is, turn start-end bins vs. middle bins, $ANOVA_{rm}$, $F_{(1,34)} = 39.77$, $p < 0.001$, $\eta_p^2 = 0.54$), with overall more presses made in turn start-end bins (M = 8.42) relative to turn middle bins (M = 4.08, $p < 0.001$). There was no significant main effect of group ($F_{(1,34)} = 1.13$, $p = 0.30$, $\eta_p^2 = 0.03$) and no overall significant interaction between bin type and group ($F_{(1,34)} = 0.10$, $p = 0.75$, $\eta_p^2 = 0.003$). Post-hoc analyses showed that within groups there were significantly more presses made in start-end bins of the CAM group (M = 8.17) and OFM group (M = 8.67) relative to turn middle bin (CAM group: M = 3.61 OFM group: M = 4.55; $p < 0.001$; $p < 0.001$; respectively). Across groups, there were seemingly comparable levels of pressing in start-end bins and middle bins ($p = 0.70$, $p = 0.06$; respectively).

Despite some differences between the groups based on the finer-grained segmentation, we next sought to compare the ratio scores across groups (see experiment 2 methods). We found no overall difference in the ratio scores between the groups across viewings (Fig. 7C; CAM: M = 0.64, SD = 0.22, OFM: M = 0.63, SD = 0.15, $t_{(34)} = 0.21$, $p = 0.84$, $d = 0.07$). This led us to examine the inter-press-interval data, asking whether the likelihood to repeatedly press at given interval was similar between the groups. A mixed repeated measures ANOVA yielded a significant main effect of time interval ($F_{(1.02, 8.18)} = 36.22$, $p < 0.001$, $\eta_p^2 = 0.82$) but not viewing ($F_{(1,8)} = 0.22$, $p = 0.65$, $\eta_p^2 = 0.03$) nor group ($F_{(1,8)} = 0.001$, $p = 0.98$ $\eta_p^2 \geq 0.01$). In addition, there was no significant interaction between time-interval and group nor viewing and group ($F_{(1.02, 8.18)} = 0.15$, $p = 0.72$ $\eta_p^2 = 0.02$; $F_{(1,8)} = 0.76$, $p = 0.41$, $\eta_p^2 = 0.09$; respectively) and no overall interaction between time-interval, viewing and group ($F_{(1.92, 15.38)} = 2.57$, $p = 0.11$, $\eta_p^2 = 0.24$). Within time-interval and viewing, post-hoc results showed that all probability estimates were comparable across groups (Fig. 7D, $p \geq 0.10$), apart from the 15-19s interval within the 2nd viewing (CAM group: M = 0.005; OFM group: M = 0.002, $p = 0.02$. See supplementary table 4 and

5 for post-hoc tests within group and viewing and within group and time interval, respectively).

5.4.2.3. Overall comparison of experiments 1 and 2 to experiment 3: event segmentation over time

A mixed repeated measures ANOVA showed no significant main effect of thirds ($F_{(2,20)} = 3.01$, $p = 0.07$, $\eta_p^2 = 0.23$), nor viewing ($F_{(1,10)} = 3.75$, $p = 0.08$, $\eta_p^2 = 0.27$), nor group ($F_{(1,10)} = 0.21$, $p = 0.66$, $\eta_p^2 = 0.02$). In addition, there was no interaction between thirds and group nor viewing and group ($F_{(2,20)} = 1.18$, $p = 0.33$, $\eta_p^2 = 0.11$; $F_{(1,10)} = 0.75$, $p = 0.41$, $\eta_p^2 = 0.07$; respectively). There was however, an overall significant 3-way interaction between thirds, viewing and group ($F_{(2,20)} = 3.65$, $p = 0.045$, $\eta_p^2 = 0.27$). Post-hoc analyses revealed that within thirds and viewing there were no differences between groups (Fig. 7E; all $p \geq 0.30$). Within group and viewing, there were no differences in the OFM group across within-maze thirds of the 1st viewing (all $p = 1.00$; 1st to 3rd third: M = 22.5, 21.75 and 20.75; respectively), and the 2nd viewing (all $p \geq 0.50$; 1st to 3rd third: M = 20.25, 24.75 and 23.00; respectively). Yet, in the CAM group, while in the 2nd viewing there were no differences across within-maze thirds (all $p \geq 0.60$; 1st to 3rd third: M = 19.63, 22.25 and 19.5), importantly, within the 1st viewing, pressing was significantly higher in the 3rd third (M = 21.88) relative to the 1st and 2nd thirds (M = 14.00 and 17.63, $p = 0.023$, $p = 0.027$; respectively. No difference between the 1st and 2nd third, $p = 0.18$). Lastly, within group and thirds, there were again no differences between in the OFM group (all $p \geq 0.27$), but in the CAM group pressing was significantly higher in the 2nd viewing for the 1st and 2nd third ($p = 0.005$, $p = 0.03$; respectively) and comparable in the 3rd third across viewings ($p = 0.30$).

5.4.3. Discussion

Robust segmentation was found in the OFM particularly as the agent was making its turn. Indeed, a comparative analysis with the CAM showed that segmentation between the OFM and CAM was largely similar. At the onset of the

turn event initiated by the agent there was increased pressing across both OFM and CAM groups, but this was to a greater extent in the OFM group compared to the CAM group. Interestingly, however, as the agent exited the turn (end of turn event) towards the middle of the corridor (centre of the maze) pressing peaked 2 bins earlier in the CAM group relative to the OFM group. It was also found, in both groups more segmentation was made in the respective mazes versus the single corridor maze, where the agent traversed in a continuous manner. Finally, only in the CAM did segmentation increase over time both within and across viewings.

5.5. Differences in segmentation strategy during the first stimulus viewing across experiments

Previous event segmentation research has shown that individuals can reliably differ in the way they segment, contributing to how well individuals subsequently remember events (Speer et al., 2003; Sargent et al., 2013). In light of such work, we sought to further examine the variability in which participants were segmenting within the first 6-corridor (straights) of their respective maze stimulus (Fig. 8A). This led us to also test an intuitive explanation that could account for some of this variability, being the latency to which participants made their first segmentation (i.e., their 1st key press). Naturally, the longer one takes to make their first segmentation, the less available time there is remaining of the stimulus. However, we do note that the segmentation task does have a relatively low behavioural cost, i.e., participants could freely press the key as fast and as much as possible in a short period of time.

5.5.1. Methods (data analyses)

These analyses focused upon participants who made ≥1 press within the first 6-corridors of their respective stimulus (i.e., prior to a break where applicable). For each participant, the total number of presses made and the timing of their 1st press were the 2 variables used. Pooled CAM data for theses analyses consisted of participants from experiment 1 and from both groups in experiment 2, initially resulting in a total of 88 participants. However, after transformation of the 2 variables

using the natural logarithm (allowing better modelling using of a simple linear regression), one outlier case was excluded based upon quartiles (where $k = 2.07$, Hoaglin et al., 1986). Thus, the final pooled dataset contained 87 participants (65 female, 18-30 years, $M_{age} = 20.43$, $SD_{age} = 3.16$).

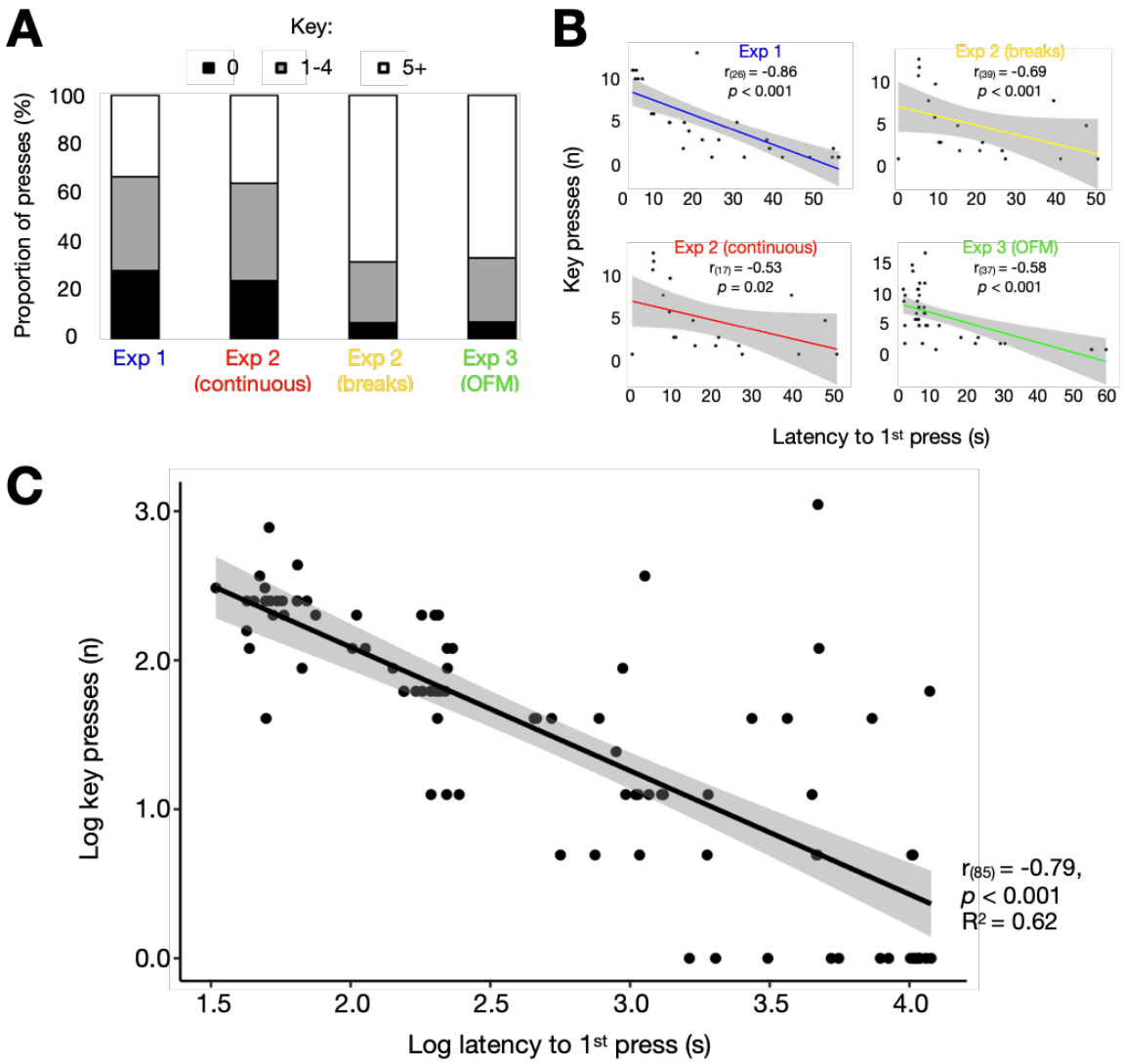


Figure 8. Differences in segmentation strategy across experiments 1 to 3. **(A)** Stacked bar graph displaying the relative proportion (%) of 0, 1-4 and 5+ key presses made (black, grey and white, respectively), across the first 6 (corridor) straights by experiment. Experiment 1 (blue), experiment 2 (*continuous* group, red; *breaks* group, yellow) and experiment 3 (open field maze, green). **(B)** Correlations between the latency to 1st key press made (s) against the number of key presses made separately for each experiment and or group in A. **(C)** Correlation between the natural logarithm of the latency to 1st key press made (s) against the natural logarithm of the number of key presses made. Data was pooled from all corridor arm experimental groups. B-C Linear lines of best fit (shaded areas are CI95%).

5.5.2. Results

Across each experimental group that viewed the agent making turns around the spatial boundaries, we found that latency to 1st press was negatively and significantly correlated with the number of key presses made (Fig. 8B; experiment 1: $r_{(26)} = -0.86$, $p < 0.001$; experiment 2 *continuous* group: $r_{(17)} = -0.53$, $p = 0.02$, experiment 2 *breaks* group: $r_{(39)} = -0.69$, $p < 0.001$). This was also the case for the OFM in experiment 3 with no inner boundaries present ($r_{(37)} = -0.58$, $p < 0.001$). This suggested that latency to which participants made their 1st press may be a common determinant across all our CAM datasets to explain some of the variability in the number of segmentations made. Indeed, across pooled CAM data. we again observed that latency to 1st press was negatively and significantly correlated with the number of key presses made (Fig. 8C; $r_{(85)} = -0.79$, $p < 0.001$). We next used a simple linear regression to assess whether latency to which participants made their 1st press could predict the number of key presses they made. We found that latency to 1st press did significantly predict the number of key presses made within the first 6-corridor straights, accounting for 62% of the variance ($F_{(1,85)} = 137.69$, $p < 0.001$, $R^2 = 0.62$, $\beta = -0.83$, $t = -11.73$, $p < 0.001$). Thus, some of individual variability in segmentation could be explained by how long it took individuals to make their first segmentation.

5.6. General discussion

Accumulating evidence shows that episodic memory and spatiotemporal related perceptual estimations depends upon event segmentation (Radvansky & Zacks, 2014; Sargent et al., 2013; Brunec et al., 2018; Roseboom et al., 2019). This makes it a crucially important neurocognitive process to understand. Despite the task instructions being arguably ambiguous and the task having a relatively low behavioural cost (that is, participants can freely and easily press a key as much as they desired), we found good agreement in segmentation as typically seen in event segmentation studies (e.g., Zacks et al., 2001; Speer et al., 2003; Ben-Yakov & Henson, 2018).

The results from our experiments can be summarised as sixfold. 1) In simple environments, people segment events more so during passive viewing of an agent's turn around a boundary relative to a straight path down a corridor (Fig. 2). And an agent's turn versus its straight path when there are no inner boundaries present in the environment (Fig. 6). 2) The aforementioned segmentation occurs in a discrete manner with more presses being made at the onset of the agent's turn and as it transitions from the turn to the middle of the corridor (centre of the environment; Fig. 3 and 7B). In essence, this demarcated the start and end of turn events, largely driving segmentation behaviour overall at turns. 3) Across repeated viewings of the

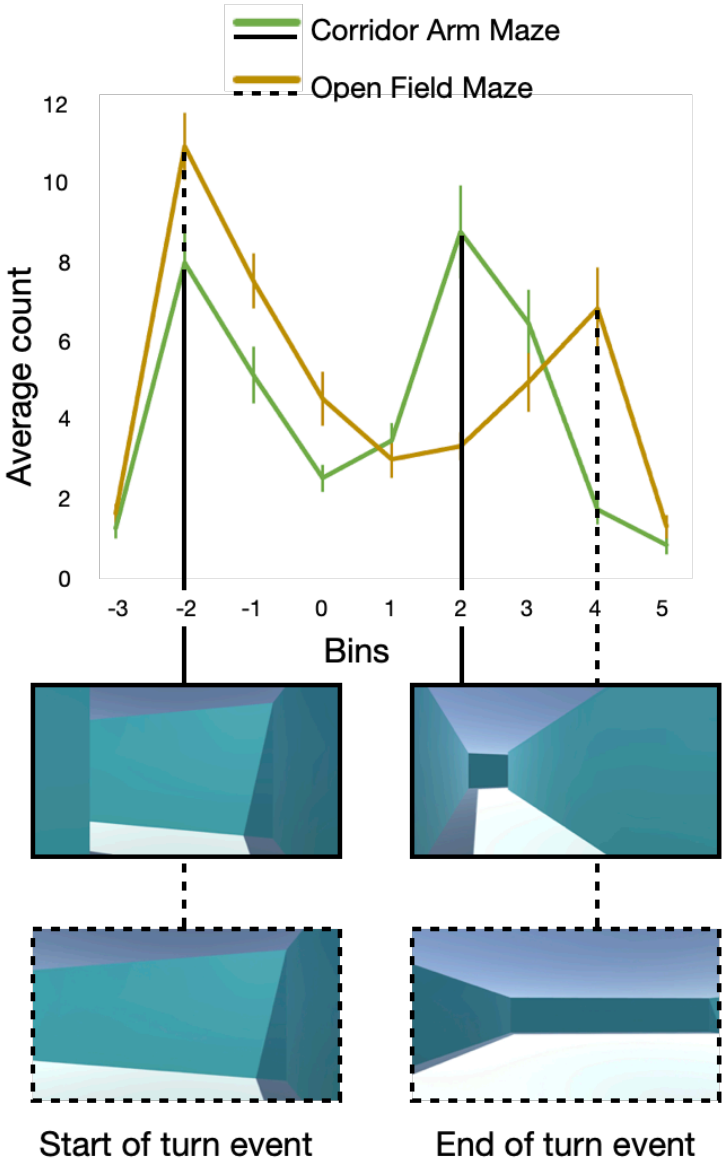


Figure 9. Discrete moments of segmentation around turns in the corridor arm and open field mazes. Same graph as in Fig. 7B, but with corresponding example video frames at peak bins of segmentation. The corridor arm environment is represented by green and solid black lines. The open field environment is represented by gold and dashed black lines.

same stimulus, breaks with a reminder of the instructions influences the magnitude in the amount of segmentation made around turns versus corridor straights (i.e., as indexed via a ratio score, see Fig. 4). Specifically, the ratio score was greater in the group that experienced breaks (only evident after the 1st break) relative to those that viewed the stimulus continuously (i.e., did not experience breaks). 4) Across viewings, more segmentation was made in simple environments (with and without inner boundaries) where an agent made turns relative to a single corridor where the agent traversed a continuous straight path. 5) There was increasingly more segmentation made within and across viewings, when participants experienced more turns in the corridor arm environment with inner boundaries present (Fig. 7E). Whereas in the open field environment without inner boundaries there were comparable levels of segmentation within and across viewings. Lastly, 6) individual differences in the number of segmentations made across the first 6-corridor arms could be partially explained by how long it took participants to make their 1st press (Fig. 8).

Previous research using more simplistic stimuli (e.g., Zacks, 2004; Hard et al., 2006) and more naturalistic complex stimuli (e.g., Newtson et al., 1987; Zacks et al., 2009), in comparison to our stimuli, have found that movement of agents/actors can cue event segmentation. Here in our cue impoverished simple environments, we found that regardless of the presence and absence of inner spatial boundaries, there was an increase in segmentation when the agent begun to make its turn (i.e., the start of the turn event; Fig. 9). The perceptual changes in the agent's movement (and optic flow) likely evoked the segmentation, as more bursts of movement changes even in simple animations using 2-D shape "characters" led to enhanced segmentation concomitant with coarser-grained segmentation (Hard et al., 2006). However, the latter peak in segmentation (what we describe as the end of the turn event) lagged by 2 seconds in the OFM relative to the CAM suggesting that unlike the start of the turn event segmentation cannot be interpreted similarly across the virtual environments .

One interpretation is that while in the OFM segmentation is cued by perceptual detection of the agent's forwards movement onset (changing from the turn), the presence of the CAM's inner boundaries shapes segmentation *before* the

agent's forwards movement onset (Fig. 9). An explanation as to why this occurs from a perceptual account, is 1) the concavity of the spatial boundaries likely constrains each corridor to feel like a separate visual scene (c.f. Cheng et al., 2021) and 2) the visual perspective of looking at the entirety of a new corridor is reminiscent of (re)establishing shots used in filmmaking, which has been seen to influence event segmentation by demarcating new spatiotemporal contexts (Cutting et al., 2012). Thus, our work adds to the existing evidence that changes in perceptual content are sufficient to cue event segmentation.

Given that many nonhuman animal species have the capacity to perceptually construct events and use episodic-like memory (Clayton et al., 2003; Allen & Fortin, 2013), it is possible that a segmentation-like process similarly occurs in nonhuman animals. We designed our experiments based on work in rats, showing that when physical boundaries are inserted into environments forming corridors (see Fig. 1), the firing of single hippocampal formation cells form discrete spatial representations of each corridor (Derdikman et al., 2009). Such physiological correlates in rats, when combined with our present results would suggest that salient changes in perceptual content (e.g., turns around spatial boundaries) may similarly cue segmentation in nonhuman animals (Ross & Easton, 2022).

The finding that spatial boundaries of the CAM facilitated an experience-dependent increase in segmentation is not well accounted for solely by prediction-based theories of event segmentation (Zacks et al., 2007). As such prediction-based theories would suggest that segmentation behaviour may decrease over time if no prediction-errors are experienced. Yet, it is neither well explained solely by changes in perceptual content which should yield consistent segmentation behaviour within and across viewings of the stimulus (as observed in the OFM; Fig. 7E). Instead, as event segmentation can occur at a more conceptual level (Swallow et al., 2018), we interpret our findings in a way that segmentation can be driven by repeating experiential units of activity (Avrahami & Kareev, 1994; see also Sun et al., 2020), becoming more 'meaningful' to an individual over time and facilitating the bounding of events. Importantly this view is conceptually consistent with the well-established function of pattern separation and its role in recognition memory (Yassa & Stark, 2011; Frank et al., 2020), providing neurocognitive and computational plausibility for

our behavioural findings.

Pattern separation describes a process typically associated with the hippocampus, where similar overlapping inputs are discretised into non-overlapping outputs (Yassa & Stark, 2011). Therefore, an intuitive hypothesis is that perceptually driven event boundaries during repetitive experiences may facilitate pattern separation computations, especially in the hippocampus (c.f. Chanales et al., 2017). However, this raises the question of what is it about spatial boundaries of the CAM that led to this increase in segmentation over time?

From the agent's first turn in the OFM one can ascertain the entirety of the spatial layout. Whereas in stark contrast, as previously stated, the geometry of the spatial boundaries likely affords each corridor to feel like a separate scene/spatial context (c.f. Cheng et al., 2021) and occludes the viewing of other corridors. Thus, in the CAM one requires the experience of more turns to ascertain the entirety of the spatial layout, leading to the realisation that the environment (and agent) was repeating itself or as a 'loop' as some participants described (Fig. 6). For example, "none of the turns seemed "meaningful" until they were the only thing that happened repeatedly" [participant 4793]. "The loop started again from the beginning (the loop being turning left then right)" [participant 4664]. "I pressed the spacebar when I felt as if the environment around me was looping – when I believed I had already taken that path before" [participant 8395]. It should be noted however, that this view does not account for the behaviour of all our participants, as some individual pressed immediately from the first turn onwards (see Fig. 8). Also, as our experiments were designed to make cross-species relatability we purposely used simple environments. Thus, segmentation could change once the environment is made more complex with more sensory cues added, this is similarly seen in the firing of spatially modulated hippocampal cells when more cues are added (Bourboulou et al., 2019; Sharif et al., 2021). Yet, given that repetitive experiences and familiarity are a natural occurrence of daily life affecting spatiotemporal cognition (Avrahami & Kareev, 1994; Mandler, 1980; Jafarpour & Spiers, 2017), future research should further explore the complex relationship between event segmentation behaviour, familiarity and episodic memory.

In conclusion, our experiments allowed for cross-species comparisons

suggesting that the perceptual changes associated with turns (especially around a spatial boundaries), may similarly cue segmentation in both humans and nonhuman animals. The simplicity of the experimental design also provided insight into a lesser developed theory of event segmentation. That is, segmentation can increase with more experience, becoming more meaningful over time due to repeating experiential units of activity. This potentially unites event segmentation and pattern separation functions to ultimately advance our understanding of spatiotemporal cognition and episodic memory.

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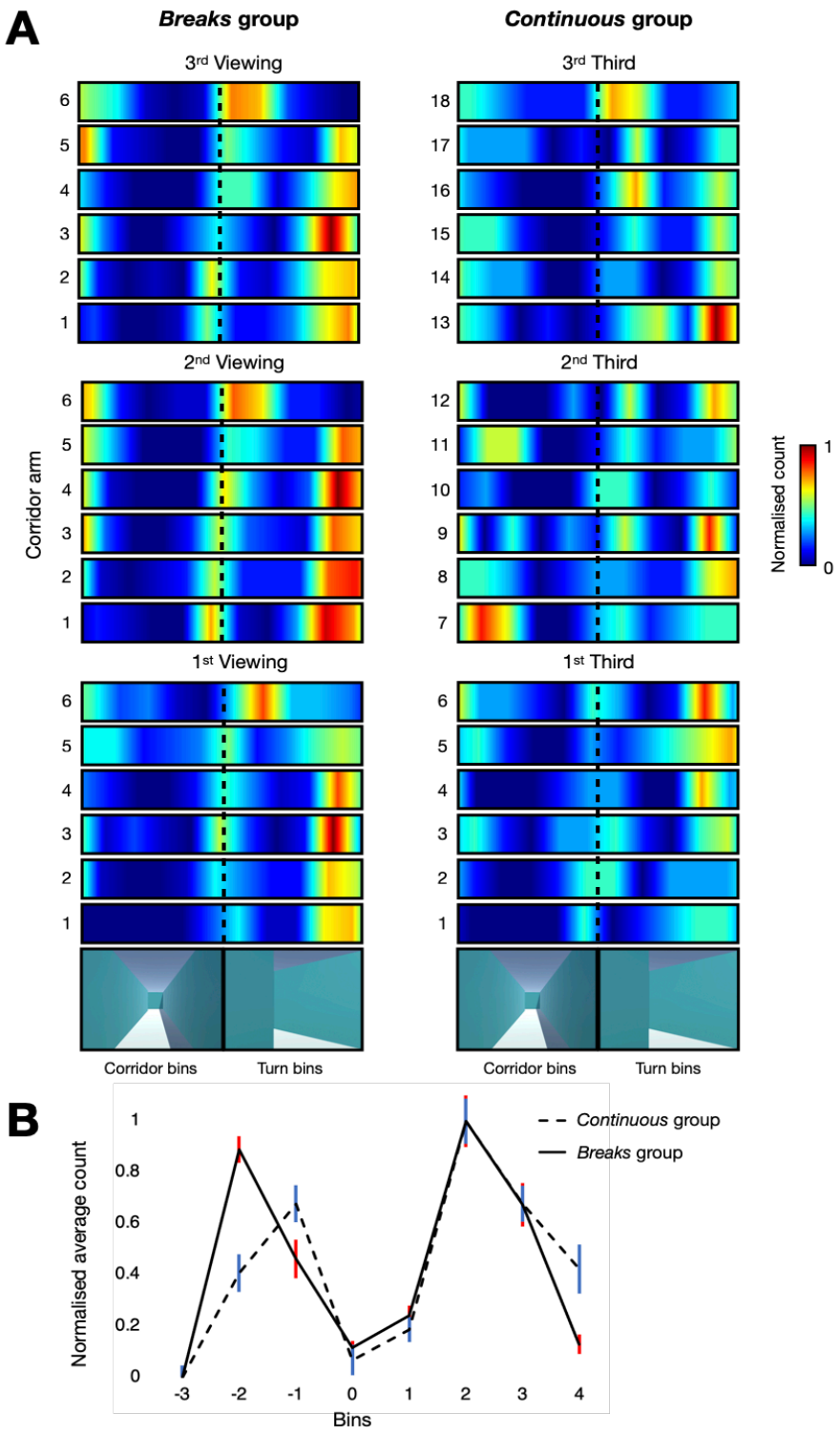
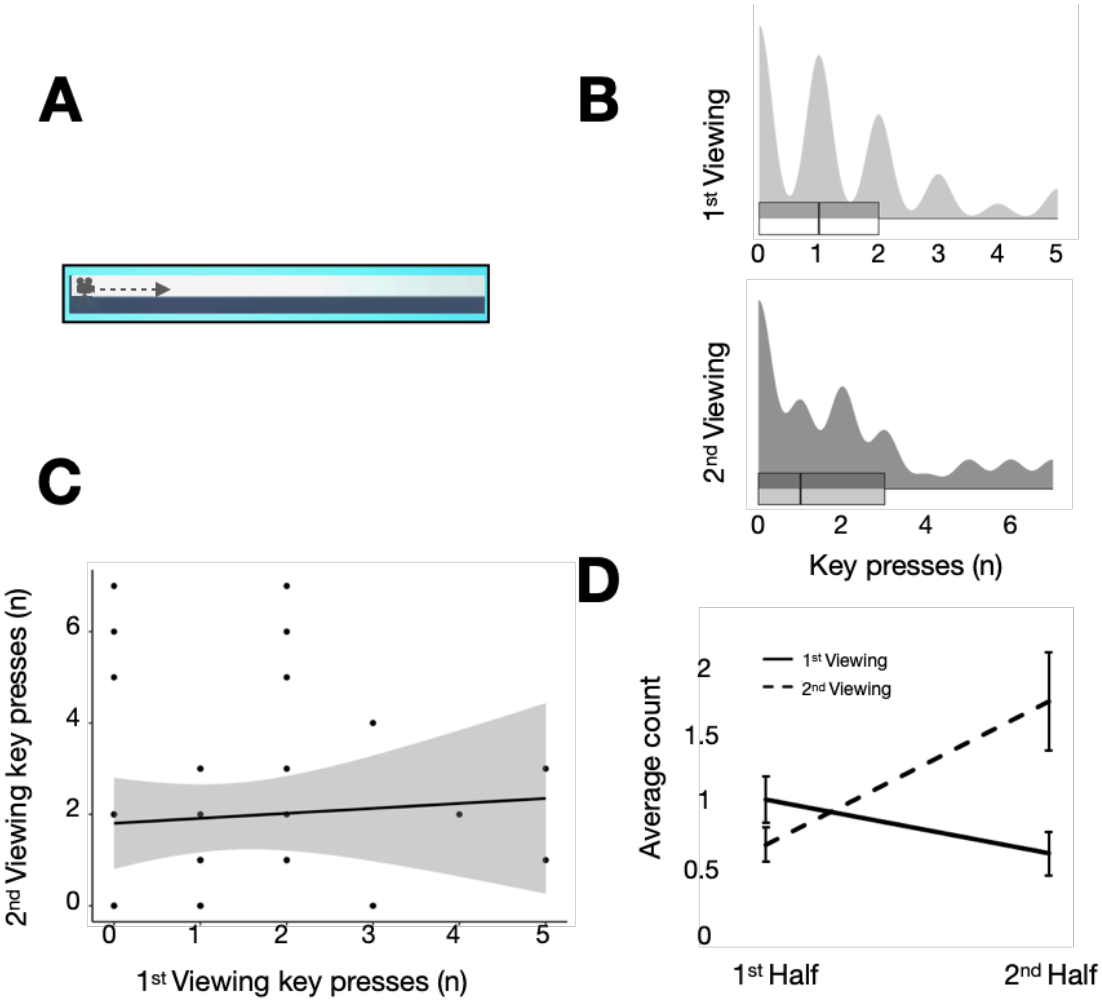
5.8. Chapter 4 supplementary material



Supplementary Figure 1. Experiment 2 event segmentation based upon finer-grained binning. **(A)** Heat maps based upon finer-grained displaying the normalised count of key presses made across the bin types (simply represented via coarser-grained binning). Left, *breaks* group (across each viewing separately). Right, *continuous* group. **(B)** Normalised average count of key presses made by turn sequence based upon finer-grained binning (averaged across all turns and viewings). *Breaks* group represented by the solid black line, *continuous* group represented by the dashed black line. Error bars denote ±1 SEM.

Supplementary text for supplementary figure 1

A mixed repeated measures ANOVA based upon coarser-grained binning similarly to experiment 1, showed a significant main effect of bin type ($F_{(1,10)}$ = 318.50, $p < 0.001$, $\eta_p^2 = 0.97$), and of group (i.e., *breaks* vs. *continuous* group, $F_{(1,10)}$ = 239.44, $p < 0.001$, $\eta_p^2 = 0.96$), but not of nor viewing ($F_{(1.22,12.19)} = 1.10$, $p = 0.33$, $\eta_p^2 = 0.01$). There was no overall interaction between viewing and group ($F_{(1.22,12.19)}$ = 0.38, $p = 0.59$, $\eta_p^2 = 0.14$), but was interaction between bin type and group ($F_{(1,10)}$ = 140.04, $p < 0.001$, $\eta_p^2 = 0.93$). There was however, no overall significant 3-way interaction between bin type, viewing and group ($F_{(2,20)} = 1.93$, $p = 0.17$, $\eta_p^2 = 0.16$). Overall, there was a greater count in turn bins (M = 24.83) relative to corridor straight bins (M = 9.33, $p < 0.001$), and there was also a greater count made by the *breaks* group (M = 25.33) relative to the *continuous* group (M = 8.83, $p < 0.001$). For the interaction between bin type and group, within bin type, there was a greater count in both turn bins and corridor straight bins for the *breaks* group (M = 38.22, M = 12.44, respectively) versus that of the *continuous* group (M = 11.44, M = 6.22, $p < 0.001$, $p = 0.004$; respectively). Yet importantly, within groups more presses were made in turn bins relative to corridor bins for both the *breaks* and *continuous* groups ($p = 0.002$, $p < 0.001$, respectively). Indeed, similarly to experiment 1, finer-grained binning focussed around turns also yielded a distribution best explained by a quartic function in both the *breaks* and *continuous* groups (SFig. 1; $F_{(1,17)} = 189.66$, $p < 0.001$, $\eta_p^2 = 0.92$; $F_{(1,17)} = 85.56$, $p < 0.001$, $\eta_p^2 = 0.83$, respectively). Thus, these results replicate the some of the main findings in experiment 1 across both experimental groups in experiment 2.



Supplementary Figure 2. Experiment 3 key presses and event segmentation for the single corridor maze. **(A)** Schematic of the single corridor maze where the agent traversed a continuous path until the end boundary. **(B)** Box plot distributions of the number of key presses made across 1st and 2nd viewings (light grey and dark grey, respectively) of the single corridor maze stimulus. **(C)** Correlation between 1st viewing number of key presses against 2nd viewing number of key presses within participant. Linear line of best fit (shared area is CI95%). **(D)** Average key press count of 1st half versus 2nd half bins by viewing. Solid black line represents the 1st viewing and dashed black line represents the 2nd viewing. Error bars denote ±1 SEM.

Table 1

Experiment 1: post-hoc comparisons within viewing for the interaction between viewing and time interval.

Viewing	Time interval	Time interval comparison	*p*
1	0-4	5-9	1.00
		10-14	1.00
		15-19	0.047*
		20-24	0.034*
		25-29	0.025*
	5-9	10-14	0.039*
		15-19	< 0.001**
		20-24	< 0.001**
		25-29	< 0.001**
	10-14	15-19	0.37
		20-24	0.25
		25-29	0.27
	15-19	20-24	< 0.001**
		25-29	0.019*
	20-24	25-29	0.80
2	0-4	5-9	0.38
		10-14	1.00
		15-19	0.23
		20-24	0.18
		25-29	0.15
	5-9	10-14	0.97

		15-19	< 0.001**
		20-24	< 0.001**
		25-29	< 0.001**
	10-14	15-19	0.71
		20-24	0.51
		25-29	0.53
	15-19	20-24	0.002*
		25-29	< 0.001**
	20-24	25-29	1.00

* $p < 0.05$ ** $p \leq 0.001$

Table 2
Experiment 1: post-hoc comparisons across finer-grained bins around turns.

Bin (Mean)	Bin comparison	*p*
-3 (1.25)	-2	0.001**
	-1	0.19
	0	1.00
	1	0.65
	2	0.037*
	3	0.046*
	4	1.00
-2 (5.00)	-1	1.00
	0	0.28
	1	1.00
	2	1.00
	3	1.00
	4	< 0.001**
-1 (3.50)	0	1.00
	1	1.00
	2	1.00
	3	1.00
	4	0.25
0 (2.50)	1	1.00
	2	1.00
	3	1.00
	4	1.00
1 (3.00)	2	1.00
	3	1.00

	4	0.76
2 (4.58)	3	1.00
	4	0.029*
3 (4.08)	4	0.09
4 (1.08)	-	-

* $p < 0.05$ ** $p \leq 0.001$

Table 3

Experiment 2: post-hoc comparisons within group for the interaction between group and time interval.

Group	Time interval (Mean)	Time interval comparison	*p*
Breaks	0-4 (0.07)	5-9	1.00
		10-14	1.00
		15-19	0.006*
		20-24	0.026*
		25-29	0.007*
	5-9 (0.09)	10-14	< 0.001**
		15-19	< 0.001**
		20-24	< 0.001**
		25-29	< 0.001**
	10-14 (0.03)	15-19	1.00
		20-24	0.33
		25-29	0.48
	15-19 (0.004)	20-24	1.00
		25-29	1.00
	20-24 (0.003)	25-29	1.00
Continuous	0-4 (0.06)	5-9	1.00
		10-14	1.00
		15-19	0.038*
		20-24	0.17
		25-29	0.02*
	5-9 (0.08)	10-14	0.008*
		15-19	< 0.001**
		20-24	< 0.001**

		25-29	< 0.001**
	10-14 (0.03)	15-19	1.00
		20-24	1.00
		25-29	0.52
	15-19 (0.01)	20-24	1.00
		25-29	0.036*
	20-24 (0.01)	25-29	0.06

* $p < 0.05$ ** $p \leq 0.001$

Table 4

Overall comparison of experiments 1 and 2 to experiment 3: post-hoc comparisons within group and viewing for the interaction between time interval, viewing and group (corridor arm maze vs. open field maze)

Group	Viewing	Time interval (Mean)	Time interval comparison	*p*
CAM	1	0-4 (0.08)	5-9	1.00
			10-14	1.00
			15-19	0.01*
			20-24	0.012*
			25-29	0.008*
		5-9 (0.08)	10-14	< 0.001**
			15-19	< 0.001**
			20-24	< 0.001**
			25-29	< 0.001**
		10-14 (0.03)	15-19	1.00
			20-24	0.69
			25-29	0.52
		15-19 (0.005)	20-24	0.79
			25-29	0.001**
		20-24 (0.003)	25-29	0.007*
		25-29 (0.0003)	-	-
CAM	2	0-4 (0.06)	5-9	1.00
			10-14	1.00
			15-19	0.06
			20-24	0.06
			25-29	0.032*

		5-9 (0.09)	10-14	0.017*
			15-19	< 0.001**
			20-24	< 0.001**
			25-29	< 0.001**
		10-14 (0.04)	15-19	0.61
			20-24	0.38
			25-29	0.38
		15-19 (0.005)	20-24	0.73
			25-29	< 0.001**
		20-24 (0.002)	25-29	0.39
		25-29 ($1.2E^{-6}$)	-	-
OFM	1	0-4 (0.07)	5-9	1.00
			10-14	1.00
			15-19	0.027*
			20-24	0.037*
			25-29	0.022*
		5-9 (0.08)	10-14	< 0.001**
			15-19	< 0.001**
			20-24	< 0.001**
			25-29	< 0.001**
		10-14 (0.04)	15-19	0.26
			20-24	0.17
			25-29	0.12
		15-19 (0.005)	20-24	1.00
			25-29	0.004*
		20-24 (0.005)	25-29	0.001**
		25-29 (0.001)	-	-

			5-9	1.00
		0-4 (0.06)	10-14	1.00
			15-19	0.041*
			20-24	0.049*
			25-29	0.032*
		5-9 (0.09)	10-14	0.07
			15-19	< 0.001**
			20-24	< 0.001**
OFM	2		25-29	< 0.001**
		10-14 (0.05)	15-19	0.26
			20-24	0.18
			25-29	0.21
		15-19 (0.002)	20-24	1.00
			25-29	0.054
		20-24 (0.001)	25-29	1.00
		25-29 (0.0001)	-	-

* $p < 0.05$ ** $p \leq 0.001$

Table 5

Overall comparison of experiments 1 and 2 to experiment 3: post-hoc comparisons within group and time interval for the interaction between time interval, viewing and group (corridor arm maze vs. open field maze)

Group	Time interval	*Viewing 1 vs. 2* *p*
CAM	0-4	< 0.001**
	5-9	0.003*
	10-14	0.011*
	15-19	0.68
	20-24	0.014*
	25-29	0.54
OFM	0-4	0.07
	5-9	0.033*
	10-14	0.08
	15-19	0.007*
	20-24	< 0.001**
	25-29	0.029*

* $p < 0.05$ ** $p \leq 0.001$

5.9. Bridging of chapter 4 and 5

The empirical work of chapters 2 to 4 address episodic processing on the cognitive-behavioural level, but at the same time have aimed to be interpretable on the biocomputational level. The methodology of chapter 5 now allows the addressing episodic processing on the level of single units. To allow good spatiotemporal resolution of single unit electrophysiological activity, a rodent model was returned to allowing the use of chronic implants for longitudinal recordings. More specifically, the same mouse strain as used in chapter 3 were the subjects of chapter 5. One of the benefits of this was that the mice from chapter 3 could act as a control group to ascertain whether successful novel object recognition behaviour could occur in a novel trial sequence design implemented in chapter 5.

As the experiments in chapter 2 have used an episodic-like approach in the form of object-place-context associations, chapter 5 also considers specific simultaneously integrated object-place-context associations to be content of episodic nature. Thus, in having experience using the object-place-context spontaneous recognition task, in combination with reviewing relevant literature of place cells (chapter 1, especially, section 2.3.), it led to a key question of whether single place cells could represent episodic content in the form of simultaneously integrated object-place-context associations.

6. Chapter 5: Do individual place cells incorporate spatial context and object specificity to form simultaneously integrated episodic representations?

6.1. Introduction

Hippocampal pyramidal cells of the cornu ammonis (CA) regions can fire in one or more restricted regions of space when a rodent traverses in their environment, hence called place cells (O'Keefe & Dostrovsky, 1971). As discussed in chapter 1 of this thesis, the activity of place cells (and generally principal cells of the hippocampal formation) can be modulated by external stimuli comprised of various sensory modalities, and collectively the activity of these cells can reflect mapping of (allocentric) spatial and non-spatial dimensions (O'Keefe & Nadel, 1979; Aronov et al., 2017; see also chapter 1, sections 2.3.1. and 2.3.2).

Previous work using objects when recording from place cells has shown that:

I) Objects can perturb the activity of place cells, for example by supressing their place fields (e.g., Rivard et al., 2004).

II) Some place cells can fire in a vector relationship, especially noticeable when multiple objects are present in an environment (Deshmukh & Knierim, 2013).

III) The heterogeneity of hippocampus affects object modulation of place cell activity (Vandrey et al., 2021; Fernandez-Ruiz et al., 2021).

IV) Possible mechanisms by which place cells reflect object-place novelty are changes in firing rate (rate remapping) and shifting/development of new place fields (Larkin et al., 2014; Burke et al., 2011; Vandrey et al., 2021).

V) Some place cells can leave 'trace' or 'misplace' firing fields relating to where objects were previously positioned (O'Keefe, 1976; GoodSmith et al., 2022; Deshmukh & Knierim, 2013; Vandrey et al., 2021, see also, Poulter et al., 2021; Tsao et al., 2013; Weible et al., 2012).

Together, such work would argue that place cells can support a representation of object positions in environments. This in turn could seem to be a necessary prerequisite for the hippocampal support of episodic memory, yet some

have theorised otherwise.

Hippocampal indexing theory describes a framework as to how an episodic memory is formed (Teyler & Rudy, 2007; Goode et al., 2020). It proposes that a behavioural experience (episode) activates a particular neocortical pattern which is ultimately projected to the hippocampus, activating a unique set of synapses, then 'stored' as strengthened connection amongst these synapses activated by the input pattern (Teyler & Rudy, 2007). Moreover, partial input of the original neocortical pattern can activate the hippocampal set of synapses (index) and project back to the neocortex to activate the entire pattern (i.e., recall the episodic memory), a computational function referred to as pattern completion (Passingham, 2017; Horner et al., 2015). In the same breath, a strong view of indexing theory argues that no content is being stored in the hippocampus, as the synaptic connectivity pattern is the mnemonic index. Teyler and Rudy go on "The hippocampus has neither the computing power nor functional organization to accomplish the analytical processing done by neocortex – so it contains no content. The content resides in the neocortex." (p. 1163, Teyler & Rudy, 2007). Indeed, another functional theory of the hippocampus which also relates to episodic memory processing is that of sequence generation (Buzsáki & Tingley, 2018). This theory, although not mutually exclusive from hippocampal indexing theory also outlines that the "hippocampus performs a general but singular algorithm: producing sequential content-free structure to access and organise sensory experiences distributed across cortical modules" (p. 853, Buzsáki & Tingley, 2018). A commonality shared by both theories implies that the hippocampus is 'blind' to the specificity of the information that it receives and performs computations on. This is seemingly at odds with a plethora of hippocampal work, not least those relating to object-related coding by place cells, which has provided evidence that place cells are modulated by content in environments, thus, the line of questioning in this chapter is based upon this evidence.

Recent work in rodents has stressed the importance of an emergent population-level code in understanding hippocampal-dependent cognition such as episodic memory (Nagelhus et al., 2023; Nieh et al., 2021; Rubin et al., 2015; Rubin et al., 2019). Place cells typically allow good decoding of an animal's position in environments, whilst also being sensitive to spatial context changes through global

remapping (Kubie et al., 2020; see also chapter 1, section 2.4.3). Indeed, the aforementioned evidence allows for a representation of object-place coding in environments. In this way, at the neural population-level of the hippocampus specific object-place-context integrations (i.e., episodic content; Eacott & Norman, 2004) can be represented and communicated to downstream regions to affect behaviour (Fig. 1, left). However, an equally plausible occurrence is that an individual place cell can integrate object and spatial context specificity to form and support episodic representations (Fig 1. right). Such place cells would be prime candidates consistent with indexing theory, except it is content of episodic nature that could define them as putative indices as opposed to 'blindly' performing an indexing computation.

To this end the main goal of these current experiments were to elucidate between these two possibilities (shown in Fig. 1). As previous work has shown that the activity of place cells can be perturbed by objects and can represent object-place memory, one can ask whether and how such single-cell activity will be impacted by a change in spatial context and when introducing an unfamiliar object in the original spatial context (in which an object-place memory may have been formed). For

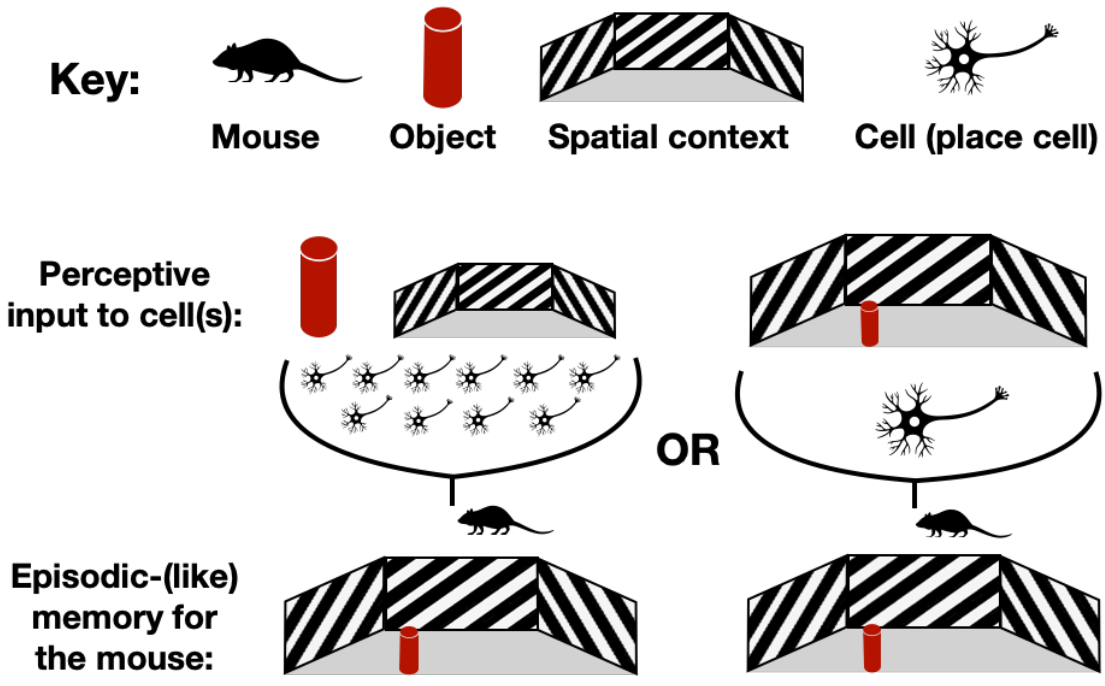


Figure 1. Example schematic of an episode being represented by the neural population or a single cell. Left: some cells represent the object (object-place) and other cells represent the specific spatial context. Thus, as a population a specific object in place and spatial context (episodic content) can be supported. Right: a single place cell that simultaneously integrates a specific object in place and specific spatial context.

example, if a place cell that was perturbed by an object or exhibited an object-place memory was later sensitive to changes in both spatial context and mismatch due to an unfamiliar object being present it could allow one to argue for discrimination of a particular episode (object-place-context integration) by an individual place cell. Thus, recording from place cells in the sequence of these experimental manipulations may offer new insight in further understanding the mechanisms of episodic-(like) memory.

6.2. Methods

6.2.1. subjects

Two B6FVBF1 male mice were bred inhouse at the life science support unit (Durham University, U.K.). At the time of surgery, they weighed 30.1-32.4g and were ~14 weeks of age. They were housed in individual caging and were equipped with a running wheel after surgery. The home room was maintained on a 12h light-dark cycle (lights off: ~09:00 - 21:00h), with daily monitoring of temperature and humidity (20 ± 1°C; 55 ± 10%; respectively). All experiments occurred during their dark phase, and after mice recovered from surgery they were food deprived throughout experiments, maintained on 85-90% weight from their initial baseline free feeding weight. The details of the control mice (not implanted) are reported in Chapter 3 (section 4.4.1.) All experiments were conducted in accordance with the U.K. Animals Scientific Procedures Act (1986), approved by Durham University AWERB and in accordance with the Home Office (procedure licence number: P7B7D2E4B).

6.2.2. Surgery and tetrode implants

Under deep gaseous anaesthesia (isoflurane 1-3%) mice were chronically implanted with two microdrives; one in each hemisphere. In the left hemisphere hippocampal area CA1 was targeted at coordinates 1.8mm medial-lateral and 2.1mm posterior to bregma. In the right hemisphere the dorsal subiculum was targeted (1.8mm M-L, 3.3mm posterior to bregma). Mice were provided with pre- and post-operative analgesia (buprenorphine, 0.1mg/kg), and these custom-made

microdrives allowed four tetrodes (17μm, platinum-iridium, California Fine Wire, U.S.A.) to be lowered vertically using a single cannula. After experiments mice were euthanised with an overdose of sodium pentobarbital and perfused transcardially with saline followed by paraformaldehyde and brains were recovered.

6.2.3. Electrophysiological recording

Mice were given 1 week to recover from surgery before electrophysiological screening began. During screening and intervals between trials mice were placed into a bedded holding cage 45 × 28 × 13cm (l × w × h). Tetrodes were slowly lowered over the course of days and weeks towards the pyramidal layer of the respective regions and were left for ~24-h after being lowered for stabilisation purposes before a recording session began on a given day. The electrophysiological data was acquired via the DacqUSB system (Axona, U.K). Signals from the electrode were passed through the headstage and then pre-amplified (gain 1,000), the recording system then filtered and amplified signals (band pass filter: 500Hz to 7kHz). The sampling rate of channels were continuously monitored at 50kHz and action potentials were stored when the signal had exceeded a given threshold (1ms, 200μs pre- and 800μs post-threshold). Two arrays consisting of infrared light-emitting diodes (LEDs) allowed for tracking of the mice being attached to the head. The tracking hardware and software (DacqUSB) used video camera input, the camera being placed above the behavioural apparatus so that the field of view included the apparatus and holding cage, to calculate the halfway position between the two arrays centred above the skull of the mice. Thus, the position of mice was taken to be this halfway position sampled at 50Hz (offline, TINT, Axona, U.K.).

6.2.4. Apparatus and objects

All experiments took place in the same experimental room and in wooden boxes measuring 40cm^2, (l × w) and 30 or 40cm high. For all spatial contexts a white curtain encircled the box and lamps lit the experimental room (60-100W). Importantly, the curtain was drawn at different distances and lamps were shining at

different directions for certain contexts (Fig. 2A).

For context ‘Grey’ (Fig. 2A, left), the walls were painted in a ‘light rain’ grey and a black runner cloth was hung to what was considered north with respect to the box, acting as a polarised extra-maze cue. Additionally, curtain was drawn so that the computer monitor was visible (which was always in the same position throughout screening and experiments, south-east with respect to the box). Lastly, one of the two lamps was switched-off for this context, with the direction of the switched-on lap being south-west to the box.

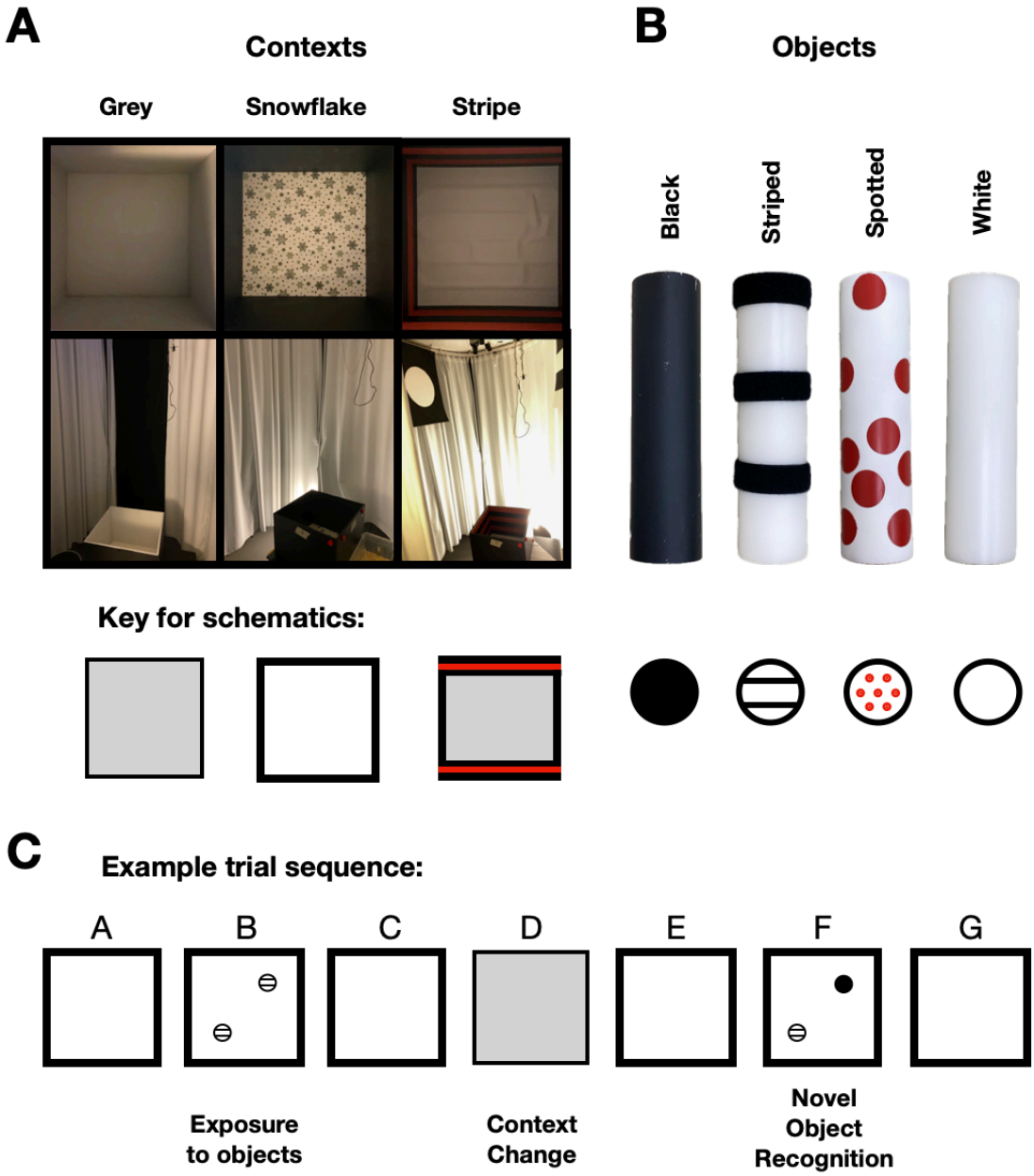


Figure 2. Examples of the spatial contexts, objects and trial sequence used in these present experiments.

For context ‘Snowflake’ (Fig. 2A, middle) this was a different box to context grey and the walls were painted black. In this box walls and floors could be easily inserted and removed. The floor of snowflake consisted of a textured white floor with a snowflake pattern. For the extra-maze cues, the black runner cloth was removed and the second lamp was positioned north-west of the box allowing dappled light to be seen in this direction, with the other lamp remaining in the same position and the encircling curtain more drawn.

Finally, context ‘Stripe’ (Fig.2A, right) was the same box as snowflake, but black and red striped walls were inserted and there was a textured grey Lego floor. The extra-maze cues consisted of polarising cue cards hung up to the east and west of the box (stripe card, east; dot card, west), and the complete white encircling curtain being closed so that the computer monitor and one of the two lamps were no longer visible. The other lamp was placed and face north-east and pointed more upwards allowing more dappled light relative to snowflake.

The objects were all the same size, being cylinders measuring 20cm in length and 5cm in diameter (Fig. 2B). However, objects differed in visuo-tactile features: black, white (a single solid colour, respectively), spotted, (white background with patterned red spots) and striped (white background, with black fluffy Velcro wrapped around in equidistant thirds). There was a minimum of three copies of each object. In object-present trials objects were placed in a diagonal manner with one object being in the north-east (or north-west) and the other south-west (if north-east, but south-east, if north-west). The positioning the objects measured 12cm from the north/south wall and 12cm from east/west wall relative to the object centroid.

6.2.5. Behaviour and trial sequence

6.2.5.1. Implanted mice

At the start of trials mice were placed into the box from the north-east corner and the recording system was initiated. During trials mice foraged for sweetened soya milk which was pipetted quasi-randomly by the experimenter to allow for good spatial coverage, and at the end of each trial mice were removed from the box and place into the holding cage in which trial interval varied between 5-30min (typically

around 10min). This allowed the experimenter to place objects or change the spatial context.

The trial sequence consisted of the following seven consecutive trials, all conducted within the same recording session:

A) Starting baseline trial where the context was empty.
B) Objects-present trial where the same object pair were placed diagonally.
C) Post-objects baseline (and pre-spatial context change baseline, empty).
D) Spatial context change.
E) Post-context change baseline (and pre-novel object trial baseline, empty).
F) Novel object recognition trial: unfamiliar object displaces one object from B.
G) Post-novel object trial baseline, empty.

Thus there were 3 manipulation trials (B,D and F), which each had an pre- and post-manipulation baseline where the spatial context was the original one as the trial sequence had started in A and it was empty. Each trial lasted for 20min and an example trial sequence is shown in (Fig. 2C).

For the novel object recognition trial (F), pipetting of the milk was delayed by 3min to allow mice to freely explore objects and not be distracted by the milk and or experimenter. After such time it was necessary to pipette milk to allow for good spatial coverage. A separate camera to the tracking camera was used to record object exploration behaviour in F. Across sessions the position of the unfamiliar (hence novel) object was counterbalanced across positions within animals.

6.2.5.2. Control mice

As this was a novel experimental design it was important to ascertain whether the post-object exposure trials (C-E) produced mnemonic interference with what mice experienced in the object exposure phase of trial B. Hence, the rationale of this control group of mice was to robustly determine whether mice are successfully able to discriminate the novel object in trial F given these post-object exposure trials, which differs to a typical novel object recognition design (e.g. Ennaceur & Delacour,

1988; Bevins & Besheer, 2006). A control group was also used because implanted mice differed in many ways to control mice. For example, they were not implanted (nor sham controlled), they were not individually housed (same-sex cage groups of 5 for control mice) and they were not food restricted. Control mice had been used in other recognition experiments presented in chapter 3, this those experiments this group of mice had been exposed to different objects, spatial contexts and conspecifics in another experimental room. They had not experienced the specific spatial contexts, objects nor the experimental room before of these currently described experiments. Lastly, approximately ten weeks had elapsed between the end of the chapter 3 experiments and the start of testing in chapter 5.

Control mice were run in a shortened version to that of implanted mice. Thus, while the trial sequence order was the same from A to F, each trial lasted only 10min for control mice (3min for the novel object trial, F). This was interleaved with an 10min interval between trials where they were placed in a holding cage the same specification as implanted mice. An additional camera was set-up above the box to record behaviour which was not used for implanted mice.

In the first session for each mouse it was a novel object recognition test trial in F (as the example shown in Fig. 2C). The spatial contexts used for this novel object recognition session were the Snowflake and Grey contexts and the black and white objects, Fig. 2A-B).

Later, this control group of mice were run in a *control* object recognition session. Where it was the same trial sequence (as the example in Fig. 2C) but objects in trial F (the previous novel object trial) were now the same objects as presented in the exposure phase of trial B. Approximately seven to ten days had elapsed between the novel object recognition session and *control* object recognition session. The spatial contexts used in this *control* object recognition session were context Stripe and Dot, (details of the dot context are not specified as implanted mice were not run in this context. The objects used were the striped and spotted objects.

In both the novel object recognition session and *control* object recognition session the spatial contexts in trial A were novel to the control mice. The order of the spatial context, objects, positions of the objects (i.e., north-east & south-west or

north-west & south-east) and position of the novel object was counterbalanced across animals.

6.2.6. General analytic procedure

The majority of the forthcoming measures were subjected to a repeated measure analysis of variance (ANOVA) examining the effect of 'trial' on a given variable (a non-parametric alternative was used where appropriate). All post-hoc testing was Bonferroni corrected to adjust for multiple comparisons. All other reported inferential statistics are reported as two-tailed tests.

6.2.7. Behavioural recognition analyses

Exploratory behaviour was measured off-line using the video footage of trial F. Active exploratory behaviour was taken to be when the mice were ~2cm of the object and were sniffing, touching, biting, and visibly whisking. The duration of exploration(s) was manually scored by the experimenter unblinded. The D2 calculation was used, resulting in a discrimination score ranging between -1 and 1, where more relative exploration towards the novel object was indicated by positive values toward 1, whereas more relative exploration towards the familiar object was indicated by negative values toward -1. Total exploration time was the total amount of recorded exploration across both objects for a given test trial F.

Both the novel object recognition session and the *control* object recognition session of the control group of mice were compared to the novel object recognition session of the implanted mice (independent samples t-test). When comparing behaviour of the control mice in the novel object recognition session versus the *control* object recognition session mice, the position of where the novel object was in the novel object session was kept the same for the control recognition session when calculating D2 scores (paired t-test).

6.2.8. Cell isolation and analyses of place characteristics

To isolate single units all trials of a given session were loaded into TINT (Axona) forming a merged dataset. Then cluster cutting was performed using principal component analysis by KlustaKwik (v.3., Kadir et al., 2014). Manual adjustments were made where necessary and once cluster cutting of the merged dataset was complete, the cell clusters were then split into individual trials from that session via MultiCutSplitter (Axona, U.K.).

Firing-rate maps for all cells were computed on TINT (Axona). The recording box was divided into a grid of spatial bins (1.1cm^2) considering the number of spikes over occupancy for each bin (spiking and position data were smoothed separately before taking n-spikes over occupancy, boxcar kernel being 5 bins, i.e. each bin being smoothed by the 5 x 5 bins centred on it). The degree of occupancy used for initial edge trimming being 3 bins. Firing rate maps were normalised to the peak rate and displayed with five gradations of firing: red (dark blue) depicts the highest (lowest) ranges of firing rates in each given map. Peak firing in Hz, with peak firing position by pixels coordinates calculated in TINT (730 pixels per 100cm). Overall firing rate (Hz) was taken to be the number of spikes fired by a cell for a given trial divided by the trial time.

Spatial information (bits per spike) of a given unit in each trial was calculated by TINT (Axona), using the Neil Burgess variant of this measure developed by Skaggs and colleagues (Skaggs et al., 1993). This measure calculates information per spike using the animal's position to estimate the mean rate at position x as per the following:

$$I = \int x \int np(x)p(n \mid x)\, log \frac{p(n \mid x)}{p(n)}$$

where n is the number of spikes (with the assumption of a Poisson distribution with a mean varying with location), x being the spatial location, $p(x)$ being the probability of the mouse being at location x and $p(n \mid x)$ is the probability of observing the mouse at location x given n. The Neil Burgess variant was selected over the Skaggs variant because it provided a better continuous measure by yielding fewer false positives of

high spatial information scores where the peak firing rate of a place cell was low (≤ 1Hz). Relative changes in spatial information between consecutive trial-pairs was the subtraction of spatial information scores of a given trial from the spatial information scores of the previous trial (within-cells).

A cell's spatial stability was assessed by correlating rate maps across trials generating a Pearson's correlation coefficient for a pair of trials (within-cells). Bins corresponding to locations in the box where the mouse did not visit in either trial were not considered to mitigate spurious estimates of the correlation coefficient. The same was completed for between-cell pairs of the same trial (between cells of the same recording session).

A correlation of spike times between-cell pairs was also conducted, binning spike times into 1s bins by trial per cell. Bins where neither cell fired were not considered again to mitigate spurious estimates of the correlation coefficient. To obtain a measure somewhat separate to spatial modulation, inter-spike intervals were used to see whether and how this differed across trials as it has been suggested that shorter intervals between spikes may convey salient information more rapidly to downstream regions (Harris et al., 2001; Zhao et al., 2022). The difference in spike times between consecutive spikes was calculated separately for each trial per cell and the probability density was computed (75 bins, 4ms per bin, 4-300ms). These probability densities were then averaged across all cells separately for each trial.

Fifty-six candidate units were identified based upon the aforementioned cell insolation procedure across sessions. For each trial the lower quartile was calculated from cells' spatial information scores and then averaged across trials to form a threshold spatial information score (0.348). Units that had a spatial information score ≤ 0.348 for 5 out of the 7 trials were excluded. These cells were examined for whether largest field had a firing rate ≥ 1Hz and was ≥ 5 contiguous bins (based upon peak firing rate from rate maps, for at least 4 out of 7 trials). Cells were also excluded if they had no discernible place field in the starting trial A (according to the above requirements derived from the rate maps). Across sessions this resulted in 36 place cells being accepted for analyses (29 cells in mouse 1 across four sessions and 7 cells in mouse 2 across two sessions).

6.2.9. Remapping analyses

For position-based remapping, the position of the peak firing rate for each trial per cell was taken and the Euclidean distance between field peak positions across trials were calculated. A shift above the threshold of 8cm was considered to be a meaningful shift of field. Vandrey and colleagues (2021) had implemented a 7.5cm threshold in a 60cm^2 (l × w) box, hence if one scaled down to the 40cm^2 box as used for these current experiments this would result in a 5cm threshold (by Vandrey et al., 2021 standards). Thus, an 8cm threshold can be considered as a conservative threshold. Some manual adjustments were made when cells had multiple fields to allow comparison between the same fields. As consistent with previous research some cells developed new fields when the objects were present (e.g., in the first objects present trial B) and occasionally peak firing was positioned in these new fields as opposed to a pre-existing field from a previous baseline trial (e.g., trial A). Therefore, a peak position was manually selected from the approximate centroid of a (pre-existing) place field to ensure comparison between the same field (and not a newly developed field). To assess whether and how cells peak firing rate fields had shifted relative to the novel object and familiar object in trial F, the peak firing rate position of cells in trial E and G were compared relative to the object centroids of where they would be (and were) positioned in F (calculated using Euclidean distance).

Rate remapping took the peak firing rate of a manipulation trial per cell (that is trial B, D and F) and compared it relative to the average peak firing rate of pre- and post-manipulation trials (trials A and C for trial B; trials C and E for trial D; trials E and G for trial F). A threshold of ⅓ fold Δ (increase or decrease) was considered to be a meaningful rate change (also used for the overall firing rate). Cells were first tested against these position-based and rate remapping thresholds as a group. Then a pre- to post- manipulation trial sequence breakdown was realised, where cells that discriminated trial B from baselines trials A-C, moved onto C-E and if they discriminated trial D from baseline trials C-E, they moved onto E-G. Thus, those cells that discriminated trial F from baseline trials E-G resulted in a subgroup of cells that

discriminated all manipulation trials from pre- and post-manipulation trials via remapping mechanisms (applying the same aforementioned thresholds). This was done to better ascertain whether any common pattern or patterns of discrimination could be observed. Any such patterns might have been obscured by analyses including non-discriminating cells. Thus, a total of 17 cells (out of a possible) 36 remained in this subgroup of 'discriminating cells', (fourteen cells from mouse 1 and three cells from mouse 2).

6.3. Results

6.3.1. Implanted mice exhibited variable object recognition behaviour

The object recognition behaviour of the implanted mice in trial F was greatly variable and not suggestive of novelty-biased exploration (Fig.3A-B; D2 score: M = -0.36, SD = 0.52, four sessions from mouse 1, two from mouse 2, no different from chance performance, $t_{(5)} = -1.70$, $p = 0.15$, one sample t-test against zero).
The trial sequence of the recording procedure involved post-object sessions where the environment was empty and included a spatial context change session before novel object recognition (NOR) test in trial F (Fig. 2C). This differs from typical NOR paradigms that typically include a single exposure session, delay, and test session (e.g. Ennaceur & Delacour, 1988; Bevins & Besheer, 2006). To this end, a separate group of control mice that were not implanted (n = 10), were ran in the same trial sequence (trial A to F, as an example shown in Fig. 2C). This was to ascertain whether post-object trials (trials C-E) may have been producing mnemonic interference for the implanted mice from the objects they had experienced in the initial object exposure phase of trial B. Yet, in contrast to the two implanted mice, these control mice were found to display recognition behaviour significantly differing to chance performance of zero, in favour of novelty-based exploration (Fig. 3A; D2 score: M = 0.25, SD = 0.35; $t_{(9)} = 2.28$, $p = 0.049$, $d = 0.72$). Accordingly, it seemed that for the control group of mice that were not implanted they could successfully discriminate the unfamiliar (hence novel) object in trial F, initially suggesting that the post-object trials were not profoundly producing mnemonic interference for mice.

In a separate *control* OR session for the control group of mice, where the objects in trial F were the same as that experienced in trial B, control mice showed no exploratory preference toward a particular object in this *control* OR session (Fig.

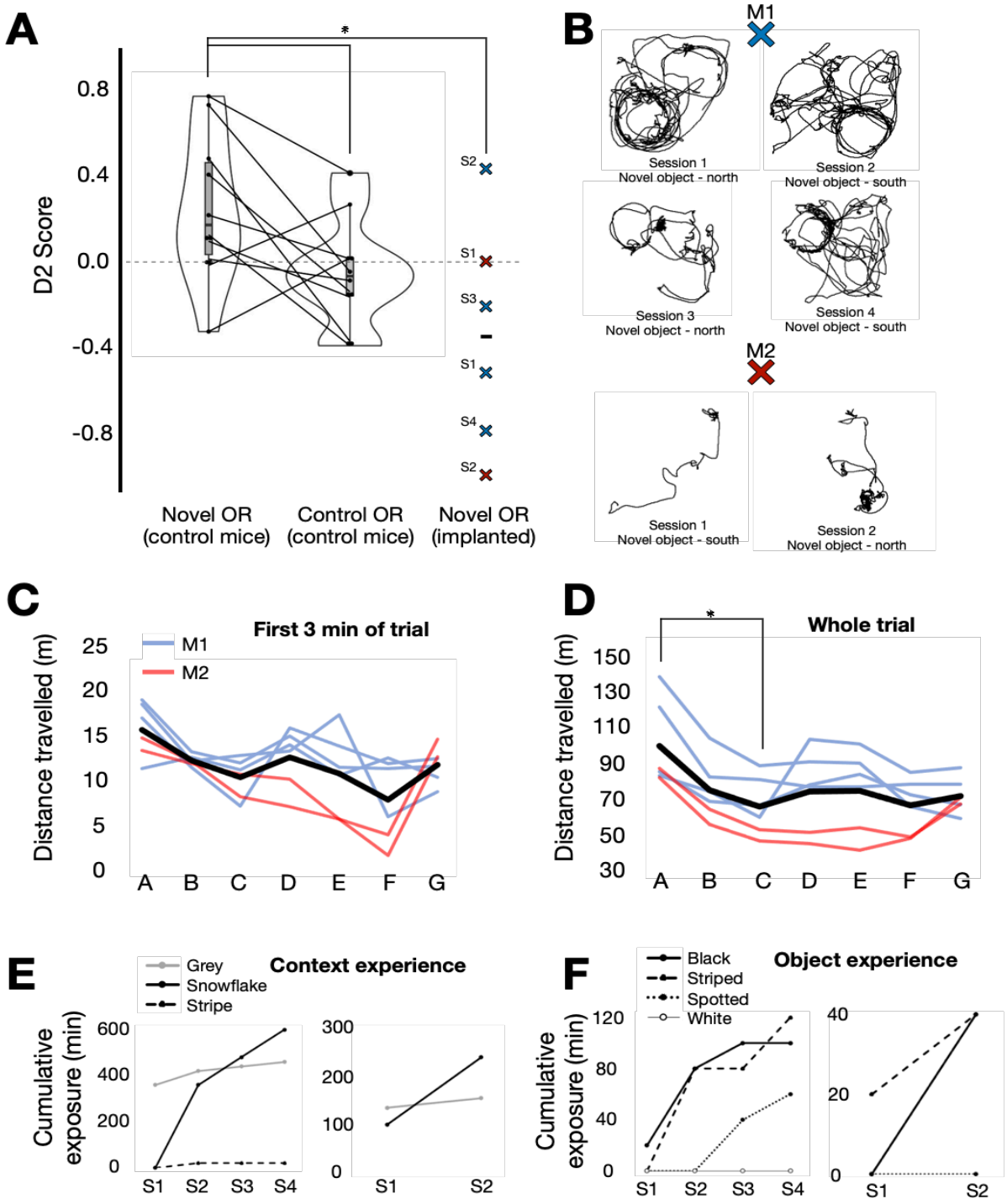


Figure 3. Behavioural results. **(A)** Novel object recognition (NOR) of the implanted and control mice in trial F. Far right: the crosses denote implanted mice (blue is mouse 1, red is mouse 2 and the black line is the mean). **(B)** Example paths of the mice during NOR by session (first 3min of the trial). **(C)** Distance travelled (m) for the first 3min of each trial. **(D)** Same as C but for the entire 20min of the trial. **(E)** Spatial context experience over time (dots denote experience before the session, left M1, right M2). **(F)** Same as E but for objects. *$p < 0.05$

3A; D2 score: M = -0.05, SD = 0.25, $t_{(9)}$ = -0.62, p = 0.55). Indeed, the D2 score was significantly greater in the NOR session of the control mice versus the *control* OR session ($t_{(9)}$ = -2.25, p = 0.043, d = 0.74, paired t-test, with comparable exploration levels across the sessions, NOR: M = 51.76s, SD = 24.45s, Control OR: M = 87.57s, SD = 45.15s, $t_{(9)}$ = -2.10, p = 0.07, d = 0.67). When comparing the NOR sessions of implanted mice versus the NOR sessions of the control not implanted mice, the D2 score was significantly greater in favour of the control group of mice ($t_{(14)}$ = -2.84, p = 0.013, d = 1.46; with comparable exploration levels, implanted mice: M = 33.02s, SD = 30.86s, $t_{(14)}$ = -1.35, p = 0.20). Whereas in contrast, the D2 scores between the *control* OR session of the control group of mice and the NOR sessions of the implanted mice were comparable ($t_{(14)}$ = -1.63, p = 0.13; with control mice showing greater exploration levels on average, $t_{(14)}$ = -2.60, p = 0.021, d = 1.34). Taken together, it can be concluded that mice are generally able to successfully discriminate the novel object in trial F (Fig. 3A) in the currently used trial sequence design (Fig. 2C).

The distance travelled in the first three minutes of the implanted mice was compared across all the trials of the A-G trial sequence (Fig. 3C), as this related to a timeframe in which object exploratory behaviour was analysed for NOR discrimination. A repeated measures ANOVA initially yielded an overall significant effect of 'trial' (i.e., trial A to G; $F_{(6,30)}$ = 4.02, p = 0.005, η_p^2 = 0.45). However, post-hoc comparisons revealed no particular differences between trials (all $p \geq 0.16$). Moreover, when considering whole-trial distances travelled across all the trials (Fig. 3D), there was also an overall significant effect ($F_{(6,30)}$ = 4.47, p = 0.002, η_p^2 = 0.47). Post hoc tests showed that significantly less distance was travelled in trial C, the post-object baseline trial (65.93m) versus trial A, the very first, and pre-object, baseline trial (99.82m, p = 0.016, there were no differences between other trial by trial comparisons, $p \geq 0.06$). This may indicate that implanted mice habituated to some initial novelty of the recording task. Lastly, figure 3 (E-F) shows the experience of contexts and object separately for each mouse over the course of recording sessions.

Overall these results suggest that in this trial sequence used for these experiments (Fig. 2C), it is possible for mice to be able to successfully recognise the

novel object in trial F from the familiar objects experienced in B (exhibited via novelty-based exploration; Fig., 3A). This would suggest that the post-object trials C to E were not profoundly producing mnemonic inference. However, implanted mice showed great variability in their recognition exploratory behaviour. As previously mentioned in the methods section (6.2.5.2), there were numerous differences between implanted mice and the control group mice. 1) Implanted mice were exposed to each trial twice as long as control mice to allow good spatial coverage for place cell interpretation, potentially being more fatigued than control mice. 2) In combination with 1, implanted mice were also food restricted and during trials were encouraged to forage for milk, again aiming to allow for good spatial coverage (although notably, in trial F milk was not given for the first 3 minutes). 3). Control mice were housed in cage groups of 5, whereas implanted were solitary caged (to mitigate damage to the implant). Thus, any one or a combination of these reasons could have contributed to the variability of the implanted mice object recognition behaviour relative to the control mice.

6.3.2. The presence of objects mediated spatial information loss by the cells over the course of the trial sequence

Across 6 recording sessions of the 2 mice, a total of 36 cells were analysed. The spatial information (SI) properties of these cells across trials were initially assessed (see methods, section 6.2.8.). There was an overall effect of 'trial' in changes of cells' SI scores (bits/spike), across trials (Fig. 4A; $\chi^2_{(6)} = 16.88$, $p = 0.01$) with the SI score being significantly greater in trial A (Mdn = 0.66 bits/spike, SD = 0.39 bits/spike), the very first pre-object baseline trial, versus trial D (Mdn = 0.44 bits/spike, SD = 0.40 bits/spike), the spatial context change trial, and trial F, the NOR trial (Mdn = 0.48 bits/spike, SD = 0.38 bits/spike, $p = 0.027$, $p = 0.033$, respectively. All other trial comparisons $p \geq 0.06$). Indeed, relative changes of cells' SI scores between consecutive trial pairs showed that there was a significant reduction in SI compared to chance from trial E (the post-spatial context change but pre-NOR baseline trial) to trial F, the NOR trial (Fig.4B; M = -0.09 bits/spike, SD = 0.25 bits/spike, $t_{(35)} = -2.26$, $p = 0.03$, $d = 0.38$, one sample t-test against zero). There

were no differences between other consecutive trial pairs and chance being zero (all $p \geq 0.07$), nor differences from each other ($F_{(2.73,95.55)} = 2.38$, $p = 0.08$, $\eta_p^2 = 0.06$, all post-hoc comparisons $p \geq 0.15$). Lastly, the net SI change from trial A to G, that is the sum of the changes across consecutive trial pairs, was negative (M = -0.19

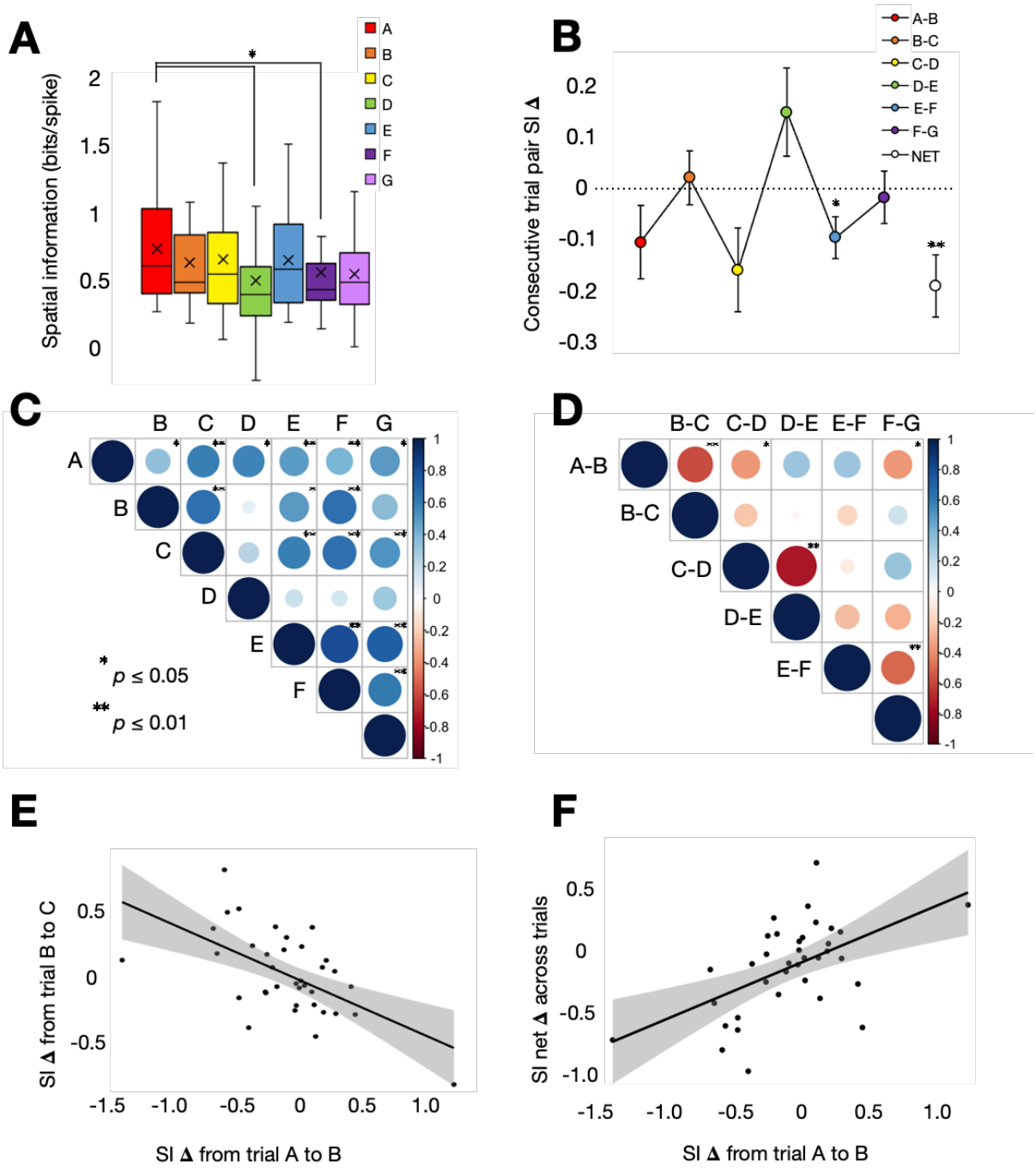


Figure 4. Spatial information results across all cells. **(A)** Spatial information (SI) by trial (bits per spike). **(B)** Relative changes in SI scores between consecutive trial pairs. Dotted line denotes zero and error bars denote ±1 SEM. **(C)** Correlogram of SI scores by trial-pair. **(D)** Same as C but for the difference between consecutive trial-pairs. **(E)** Example correlation between relative SI change from trial A to B plotted against relative SI change from trial B to C. **(F)** Example correlation between relative SI change from trial A to B plotted against net SI change across trials. *p ≤ 0.05 **p ≤ 0.01

bits/spike, SD = 0.36 bits/spike) and differed significantly from chance ($t_{(35)}$ = -3.09, p = 0.004, d = 0.52, one sample t-test against zero). Altogether, this suggested that on average there was a reduction of SI from trial A to G, mediated particularly by the spatial context change manipulation (in trial D) and introduction of an unfamiliar object (i.e., NOR) in trial F.

To further explore the relationship between SI scores across trials and the net reduction of SI, correlations were performed between trials and consecutive trial pairs (Fig. 4C-D). The SI scores of cells across trials were generally moderately to strongly positively correlated (R ranged from 0.35 to 0.80, excluding correlations involving trial D), suggesting that cells that had a greater SI score in certain trials tended to have greater SI score in other trials. There was a noticeable exception for correlations involving trial D, the spatial context change (R ranged from 0.09 to 0.56), a preliminary indication that cells were remapping between spatial contexts.

When correlating consecutive trial pairs, there were some moderate to strong negative relationships between some consecutive trial pairs and preceding consecutive trial pairs e.g., the starting pre-object baseline trial and the first objects present trial (A-B) against trial B and the post-object, but pre-spatial context change, baseline trial C (Fig. 4E). This suggested that cells which showed a decrease in SI from, for example trial A to B, tended to show an increase in SI from trial B to C. Conversely, cells which showed an increase in SI from trial A to B tended to show a decrease in SI from trial B to C. In other words, if the presentation of objects reduced a cell's SI, removing objects tended to increase the SI again. Similarly, if object presentation increased a cell's SI, removing the objects tended to reduce the SI again. Despite the consecutive trial pair of E to F yielding the only robust change relative to chance, it did not correlate with net change ($r_{(34)}$ = -0.016, p = 0.42). However, change in SI from trial A to B and trial D to E did positively correlate significantly with net change (Fig. 4F; $r_{(34)}$ = 0.54, $p < 0.001$; $r_{(34)}$ = 0.35, p = 0.036, respectively, all other correlations $p \geq 0.20$). Indeed, change from trial D to E also significantly predicted net change from trial A to G, but only accounted for 12% of the variance ($F_{(1,35)}$ = 4.77, p = 0.036, R^2 = 0.12, β = 0.35, t = 2.18, p = 0.036, simple linear regression). On the other hand, change in SI from trial A to B significantly predicted net change accounting for 29% of the variance ($F_{(1,35)}$ = 14.14, $p < 0.001$,

$R^2 = 0.29$, $\beta = 0.54$, $t = 3.76$, $p < 0.001$,).

Finally, a linear regression model including changes in SI from trials C-D, D-E, E-F and F-G accounted for 49% ($F_{(4,35)} = 7.44$, $p < 0.001$, $R^2 = 0.49$, D-E: $\beta = 1.18$, $t = 4.77$, $p < 0.001$, F-G: $\beta = 0.75$, $t = 4.28$, $p < 0.001$; E-F: $\beta = 0.72$, $t = 3.79$, $p < 0.001$; C-D: $\beta = 0.55$, $t = 2.54$, $p = 0.016$). Yet, strikingly, a model with only changes in SI from trial A to B and trial E to F also significantly predicted net change accounting for 50% of the variance ($F_{(2,35)} = 16.39$, $p < 0.001$, $R^2 = 0.50$, A-B: $\beta = 0.72$, $t = 5.44$, $p < 0.001$, E-F: $\beta = 0.49$, $t = 3.67$, $p < 0.001$). Hence, transitions only from preceding empty context trials to object present trials (A-B and E-F), predict as much variance in cells' overall net SI change, compared to when considering transitions from C-G, more than half of all consecutive transitions. Taken together as a whole group of cells, the relationship between pre-object and object-presence trials was particularly powerful in explaining net SI change across the trial sequence. Thus, in summary, the presence of objects tended to reduce the SI of place cells on average. This could be explained by the fact that objects suppressed pre-existing place fields or developed new place fields.

6.3.3. Positional remapping changes: a strong effect of spatial context change

The next step in the analyses examined whether the group of place cells (n = 36) could use positional remapping changes to discriminate the object and spatial context manipulation trials (B, D and F) from pre- and post-empty baseline trials (A,C, E and G). On average fields shifted significantly relative to chance (taken to be an 8cm threshold, see methods) in consecutive trial transitions from the starting pre-object baseline trial A to trial B, the first objects present trial (Fig. 5A; Mdn = 12cm, SD = 12cm, $Z = 2.23$, $p = 0.026$, r = 0.37, one sample t-test against a value of 8). Fields also shifted significantly relative to chance in the post-object but pre-spatial context change baseline trial C to trial D, the spatial context change trial (Mdn = 18cm, SD = 10cm, $Z = 4.36$, $p < 0.001$, r = 0.73) and trial D to trial E, the post-spatial context change but pre-NOR baseline trial (Mdn = 18cm, SD = 10cm, $Z = 4.33$, $p < 0.001$, r = 0.72). All other transitions between consecutive trials did not yield a

significant shift in field. $p \geq 0.08$). This suggested that as a group of cells, the first objects present trial B could be discriminated relative to the pre-object baseline trial A via position-based remapping of place fields. Similarly, as a group of cells the spatial context change trial D could be discriminated from the pre- and post-baseline trials (C and E) position-based remapping of place fields.

When comparing consecutive trial pairs across the entire trial sequence (A-B to F-G), there was a significant overall effect ($\chi^2_{(5)} = 15.93$, $p = 0.007$), with the above-mentioned field shifts in D-E being significantly greater than in the post-spatial context change but pre-NOR baseline trial E to trial F, the NOR trial (Fig. 5A; Mdn = 5cm, SD = 9cm, $p = 0.008$, all other comparisons $p \geq 0.06$). In other words, place fields shifted to a greater extent on average when returning to the original spatial context (D to E) that the trial sequence had begun in (i.e., that of trial A-C) more than when an unfamiliar object and familiar object was introduced in the NOR trial F. Thus, this suggested a preliminary indication that the spatial context change manipulation produced stronger remapping effect than the NOR manipulation.

Lastly, there were no significant shifts in fields between consecutive empty baseline trials (A-C, C-E and E-G) relative to the 8cm threshold (Fig. 5B; all $p \geq 0.46$, nor were there differences between them, $\chi^2_{(2)} = 3.38$, $p = 0.18$, all pairwise comparisons, $p \geq 0.23$). This preliminarily indicated that on average there was good spatial stability of place fields between baseline trials.

6.3.4. Rate-based remapping: a strong effect of spatial context change but not for object presence

Here the next set of analyses focused upon rate-based remapping, where place cells may differentiate certain trials using changes in their firing rate (that is, change in their peak firing rate or overall firing rate, Hz, methods section 6.2.8-to-9).

There were no changes in peak firing rate on average across trials ($\chi^2_{(6)} = 7.74$, $p = 0.26$, all post-hoc comparisons were $p \geq 0.32$). However, in terms of overall firing rate there was an overall significant effect of trial ($\chi^2_{(6)} = 20.92$, $p = 0.002$). Post-hoc comparisons showed that there was a significantly greater firing rate in the first objects present trial B (Mdn = 0.74Hz, SD = 0.72Hz) relative to the post-object

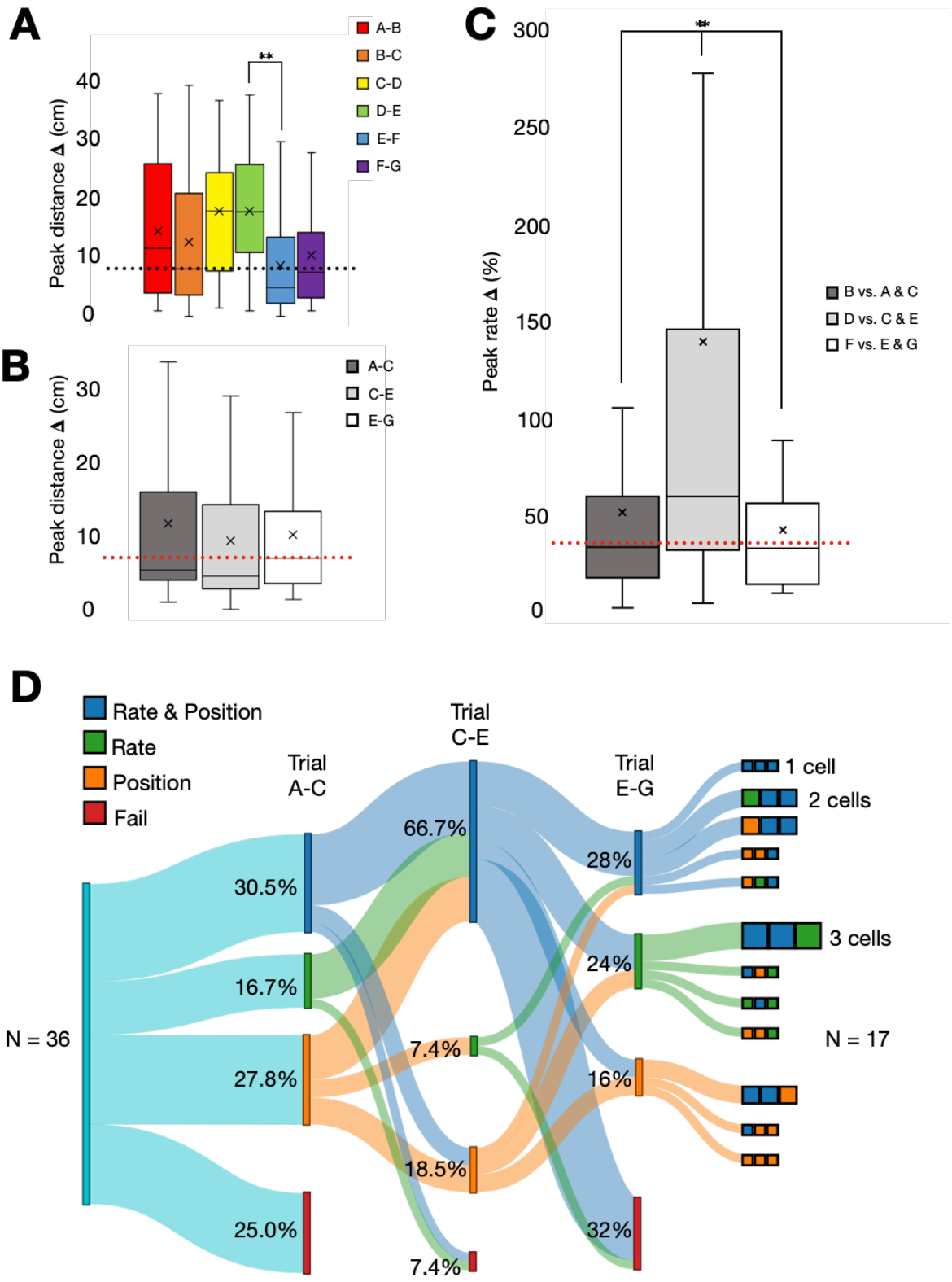


Figure 5. Position-based and rate-based remapping results across all cells. **(A)** Position of peak firing change between consecutive trial-pairs (cm). Dotted line denotes 8cm threshold. **(B)** Same as A but between consecutive baseline (empty trials). **(C)** Peak firing rate changes (Hz) between manipulation trials relative to pre- and post-baseline trials. Dotted line denotes 33.33% threshold. **(D)** Sankey plot displaying the proportion of cells that passed discrimination of manipulation trials from pre- and post-threshold baselines (i.e. showed above-threshold remapping). $^{**}p \leq 0.01$

but pre-spatial context change baseline trial C (Mdn = 0.52Hz, SD = 0.55Hz, p = 0.009). Also, the overall firing rate of trial B was also significantly greater than that of trial D, the spatial context change trial (Mdn = 0.60Hz, SD = 0.80Hz, p = 0.025). Indeed, the overall firing rate of trial F, the NOR trial, (Mdn = 0.88Hz, SD = 0.55Hz) was also significantly greater than that of trial C (p = 0.033, all other comparisons, p $p \geq 0.08$). This initially suggested that rate-base changes in overall firing rate could be used discriminate certain trials, with a tendency for the average overall firing rate to increase in the objects present trial B and (NOR) trial F (relative to trial C and trial D).

As previously mentioned, the A to G trial sequence design sandwiched manipulation trials (B, D and F) in between pre- and post-baseline trials (A, C, E and G), where the spatial context was empty (Fig. 2A). Therefore, one can ask whether there was a significant rate change, regardless of rate increase or decrease (using a ⅓ fold Δ threshold) when averaging across pre- and post-baseline trials relative to the manipulation trial in between them (i.e., B vs. A and C; D vs. C and E; F vs. E and G). Thus, potentially allowing rate-based remapping to discriminate manipulation trials from pre- and post-baseline trials. Despite the above mentioned trial differences regarding the overall firing rate, examining rate-remapping in this way showed that the overall firing rate of cells (n = 36) could not discriminate manipulation trials from their pre- and post-baseline trials (trial B: Mdn = 31.4Δ%, SD = 27.7Δ%; trial D: Mdn = 32.5Δ%, SD = 109.6Δ%; trial F: Mdn = 22.5Δ%, SD = 39.9Δ%; Z = -0.99, p = 0.32; Z = 1.10, p = 0.27; Z = -1.54, p = 0.12; respectively, one-sample Wilcoxon signed rank test against ⅓). Interestingly, however, the overall firing rate change relative to pre- and post-baseline trials was greater in trial D, the spatial context change trial versus the NOR trial F ($\chi^2_{(2)}$ = 10.06, p = 0.007, post-hoc comparison, p = 0.007. No other significant comparisons, $p \geq 0.08$). In brief, although one could not discriminate manipulation trials from pre- and post-baseline trials using overall firing rate (relative to a ⅓ fold threshold) there were hints that the spatial context change (trial D) elicited a stronger rate-remapping effect. This was indicated by the great variance in rate change of trial D and that its change was significantly greater than that of trial F.

When assessing rate-based remapping using peak firing rate, it was found

that the peak rate change was significantly above the ⅓ fold threshold for the spatial context change trial D (Fig. 5C, Mdn = 57.2Δ%, SD = 188.1Δ%, $Z = 3.41$, $p < 0.001$, r = 0.57, one-sample Wilcoxon signed rank test against ⅓). Yet, in contrast, there were no peak rate change differences in first objects present trial B versus an average of A and C (Mdn = 31.3Δ%, SD = 57.1Δ%), nor in F versus an average of E and G (Mdn = 30.5Δ%, SD = 32.1Δ%, all $p \geq 0.67$). Lastly, the relative rate change in trial D was greater than in B and F, ($\chi^2_{(2)} = 12.06$, $p = 0.002$, post-hoc comparisons $p = 0.01$, $p = 0.007$, respectively. No difference between B and F, $p = 1.00$). Again, an indication of stronger spatial context remapping versus the object manipulations.

In overall summary of the remapping results, there was evidence of remapping between spatial contexts as indexed via position- and rate-based remapping (when using peak firing rate). This was also preliminarily reflected in the SI score analyses and overall suggests that as a group of cells, there was clear discrimination between spatial contexts. There was some evidence of discrimination of the first objects-present trial from the preceding baseline (i.e., A from B) in terms of position-based remapping, but not rate-based remapping. Finally, there was no discrimination of the latter objects-present trial (F) from the pre- and post-baseline trials (E and G, respectively) as a group of cells.

To follow on from these group-level cell analyses, cells that did not have above threshold position and peak rate changes were filtered out versus cells that did, resulting in a sub-group of place cells that discriminated all manipulation trials relative to pre- and post-baseline trials (see Fig. 5D). One key motivation in looking at this ‘discriminating’ sub-group of place cells was to ask if a common pattern or patterns of discrimination could be observed. Any such patterns might have been obscured by analyses including non-discriminating cells. In this way, it resulted in total of 47% of cells (n = 17/36) that successfully discriminated all manipulations from baseline trials, hence subsequent analyses focused upon these cells (Fig. 6, displays example discriminating cells and non-discriminating cells from the same recording session).

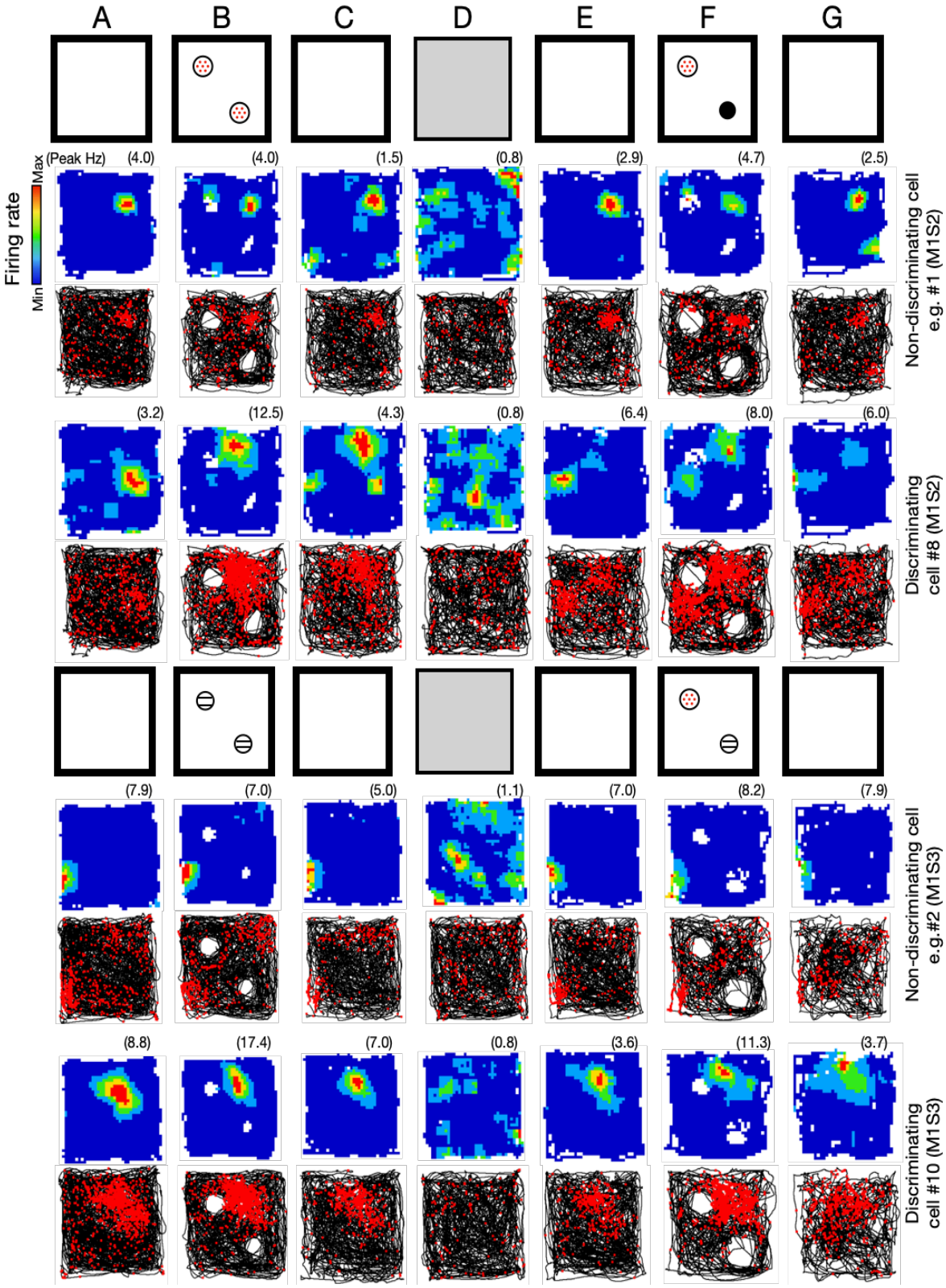


Figure 6. Example discriminating cells that did and did not pass all discriminations of manipulation trials from pre-baseline and post-baseline trials. Each row is a cell. Upper: shows cell rate maps by trial with five gradations of firing rate (red denotes the firing rate peak, Hz, in the brackets). Lower: shows mouse's path in black with all spikes of the cell during the trial overlayed in red.

6.3.5. The discriminating sub-group: again a loss of spatial information over course of trial sequence

Reanalysis of SI scores in these sub-group of cells, showed that there was a significant overall effect ($\chi^2_{(6)} = 13.49$, $p = 0.036$). Post-hoc test revealed greater SI scores in the very first pre-object baseline trial A (Fig. 7A; Mdn = 0.88 bits/spike, SD = 0.42 bits/spike) relative to the NOR trial F (Mdn = 0.53 bits/spike, SD = 0.22 bits/spike, $p = 0.018$, all other comparisons $p \geq 0.12$). Relative changes of cells' SI between consecutive trial pairs showed that there was a significant difference to chance from trial A to trial B, the first objects present trial (Fig. 7B; M = -0.24 bits/spike, SD = 0.44 bits/spike, $t_{(16)} = -2.25$, $p = 0.039$, $d = 0.55$, one sample t-test against zero). Yet, all other consecutive trial pairs showed no difference to chance (all $p \geq 0.13$), nor from each other ($F_{(2.56, 41.01)} = 1.83$, $p = 0.16$, $\eta_p^2 = 0.10$, post-hoc comparisons all $p \geq 0.47$). However, similarly to when all cells were considered, these discriminating sub-group of cells again showed a significant net reduction of SI across trials A to G (M = -0.29 bits/spike, SD = 0.41 bits/spike, $t_{(16)} = -2.94$, $p = 0.01$, $d = 0.71$, one sample t-test against zero). Indeed, again as was observed when considering all cells, change in SI from trial A to B of discriminating cells was significantly positively correlated with cell's overall net change $r_{(15)} = 0.48$, $p = 0.05$, with SI change from trials A to B being able to significantly predict net change accounting for 23% of the variance in overall net change ($F_{(1,16)} = 4.56$, $p = 0.05$, $R^2 = 0.23$, $\beta = 0.48$, $t = 2.14$, $p = 0.05$, simple linear regression). Thus, this suggested that similarly to the when the entire group of cells were analysed, the transition from the very first pre-object baseline trial A to trial B, the first objects present trial, was important in determining the overall net SI change of cells across all trials. Again, this is suggestive of the objects in trial B perturbing pre-existing place field and or eliciting the generation of new place fields. An example of place field suppression is displayed in upper Fig. 7C, where in trial A the SI score for this place cell was 1.06 bits/spike which reduced to 0.48 bits/spike in trial B. And an example cell that developed a new object-related place field in trial B, which was not present in trial A is displayed in lower Fig. 7C (the SI score for this cell in trial A was 1.87 bits/spike which reduced to 0.46 bits/spike in trial B). Such object related changes are in

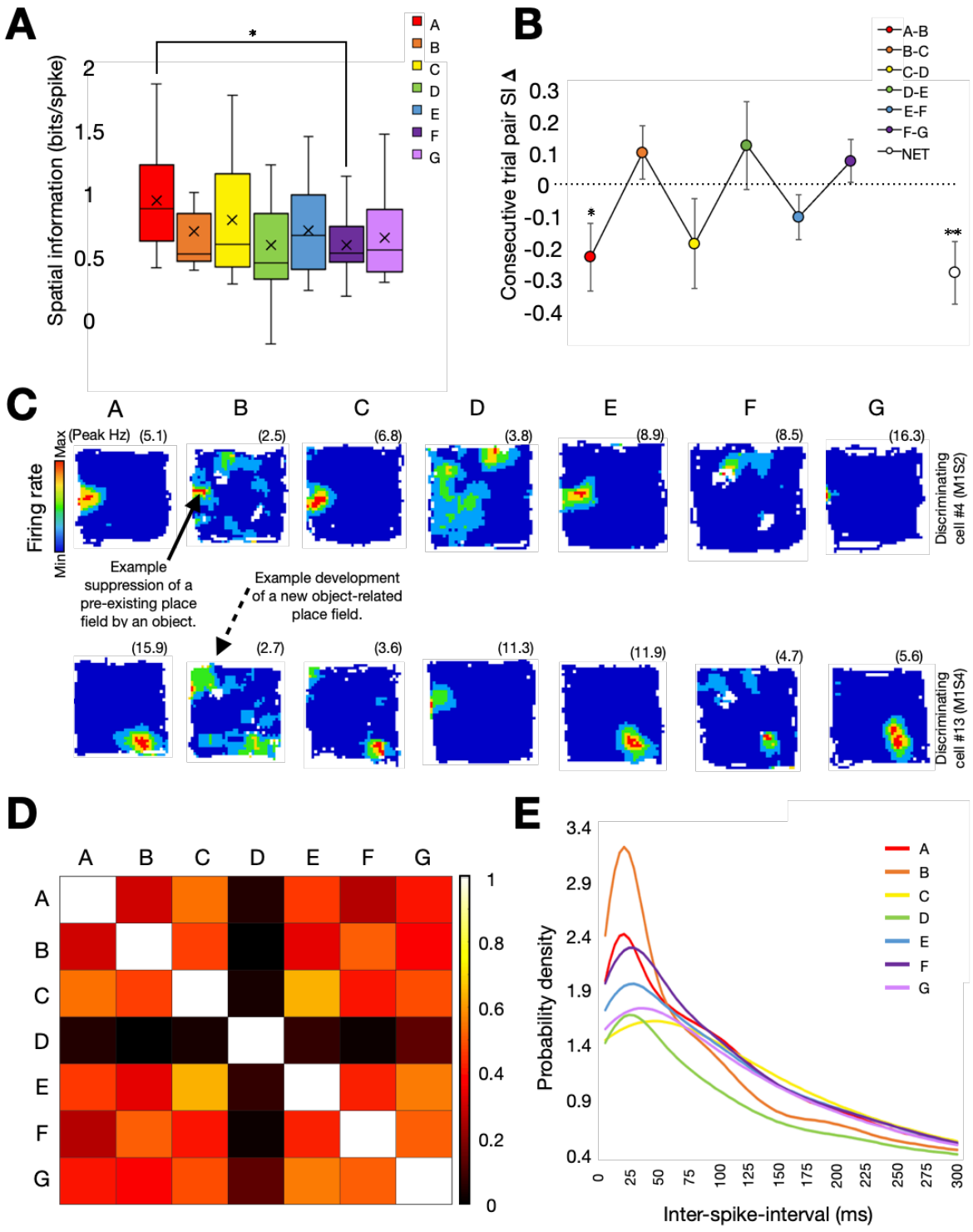


Figure 7. Properties of the sub-group of discriminating place cells. **(A)** Spatial information (SI) scores by trial (bits per spike)**. (B)** Relative changes in SI scores between consecutive trial-pairs. Dotted line denotes zero and error bars denote ±1 SEM. **(C)** Upper: example rate maps of a discriminating place cell whose pre-existing place-field from trial A was suppressed by the first presentation of objects in trial B (solid black arrow, note the reduction in peak firing rate, Hz). Lower: example place cells who putatively developed a new object-related place field in trial B that was not present in trial A (dashed black arrow). **(D)** Correlation matrix displaying the average spatial stability across trials (from within-cell rate map Pearson's correlations). **(E)** Probability distributions of inter-spike-interval averaged across cells. *$p \leq 0.05$ **$p \leq 0.01$

accordance with previous research (e.g., Rivard et al., 2004; Burke et al., 2011; Vandrey et al., 2021).

6.3.6. The discriminating sub-group: changes in spatial stability and the intervals between cell's spikes across trials

Spatial stability of the sub-group of cells was next assessed. This was realised by correlating a given cell's trial rate map against other trials (see methods, section 6.2.8. for more details). There an overall effect of trial pairings on the spatial stability of cells (Fig. 7D; $F_{(20,320)} = 16.60$, $p < 0.001$, $\eta_p^2 = 0.51$). Post-hoc comparisons showed that stability in trial A-B (M = 0.31) was significantly lower than between baseline trials A-C (M = 0.54, $p = 0.032$) and trials C-E (M = 0.64, $p = 0.033$), and in general, stability between a given trial and trial D were significantly lower that stability between other trials (see supplementary table 1). Thus, consistent with the remapping and the above SI analyses, this shows that place cells were less spatially stable and consequently less spatially informative when transitioning from the very first pre-object baseline trial A to the first objects present trial B (relative to the pre- and post-baseline trials in between trial B, that is, trials A and C).

A complementary analysis next looked at the probability density of inter-spike-intervals across trials, where it has been previously suggested that when place cells fire with a shorter latency between spikes this may more rapidly convey salient information to downstream regions (Harris et al., 2001; Zhao et al., 2022). Indeed, it was found that there was an overall significant effect of trial (Fig. 7E; $\chi^2_{(6)} = 265.98$, $p < 0.001$), with all post-hoc comparisons displayed in supplementary table 2. In brief, the main post-hoc comparative findings were that the probability density distribution (as a function of inter-spike-interval) for the first objects present trial B differed significantly from trial A, C, D, E and F (all $p < 0.001$, the distribution between trial B vs G were comparable, $p = 1.00$). Also, the probability density distribution of the spatial context change, trial D, differed from all other trials (all $p < 0.001$). This is interesting because in this sub-group of discriminating cells the overall firing rate across trials was comparable ($F = _{(6,96)} = 1.81$, $p = 0.11$, $\eta_p^2 = 0.10$, all post-hoc comparisons, $p \geq 0.32$). And similarly, the peak firing rate across trials was

comparable ($F_{(6,96)} = 0.85$, $p = 0.54$, $\eta_p^2 = 0.05$, all post-hoc comparisons, $p \geq 0.47$).

Altogether, this shows that despite no rate-based changes on average in this sub-group of discriminating cells, there was seemingly a greater likelihood of there being a shorter latency between spikes on average (peaking at ~20-25ms) in the first objects present trial B versus all other trials (bar trial G). On the other hand, there was generally a lower probability density for trial D, the spatial context change trial relative to all other trials. This latter result is consistent with the effect of strong remapping between spatial contexts. However, the former result regarding the first objects present trial B is adds an interesting detail in the context of the above reported results. Specifically, this sub-group of discriminating cells became less spatially informative when transitioning from the first baseline pre-object trial A to trial B (Fig. 7B-C). Which was mirrored in a reduction in place field stability between trial A and B (vs. trial A-C, Fig. 7D and supplementary table 1). However, this was accompanied by there being a shorter time between spikes (as seen by a disproportionate, increased probability density of inter-spike-intervals, < 25ms, Fig. 7E) relative to other trials, despite the overall firing rate and peak firing rate remaining comparable across trials. Thus, this may corroborate with the idea that because of the shorter average latency between spikes, the first presentation of objects in trial B was a salient information change that needed to be rapidly conveyed to downstream regions (Harris et al., 2001; Zhao et al., 2022). Another possibility is that this may potentially be a marker of object-memory cell assembly formation in the hippocampus (Harris et al., 2003; Larkin et al., 2014; Vandrey et al., 2021). Future work would be needed to ascertain whether this was the case because the object trial (B) was the first manipulation of a given session and not due to the first object presentation per se. One idea would be to have the spatial context change manipulation (trial D in the sequence of this presently described trial design) as the first manipulation of the session, as opposed to the object presentation (i.e., swapping trial D with trial B). This, however, is a subsidiary question to the goal of these currently described experiments which to reiterate, is addressing whether individual place cells can represent content of episodic nature. The next set of analyses takes a bigger step towards having some answer to this question.

6.3.7. Preliminary evidence that the sub-group of discriminating cells retained memory for the position of the novel object

The above analyses have shown that the sub-group of discriminating place cells clearly differentiate the first objects present trial B and spatial context trial D. To remind the reader, this sub-group of cells also displayed above threshold position- and or rate-based remapping changes to discriminate the novel object trial F from the pre- and post-baseline trials E and G (Fig. 5D, non-discriminating cells were filtered out). Thus, a key goal of the following analysis was to further explore whether there was any consistency in how the sub-group of cells discriminated the NOR trial (F) from the pre-NOR baseline trial E and post-NOR baseline trial G.

One can take the peak firing rate position of cells in trial E and G and ask whether there was a relative distance change between the novel object centroid versus familiar object centroid (Fig. 8A). For trial E, this is where objects will have been placed in trial F and for trial G, this is where objects were placed from trial F. When examining peak position in this way, it was found that for trial E (Fig. 8B) there was no difference between cell's peak position distance to the novel object centroid (M = 13.5cm, SD = 6.3cm) versus the familiar object centroid (M = 18.3cm, SD = 8.9cm; ($t_{(16)}$ = 1.56, p = 0.14, d = 0.38, paired t-test). However, for trial G (Fig. 8C) there was a marginal trend towards cell's peak positions being a significantly shorter distance from where the novel object centroid was positioned in trial F (M = 12.7cm, SD = 8.0cm) versus where the familiar object centroid was positioned in trial F (M = 19.1cm, SD = 6.8cm, $t_{(16)}$ = 2.10, p = 0.052, d = 0.51, paired t-test). Thus, there was some preliminary evidence to suggest the sub-group of discriminating cells not only differentiated the NOR trial F via position- and or rate-based remapping, but arguably displayed mnemonic retention for the novel object position in trial G, the post-NOR empty baseline trial.

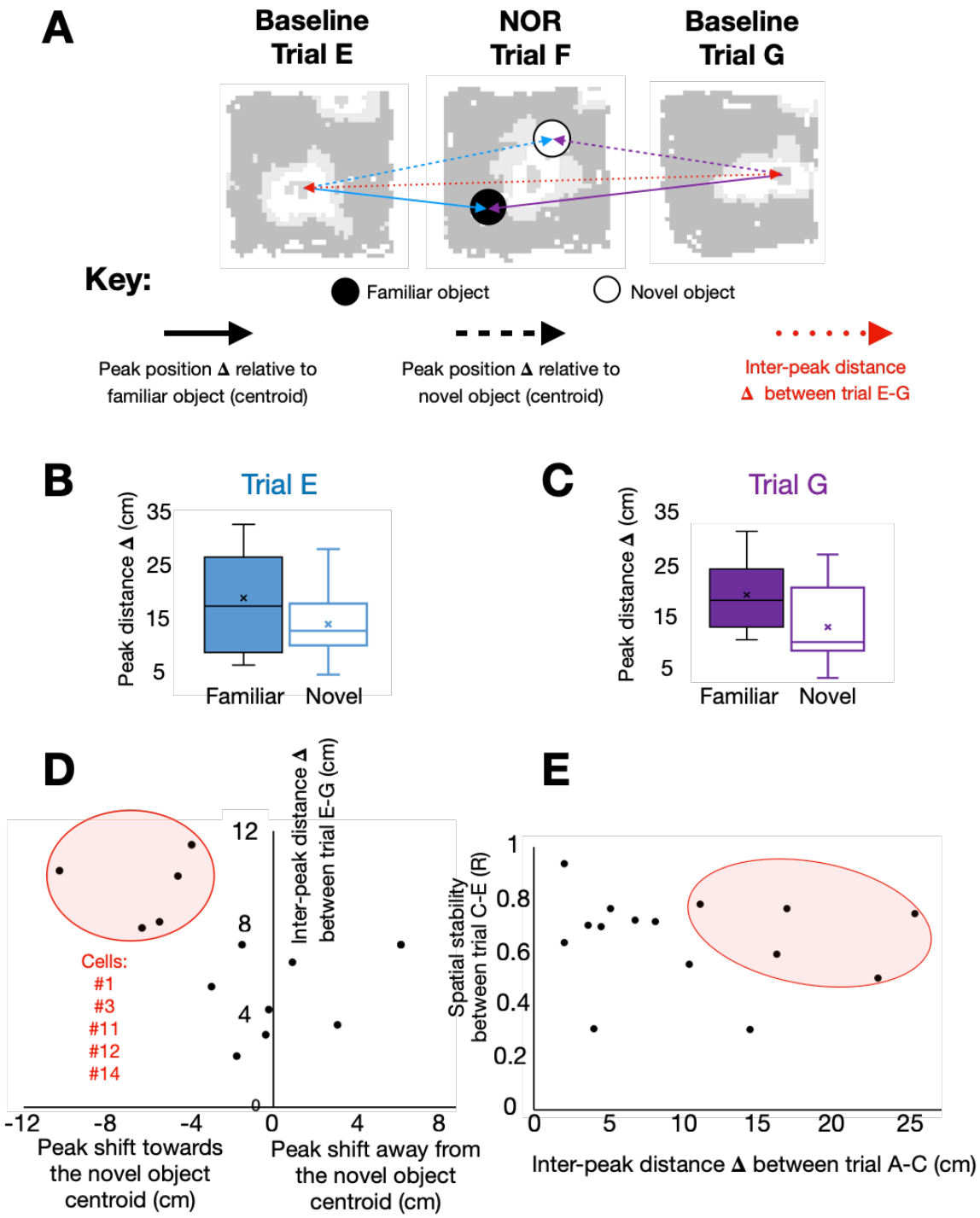


Figure 8. Consistency in how the discriminating sub-group of cells differentiated the novel object in trial F. **(A)** Schematic displaying the measures used in B right and C. Position of a cell's peak firing rate distance change relative to the centroid of the familiar object versus the novel object centroid (cm). **(B)** As calculated in A for the pre-novel object recognition (NOR) baseline Trial E. **(C)** Same for B but for the post-NOR baseline trial G. **(D)** Peak position change relative to the centroid of the NO (taking from trial E to G, hence showing shifting toward or away from the NO centroid, x-axis) plotted against inter-peak peak distance change between trial E and trial G (y-axis). **(E)** Inter-peak distance change between trial A and trial C (x-axis), plotted against spatial stability between trial C and trial E (y-axis). For D and E, not all cells are displayed as they had no discernible place field in respect to the relevant trial in the plotted axes. The red circle highlights discriminating cells with noticeably high values upon both variables in D and E (rate maps are provided in Fig. 9).

6.3.8. Preliminary evidence that place cells can represent content of episodic nature

It should now be made clear that just because this sub-group of place cells individually discriminated all manipulation trials from pre- and post-manipulation baseline trials does not necessarily mean that they represent content of episodic nature. For example, a cell may show a reduced firing rate each time any manipulation is encountered, yet this would still lead to successful (objective) discrimination. Equally, a place field of a place cell that drifted (in a above threshold manner) each time a manipulation was encountered would also lead to successful discrimination by the standards set in this chapter but may just be considered as an instable place cell, as opposed to representing content of episodic nature. However, it may be considered that being able to discriminate all manipulations trials, (B, D and F, from pre- and post-baseline trials) is a necessary prerequisite phase in order to begin examining the possibility as to whether place cells represent episodic content.

The next step plotted the relative cell peak position shift toward (or away from) the novel object centroid, against the inter-peak distance change between actual cell peaks from pre-NOR baseline trial E to post-NOR baseline trial G (Fig. 8D). This highlighted 5 place cells whose field peaks in G had shifted approximately ≥4cm towards where the novel object had been in trial F *and* whose field peak had been shifted approximately ≥8cm from trial E to trial G. Thus, one could argue that these cells not only discriminated the NOR trial but retained memory for the position of the novel (in accordance with the finding when all the sub-group of discrimination cells were considered, Fig. 8C).

Next, the inter-peak distance change between the very first pre-object baseline, trial A, and post-object but pre-spatial context change baseline trial C, was plotted against spatial stability between trial C and the post-spatial context change but pre-NOR baseline trial E (Fig. 8E). This revealed that the above highlighted 5 cells (that shifted towards the novel object, see Fig. 8D), were not only perturbed by objects in B displaying a peak field shift from A to B (ranging from 8.9cm to 26.9.cm),

but their peak fields had also shifted from A to C (ranging from 11.1cm to 25.3cm, Fig. 8E). Thus, one can argue that these cells displayed mnemonic retention of the object perturbation from trial B in trial C relative to the initial baseline in A (Fig. 9 displays the 5 highlighted cells from Fig. 8D-E and other discriminating cells for comparison, see also Fig. 6 and 7C for more example discriminating cells). Moreover, consistent with the averaged results, these 5 cells also showed low spatial stability when transitioning to and from trial D (i.e., spatial context remapping, R ranging from -0.08 to 0.08, an average of trial C-D and trial D-E). Yet, importantly, spatial stability between trial C and trial E was moderate to strong (R ranging from 0.50 to 0.78; see Fig. 8E). Hence, this further suggests that for these 5 highlighted cells, mnemonically retained object-related place fields exhibited in trial C (from trial B), were not expressed during the spatial context change of trial D (as cells remapped) but were 're-activated' when returning to the original spatial context of trials A to C). In this way, one may argue that the object-mnemonic fields of these 5 highlighted place cells were spatially context-dependent (Fig. 9; Tsao et al., 2013, similarly report context-dependent of object traces in single cells of the lateral entorhinal cortex). To reiterate and come full circle, these highlighted 5 cells discriminated the NOR trial and shifted their peak positions towards where the novel object was located in trial F (while, also shifting their peak approximately ≥8cm from trial E to trial G). Thus, one may argue that the context-dependent object-memory was 'updated' due to the presence of the novel object, allowing one to retrospectively interpret that the object memory (indexed via place-field formations) was not only context-dependent but also sensitive to object feature (object were all of the same size and shape, Fig. 2B). Altogether, a combination of the above findings allows one to argue that individual place cells (for at least these 5 highlighted cells, Fig. 9) are able to represent a specific object in place (due to place fields) and particular spatial context. In other words, a simultaneous object-place-context integration, arguably a content representation of episodic nature (Fig. 1).

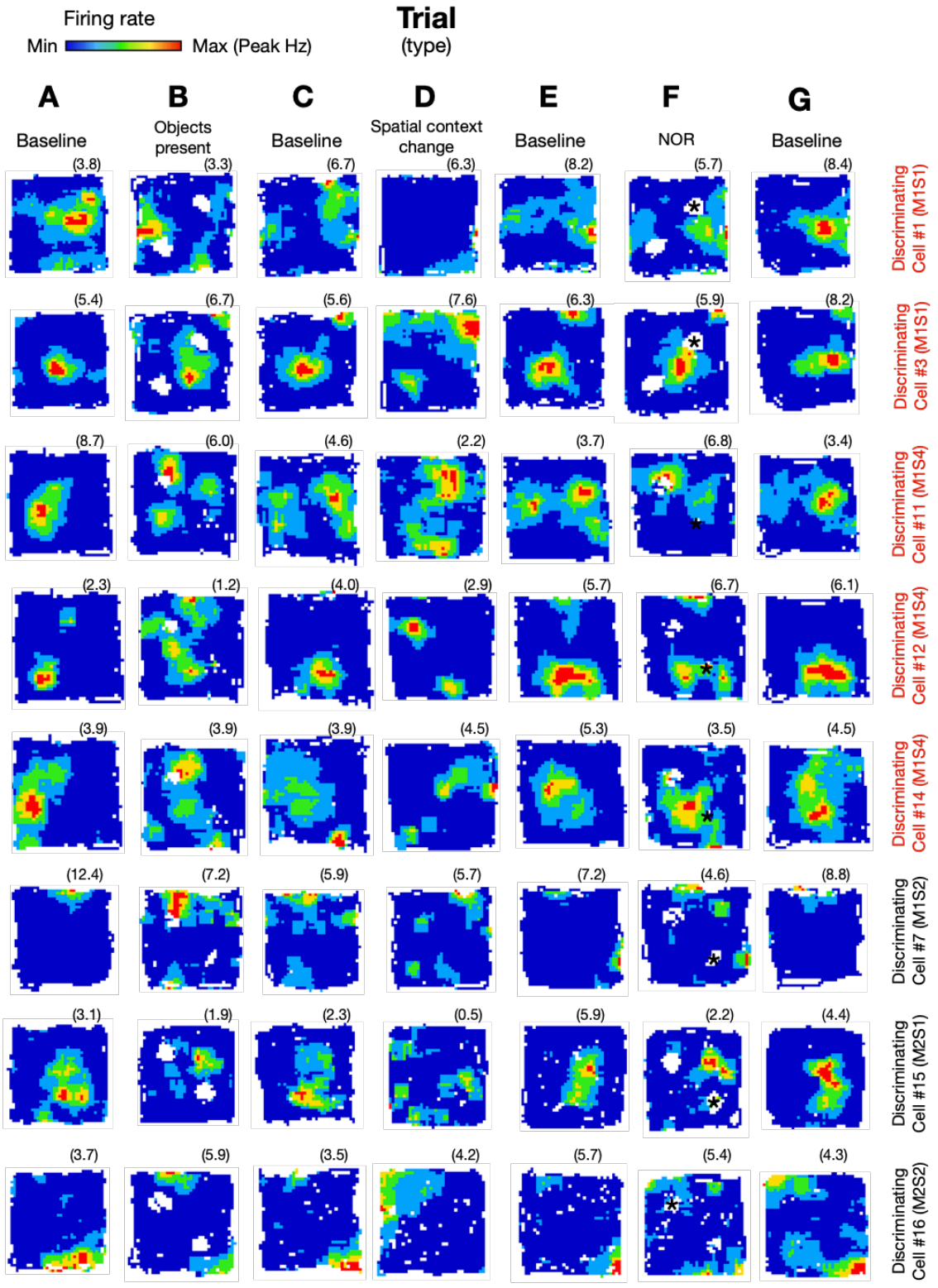


Figure 9. Rate maps of the discriminating cells whose place fields in trial G shifted towards where the novel object was positioned from trial F. Each row is a discriminating cell, showing the rate maps by trial with five gradations of firing rate (red denotes the firing rate peak, Hz, in the brackets). The first five rows display the cells highlighted in Fig. 8D-E (red labelled text). The following three rows provide more examples to visually compare (examples of other discriminating cells are provided in Fig. 6 and Fig. 7C). Overlayed asterisks in black denote the location of the novel object in trial F.

6.3.9. Preliminary evidence that discriminating place cells become more spatially overlapping due to the presentation of a novel object and a familiar object.

It is emphasised that these findings should be considered as preliminary given the low number of cells and animals recorded from. In the same breath, even if it turns out to be a well replicated finding that individual place cells do represent episodic content, this is not to say that an individual place cell alone can support the formation and retrieval of an episodic-(like) memory. For example, accumulating evidence suggests that hippocampal dependent memory and likely episodic memory is supported via cellular assemblies (e.g., Harris et al., 2003; Malvache et al., 2016). Taking advantage of cells recorded in the same session, one could ask how the activity between cell-pairs evolved over trials (n = 14, within-session cell-pairs, across all sessions). This was realised in two ways. Firstly, correlations based on spikes times, where all spikes of a given cell were summed into 1s bins and correlated with another cell of the same session (i.e., a within-session cell-pair). And secondly, rate map correlations, where the trial rate map of a given cell was correlated with the same corresponding trial rate map of another cell within the same session (see methods, section 6.2.8. for more details).

Analyses on the spike times correlations yielded an overall significant effect of 'trial' (Fig. 10A; $F_{(6,78)} = 2.75$, $p = 0.018$, $\eta_p^2 = 0.18$). Post-hoc comparisons showed a greater negative correlation on average in the spatial context change, trial D (M: R = -0.57) versus the post-spatial context baseline trial E (M: R = -0.44, $p = 0.023$) and post-NOR baseline trial G (M: R = -0.42, $p = 0.036$; all other comparisons $p \geq 0.13$). Indeed, relative differences between consecutive trial pairs showed a significant difference from chance in the post-object but pre-spatial context change baseline trial C to trial D (Fig. 10B; M: R = -0.10, $t_{(13)} = -2.84$, $p = 0.014$, $d = 0.76$, one samples t-test against zero) and trial D to trial E (M: R = 0.13, $t_{(13)} = 4.16$, $p = 0.001$, $d = 1.11$, one samples t-test against zero). No differences in other consecutive trial pairs and no overall net change (all $p \geq 0.26$ and $p = 0.20$, respectively, one samples t-test against zero). Lastly, there was a significant difference from transitioning from trial D-trial E relative to trial C-trial D ($F_{(5,64)} = 4.77$, $p < 0.001$, $\eta_p^2 = 0.27$, post-hoc

comparison of C-D and D-E, $p = 0.012$, all other comparisons $p \geq 0.10$). Thus, the spike time correlations between within-session cell-pairs suggested that cells

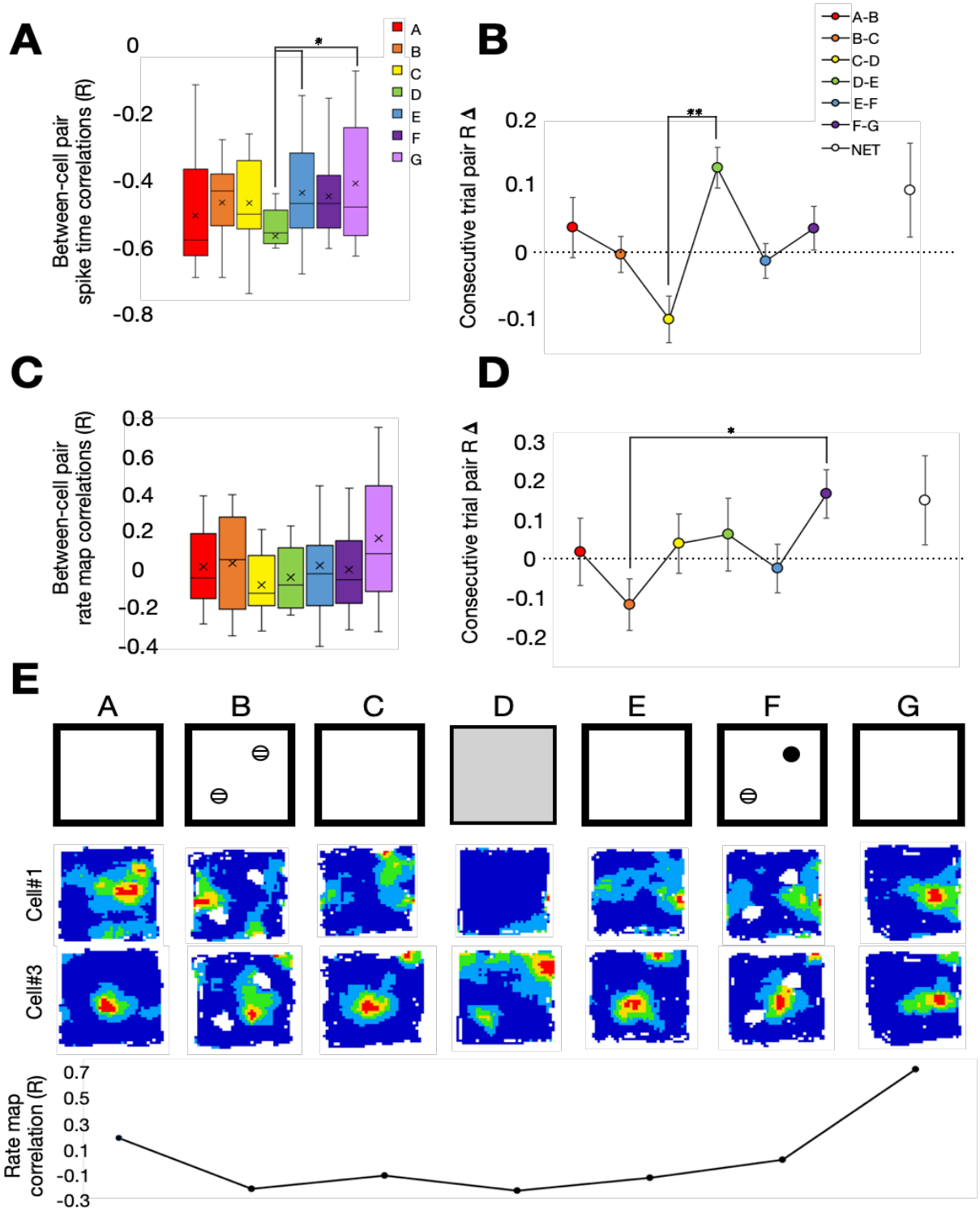


Figure 10. Between cell-pair correlation results from the sub-group of discriminating cells. **(A)** Spike time correlations between cell-pairs by trial. **(B)** Same as A but between consecutive trial-pairs. Dotted line denotes zero and error bars denote ±1 SEM. **(C)** Rate map correlations between cell-pairs by trial. **(D)** Same as C but between consecutive trial-pairs. **(E)** An example within-session cell-pair across trials (cell rate maps were already displayed, see Fig. 9 for further details). Upper: rate maps, lower: rate map correlations. *$p \leq 0.05$ **$p \leq 0.01$

became significantly more negatively correlated when the mouse experienced a spatial context change and became less negatively correlated once again when returning to the original spatial context in which the trial sequence had begun (in trials A to C).

In regard to the rate map-based correlations, there was no overall effect of trial (Fig. 10C; $F_{(6,78)} = 1.66$, $p = 0.14$, $\eta_p^2 = 0.11$, all post-hoc comparison $p \geq 0.24$). However, relative differences between consecutive trial pairs showed that transition from the NOR trial F to post-NOR baseline trial G (M: R = 0.17) there was a significant difference to chance (Fig. 10D; $t_{(13)} = 2.78$, $p = 0.017$, $d = 0.73$, one sample t-test against zero). For all other consecutive trial pairs and overall net change there were no differences to change ($p \geq 0.10$, $p = 0.21$, respectively, one sample t-test against zero). Finally, the within session cell-pair correlation change in trial F-G was significantly greater than the correlation change from the first objects present trial B to trial C (M: R = -0.12, $F_{(5,64)} = 1.40$, $p = 0.24$, $\eta_p^2 = 0.10$, post-hoc comparison between F-G and B-C $p = 0.041$, for all other comparisons $p = 1.00$). In this way, the within-session between cell-pair rate map correlations suggested that place fields became more positively correlated (overlapping) when the mouse transitioned from the NOR trial F to the post-NOR baseline trial G (an example cell-pair is shown in Fig. 10E, corroborating the novel and familiar object peak distance analysis, Fig. 8A-C). This relative increase between within-session cell-pairs from trial F to trial G was greater than that when the mouse transitioned from trial B to trial C (the first object-presence trial and the post-object but pre-spatial context change trial, respectively), which is again potentially suggestive of memory 'updating' due to the presence of the novel object in trial F (further elaborated upon in the discussion section). In conclusion, the cell-pair rate map-based correlation analyses provide some evidence to argue against an instability/random drifting of place fields perspective, which is an alternative interpretation to the preliminary support that place cells can represent episodic content presently argued for. In other words, it would seem too coincidental that cells would show a consistent instability/random drifting towards the same place from trial F to trial G. Instead, one speculative explanation is that some cell-pairs formed a new cell assembly that supported a NOR-related memory of trial F that manifested in trial G resulting in more

overlapping place fields (Harris et al., 2003, Gava et al., 2021), yet future work may explore this possibility.

6.4. Discussion

Previous work has argued that cells of the hippocampal formation can support episodic memory at a network level (see chapter 1, section 2.3.). Specifically, place cells (and other hippocampal formation cellular mechanisms) allow a means to represent not only 'what', for example objects, but also 'what-where' via place and vector coding (Deshmukh & Knierim, 2013; Nagelhus et al., 2023; Vandrey et al., 2021). Additionally, spatiotemporal context is also represented via mechanisms of remapping and temporally-structured coding relating to stimulus offset or repetitive stimuli markers (Leutgeb et al., 2005; Kubie et al., 2020; Kraus et al., 2013; Sun et al., 2020). For example, Leutgeb and colleagues (2005) conclude, "The existence of independent population codes for location and cue-configurations implies that hippocampal cell ensembles may simultaneously convey information related to where an animals is located and what is currently present in that location" (Leutgeb et al., 2005, p. 622). In this way, through a 'sum of its parts'-based formulation, one that has been explicitly made (e.g., Sugar & Moser, 2019), cells of the hippocampal formation facilitate episodic processing when considered at this network (cross-region) level. Indeed, Sugar and Moser (2019) state "The binding of sensory stimuli into a cohesive and unique episodic memory likely depends on neuronal activity in the entorhinal cortex that signals temporal relationships ("when"), a spatial universal metric ("where"), and the experience itself ("what")" (Sugar & Moser, 2019, p.1199). However, as other studies have found single cell correlates of object in place coding and memory, these present preliminary experiments have attempted to extend upon such evidence, addressing the question as to whether individual place cells can represent episodic content, which was here taken to be a specific object-place-spatial context integration.

One result of this present work was that place cells became less spatially informative over the course of the trial sequence, being particularly mediated by the object-presence trials (Fig. 4 and Fig, 7). Consistent with previous research, some

cells showed a decrease in spatial information (bits/spike) seemingly due to shifting of fields, suppression of firing fields, development of new fields (e.g., Fig. 5A and 7C; Rivard et al., 2004; Burke et al., 2011; Nagelhus et al., 2023). Yet, notably, as shown by the correlation analyses, other cells exhibited an increase in spatial information when objects were present (Fig. 4E). Thus, even in this small sample size of cells from 2 mice, heterogeneity in how cells responded to the presence and absence of objects was apparent, echoing converging evidence that hippocampal pyramidal cells are a heterogeneous population (Vandrey et al., 2021; Sharif et al., 2021; Cembrowski & Spruston, 2019).

Of the total 36 cells 13.9% (5 cells highlighted in Fig. 8D-E and Fig. 9) passed the threshold criteria that differentiated manipulation trials from pre- and post-manipulation baseline trials. Additionally, these cells also seemingly developed new fields in the presence of the objects in trial B which were retained in the subsequent baseline trial C, arguably object-place mnemonic activity. These cells then remapped when there was a spatial context change and showed moderate to high spatial stability between trial C and E, suggesting that the object-place memory activity was spatially context-dependent. Lastly, in trial G after the NOR trial F, these cells shifted their field peaks towards where the novel object had been placed in F and their field peaks had shifted from the pre-NOR baseline trial E. These occurrences together preliminarily indicated that:

I) These place cells represented an integration of object and context specificity in trial B, which can be considered content of episodic nature as it specifies a unique simultaneously integrated object-place-spatial context association.

II) The fact that these cells discriminated the novel object based on the activity changes from E to G allows the argument to be made that they were not only sensitive to the object's feature, but potentially mismatched this object in F to what previously occurred in trial B.

Consequently, one possible explanation of both I and II is that these place cells had 'updated'; this would be consistent with multiple memory trace/trace transformation theory (Nadel & Moscovitch, 1997; Nadel et al., 2012; Mau et al., 2020). This proposes that, in the NOR trial F, re-activation of a hippocampal memory trace occurs in this altered neural and experiential context and a new

hippocampal trace (cell assembly) would be formed or existing traces may be 'updated' to reflect novel episodic relevant information (Nadel & Moscovitch, 1997; Nadel et al., 2012; Mau et al., 2020). Indeed, it has also been argued that CA1 can perform a mismatch detection computation, comparing inputs of previously learned information from CA3 with currently perceived information from direct inputs from the entorhinal cortex (Duncan et al., 2012; Hasselmo, 2006; Brun et al, 2002). Therefore, these current observations offer preliminary support for an updating view. However, a caveat of the experimental approach used and consequential argument put forth here is that an activity change by cells in trial E, the post-spatial context change but pre-NOR baseline trial, to trial G, the post-NOR baseline trial, is required to make an inference that the representation was object (feature) specific (and hence episodic) and not a gist-like spatial representation, agnostic to stimuli's identity (c.f. Gilboa & Moscovitch, 2021). In this way, it is ambiguous whether cells that do not 'update' based on trial E to trial G do represent episodic content but remain episode specific or whether their activity represents a more gist-like spatial representation.

Another alternative explanation is that the place fields of place cells were simply reflecting instability and or random field drift (not being related to the objects per se). There was some evidence to argue against this view, the first being that spatial stability between the first objects present trial B and post-object baseline trial C and between trial C and the baseline trial E was moderately high (R = 0.47, R = 0.64, respectively, average across within-cell rate map correlations of the sub-group of discriminating cells, n = 17, see Fig. 7D and supplementary table 1). This suggests that whether place field changes were a result of the objects presence or due to general instability, fields were remarkably stable especially between trial C and E, given the spatial context change of trial D was sandwiched in between them (where spatial stability was low, R = 0.06, an average between trial C-D and trial D-E). Secondly, after the NOR trial F, cells of the discriminating sub-group within the same session became more spatially overlapping with other cells of the same session, in the post-NOR baseline trial G (Fig. 10C-E). This, highlighting some consistency in place field shifting of place cells, which again argues against seemingly stochastic instable drift. However, it is emphasised that these findings need to be replicated in more animals and in larger quantities to be considered

robust phenomena, although it should be noted that in existing published literature, only a small proportion of CA1 cells (~5-20%) show putative object-place mnemonic activity (18.3%, 218/1189, Nagelhus et al., 2023; 19.3%, 48/249, Vandrey et al., 2021; 4.7%, 3/64, Deshmukh & Knierim, 2013). Notably, some differences between the methodology of previous work and the currently reported work was that they did not always use empty spatial context baseline trials before and after a trial that contained a manipulation (e.g., Deshmukh & Knierim, 2013; Vandrey et al., 2021). This can for example make it hard to interpret where a given place cell's place field was located *before* the objects were presented potentially confounding results related to the object-related activity. Finally, despite these results being considered preliminary many questions arise.

I) How and why does only a fraction of place cells develop new object related fields that are retained after object removal?

II) Are these place cells part of a cellular assembly?

III) Are they more likely to act as index cells?

IV) How does the activity of these cells map onto behaviour?

V) Does similar activity occur in cells of other species and in more complex and naturalistic episodes? These questions will be discussed below.

6.4.1. How and why does only a fraction of place cells develop new object-related fields that are retained after object removal?

It has been shown that CA1 pyramidal cells that displayed a lower action potential threshold and were more 'bursty' (that is the tendency to fire ≥2 spikes within short inter-spike-intervals ~6ms or less) were also more likely to go to form place fields in a novel spatial context than regular spiking cells that tended to be silent i.e., have no place fields (Epsztein et al, 2011). This suggested that a given cell's intrinsic excitability contributes in its likelihood to participate in the spatial coding of an environment in the future (Epsztein et al, 2011; Josselyn & Frankland, 2018). In a similar vein, others have argued that there are pre-existing dynamics between ensembles of place cells which are present before an animals will explore an environment that later manifest into a code representing the environmental

experience (Dragoi & Tonegawa, 2011; Farooq & Dragoi, 2019). Once the animal is in the environment, studies have shown that small current injections or opto-stimulations can bias previously silent cells into cells that have stable place fields, or re-tune active place cells to other environment locations (Lee et al., 2012; Diamantaki et al., 2018; McKenzie et al., 2021). Additionally, it has recently been found that plasticity and activity of inhibitory cells facilitate the emergence and stabilisation of place fields (Grienberger et al., 2017; Geiller et al., 2022), but normal functioning of protein synthesis and *N*-methyl-D-aspartate receptors also contributes to the long-term stability of newly formed fields (Kentros et al., 1998; Agnihotri et al., 2004). Together, these studies would suggest an intricate relationship between excitability and inhibitory dynamics, and molecular processes allow the rapid formation and long-term stabilisation of place fields, which may underlie the retention of cue (object) related field once the cue (object) is no longer present. Notably, the spatial context may facilitate mnemonic field retention/re-activation by acting as a partial cue to aid retrieval (via pattern separation, Passingham, 2017; Horner et al., 2015).

As mentioned previously, hippocampal pyramidal cells are a heterogenous population. Recent evidence demonstrates that only a small fraction of hippocampal cells are instantaneously active (when an animal is first introduced into an environment), exhibit a higher overall firing rate and tend to express a higher number of place fields. In contrast, relative to the majority of cells, which are not as active, express a lower number of fields and require more experience/time to stabilise (Grosmark & Buzsáki, 2016; Lee et al., 2020; Gava et al., 2021). Another study differentiated between feline osteosarcoma (Fos) expressing CA1 place cells versus Fos negative place cells (Fos is an immediate early gene which is typically implicated in long-term synaptic plasticity, Yap & Greenberg, 2018). Fos^+ Place cells exhibited less spatial information per spike than Fos^- negative cells, were particularly sensitive to discriminating a novel spatial context via rate-based remapping and were interpreted as being candidate cells to support indexing theory due to this context-dependent activity (Tanaka et al., 2018). However, more recent evidence has reported that Fos^+ CA1 cells actually had a higher place field prevalence, showed more correlated activity with other Fos^+ cells and were more spatially stable across

trials within a session, hence being more spatially informative than Fos^- negative counterparts (Pettit et al., 2022). This discrepancy can potentially be explained by the fact that the former study exposed animals to a familiar (virtual) spatial context whereas the latter study used a novel spatial context, in which it has been shown that membrane potential ramps underlying place field spiking (sub- to the action potential threshold) change in an experience-dependent manner (i.e., as a novel spatial context becomes more familiar, Cohen et al., 2017). This suggests that to fully understand place cell dynamics and between-cell differences in CA1, it is important to compare activity in novel spatial contexts, familiarised spatial contexts and the transition between a novel context becoming more familiar. The present experiments can at least partially offer such comparisons, and this was one of the motivations underlying the design of the experiment.

In the present experiments, mouse 1 had been run in sessions where the starting baseline trial begun in a novel spatial context and there were other sessions where it had become more familiar (Fig. 3E). Yet, given the low number of recorded cells data was pooled across all sessions to increase statistical power. Although it is likely that some of the recorded cells may have been Fos^+ due to novel context and or object exposure (Albasser et al., 2010; Kinnavane et al., 2017), it would therefore be interesting if future work explored whether similar differences in object-place-spatial context discriminations were upheld between Fos^+ versus Fos^- place cell populations recorded in this present trial sequence, particularly when the starting baseline is a novel spatial context versus a familiar spatial context.

The above evidence indicates that many factors contribute to why certain cells form place fields. However, nearly all the above evidence has been conducted in empty cue impoverished environments. While it is likely that the determinants for object fields (and more generally cue driven fields) will be similar to place fields recorded in cue impoverished environments, vector relationships, proximity to boundaries, valence and salience may be important aspects to consider for the likelihood of cue-fields forming (Deshmukh & Knierim, 2013; Vandrey et al., 2021; Jin & Lee, 2021; Sarel et al., 2022). It is therefore also important to continue examining place cells and other spatially modulated cells in more cue rich environments to

further understand the mechanisms involved in more naturalistic settings (later discussed in further detail)

6.4.2. Are these discriminating place cells acting as part of a cellular assembly?

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Presently, it was found that pairs of cells (n = 14 pairs, of the 17 sub-group of discriminating) recorded in the same session became more negatively correlated when transitioning to trial D, that of the spatial context change, and became more correlated once returning to starting spatial context for that session. As well as indicating remapping, it is also in accordance with evidence showing that hippocampal place cells representing a given spatial context can be modelled as an attractor network (with certain synaptic connectivity patterns between cells and plasticity affording a set of stable states; Tsodyks, 1999; Wills et al., 2005). Thus, it is likely that these cells were part of a larger attractor network representing the starting spatial context for a given session. Moreover, hippocampal replay of place cell sequences describes the finding that when an animal traverses a path, place cells with overlapping fields can be active in a sequential manner and can re-activated sequentially during periods of awake rest and during sleep (e.g., Lee & Wilson, 2002; Diba & Buzsáki, 2007). This phenomenon, in part, has been used to argue that some place cells together form a cellular assembly (Malvache et al., 2016; Harris et al., 2003).

To reiterate, one finding in this current data was that in transitioning from the NOR trial F to post-NOR baseline trial G, rate map correlations between pairs of cells of the same sessions showed that they tended to became more correlated on average (i.e., place fields became more overlapping in space) and this trial F-G change was greater than transitioning from trial B to C, the first objects present trial and post-object baseline trial, respectively. Thus, it is plausible that in trial G cells formed part of a new cellular assembly and one can speculate that it was the novelty-related change of the NOR trial and changes in neuromodulatory activity (e.g. dopaminergic) that afforded this (Larkin et al., 2014; Duszkiewicz et al., 2019). Future experiments may further realise these possibilities, but it may be necessary to

have a control object trial (where the same objects as in trial B would be placed in tiral F) to see whether increased convergence of place fields between co-recorded place cells does reflect a novelty-related mechanism. To summarise, despite the low number of recorded cells there are indications that these cells do function as part of larger cell assemblies and networks.

6.4.3. Are these discriminating place cells more likely to act as index cells: a chicken and egg problem potentially solved with behaviour?

Indexing theory remains an attractive theory to explain, at least in part, how and why episodic recollection strongly depends on a healthy functioning hippocampus (Teyler & Rudy, 2007; Goode et al., 2020). On the surface, it would seem that these place cells that readily integrate episodic content are candidate cells to be recruited for an episodic-supporting index. However, from these preliminary experiments alone a 'chicken and egg problem' arises. Specifically, are these cells performing the indexing function or are they the remnants of an episodic representation already retrieved via other indices? Without any means of causal interrogation (e.g., electrical stimulation or optogenetic stimulation/silencing), such hypotheses cannot begin to be tested, but even with appropriate methodology there may be complexities…

The majority of evidence potentially implicating hippocampal principal cells as indexing cells has used valanced behavioural tasks, especially negatively-valanced such contextual fear conditioning (Goode et al., 2020; Tonegawa et al., 2015). For example, Ohkawa and colleagues (2015) tagged CA1 cells in mice that were active in a spatial context (albeit these not being explicitly confirmed to be place cells), and basolateral amygdala cells (BLA), which were active in another spatial context where a foot shock was presented in that spatial context. Despite these events being seemingly independent, optogenetic activation of both the CA1 and BLA cells could artificially associate the shock to the spatial context it was not sensorily experience in. This led to higher freezing behaviour in optogenetically activated mice in this spatial context relative to control mice who did not express the opsin (Ohkawa et a., 2015). This would argue that CA1 cells in this study were successfully indexing the

initial spatial context where the shock was not experienced. Moreover, Robinson and colleagues (2020) optogenetically activated place cells covering the reward zone of a virtual track and they reported that this stimulation drove mice to increase their licking behaviour and with more experience of stimulation sessions over time, better reward-anticipatory behaviour as indicated via deceleration in running (Robinson et al., 2020). However, it is unknown how these findings relate to behaviour in tasks not explicitly using valence e.g., object recognition.

An intriguing finding here was that in sessions where arguably the best examples of episodic content representing place cells were recorded (session 1 and 4 of mouse 1, see Fig. 9), the mouse's D2 scores were negative (-0.51 and -0.79, respectively, of the NOR trial F), i.e. showing more exploration of the familiar than novel object. While the recognition behaviour of these implanted animals was overall variable (Fig. 3), it is an interesting possibility that some place cells discriminated the novel object despite such extreme negative D2 scores (usually reflecting robust familiarity-based exploration; e.g., Contreras et al., 2019). For example, will one observe such novel object discriminating activity by place cells regardless of the animal's object recognition behaviour? If one were able to silence these place cells would this lead to variable object recognition behaviour? It is noted, that previous evidence has shown that an intact hippocampus is not functionally necessary for successful novel object recognition behaviour in rodents (Barker & Warburton, 2011; Albasser et al., 2012), although there are some complexities as object-responsive place cells of the hippocampus are still sensitive to NOR (Fig. 8-10; Larkin et al., 2014; Vandrey et al., 2021) and may be necessary for successful remote NOR, beyond a one-week delay, in rodents (Sawangjit et al., 2018). To this end, a better goal for future research may be to manipulate such putative episode integrating place cells in an episodic-like behavioural task (such as the object-place-context task) with questions being asked, as to how stimulation and silencing impacts context-based or recency-based recognition behaviour (see chapters 2 and 3). This may be a better methodology to falsify this view, as one would be able to examine the relationship between arguably objective episodic representing cells and episodic-like behaviour. Thus, pursuing such experiments would likely shed light upon the chicken and egg problem raised earlier with a possible outcome being both. That is,

these cells perform an indexing function and at the same time seemingly display remnants of an episodic representation being retrieved via re-activation.

6.4.4. Would place-(like) cells of other species also be able to represent content of episodic nature and how does this occur for more complex episodes?

Place cells or place-like cells have been observed in numerous species (see chapter 1, sections 2.3.1. and 2.3.2.) and one may hypothesise that in such species episodic representing activity by place cells would be observed. For example, recent work from the Ulanovsky lab in bats has shown that an individual place cell can display a 'mulitscale code' when bats flew in a large-scale space (200m; Eliav et al., 2021). This meant that a single cell had multiple place fields of variable field sizes (Eliav et al., 2021; similar findings were reported in rodents, Rich et al., 2010; Harland et al., 2021). Notably, there were example place cells with multiple place fields in this presently reported work (e.g., Fig. 9). In subsequent work, the Ulanovsky lab has also shown that different place fields of the same cell could represent and switch between qualitatively distinct information (Sarel et al., 2022). That is, the same cell could reflect coding relating to the self-position of the bat and its distance from a moving conspecific bat. The distance-from-conspecific firing component in these cells echoes another recent finding in subicular vector trace cells of rats, whereby a given cell fires at a particular distance (and direction) from a (static) stimulus. The cells' firing in an object field displayed earlier-going phase shifts relative to the theta cycle during object present trials and not pre- or post-object trial. In contrast, wall fields of the same cells showed no such phase shift across trials (Poulter et al., 2022), suggesting a difference between the representation of the objects and the walls by the same individual cell via spatially modulated firing fields (c.f. Lee et al., 2021). These findings in other species highlight that different spatially modulated fields of the same cell may represent different information and may bare importance to the object-related fields versus other place field of place cells recorded in this present study (Fig. 9).

Associative coding by hippocampal neurons has also been reported in

humans (Quiroga et al., 2005; Quiroga et al., 2009; Ison et al., 2015). For example, concept cells were argued to represent content in a multimodal manner, i.e., firing to pictures of a person's face as well as their written name and their name verbally pronounced. In addition, some cells in the human hippocampal formation were selectively active during particular short video clips and became active again once participants had freely recalled what they had watched (Gelbard-Sagiv et al., 2008). The activity of concept cells was claimed to be human-specific (e.g., Quiroga, 2020) but recently it has been shown that the same hippocampal cells in marmosets will respond to the face of a particular conspecific as well as upon hearing that conspecific's vocalisation (Tyree et al., 2023). Moreover, another recent study reported that hippocampal cells in mice can display 'movie-fields', where cells show enhanced firing during particular movie segments and were sensitive to the visual sequence (mice passively viewed the stimulus, while being head-fixed and were largely immobile. Purandare & Mehta, 2023). Together, these highlighted studies demonstrate the similar hippocampal coding mechanisms in non-human animals to that of humans in favour of episodic memory having a long evolutionary history (Allen & Fortin, 2013). This may suggest that if place cells do represent content of episodic nature (more replication is needed of the preliminary finding reported here), it is likely an evolutionary conserved mechanism.

Kolibius and colleagues (2023) recently distinguished between concept cells and episode-specific neurons in the hippocampus of humans, which has particular relevance to the present findings reported here. When participants had to create a vivid mental story consisting of cues that were to be associated (animals, faces and faces), these episode-specific neurons would fire during the perceptual-mentalised association and also fire specifically during the retrieval when a partial cue was given. Indeed, 86% (117/136) episode-specific neurons represented a single episode, whereas the rest coded for more than one episode. Importantly, these cells were not found to be coding for the visual properties of the images. The experimenters contextualise their findings with index theory, stating "hippocampal neurons that perform this indexing function should have no initial tuning and are allocated to specific episode during memory formation" (Kolibius et al., 2023, p. 1974). Thus, such findings resemble the associative nature by hippocampal cells

preliminarily reported here, (some place cells readily integrated specific object and spatial context information). However, there are some discrepancies between what the experimenters report and argue for and what is presently observed. Specifically, episode-specific cells should have no initial tuning prior to being allocated to a specific episode. (as determined by the experimental design). This somewhat reflects the content-free indexing view as earlier discussed. In contrast, the cells reported here were active place cells before potentially representing the episode in trial B, the first objects present trial. To this end, how do these cells and coding mechanisms relate to representation for more complex and naturalistic events?

In truth both these present experiments and the Kolibius et al., (2023) study are designed to meet the minimal requirements to be constituted as an episode and are inherently simple. As discussed earlier in this thesis (chapter 1), events outside the lab are not subject to the discrete parameters imposed by experimenters. One can envisage the idea of an episode-specific neuron as defined by Kolibius et al., (2023) if activated at or prior to the onset of an event boundary (c.f. Zheng et al., 2022). Without the role of event boundaries, a set of hippocampal episode specific neurons would have to be active for every (fine-grained) change during continuous experience, which would likely lead to capacity issues (Qiao et al., 2023). In contrast, a set of place cells (and other cells) equipped with remapping mechanisms (gradated and discrete) arguably provide a more computationally plausible manner in which specific episodes can be represented. According to this view an episode-specific coding scheme as reported by Kolibius et al., (2023) would be more scarcely implemented, likely reserved for salient moments around certain event boundaries (Zacks et al., 2007; Ben-Yakov & Henson, 2018). Finally, with the ‘multiscale’ coding reported by Eliav et al., (2021), that is, multiple place fields expressed by individual place cells acting interpedently with population-level coding (e.g., Nagelhus et al., 2023), one can begin to imagine how more complex events in naturalistic settings can begin to be represented, beyond two objects in a spatial context like mice experienced here.

6.5. Conclusion

The data from these preliminary experiments supports the view that individual place cells can represent episodic content (Fig. 8 and Fig. 9). Here, ‘content of episodic nature’ was taken to be specific simultaneously integrated object-place-spatial context associations (Eacott & Norman, 2004) To emphasise, this is not to argue that episodic-(like) memory is supported by a single place cell. Instead, it is arguing that individual place cells may form an integrated code that is spatio-temporally finite (Tulving, 1972) from continuously perceived experience. The place cells likely operate together with other cells (cell assemblies) to support an episodic-(like) memory. A nice analogy is provided Sugar and Moser (2019), “we can imagine a process where entorhinal cortex presents a “movie” of ongoing experience to the hippocampus that acts as an editor of this continuous flow of information” (Sugar & Moser, 2019, p. 1201). Based upon the preliminary reported evidence here one can extend upon this analogy. Individual place cells can represent a short ‘clip’ from this ‘movie’ of ongoing experience (Fig. 1).

6.6. References

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6.7. Chapter 5 supplementary tables

Table 1

Post-hoc comparisons of trial-to-trial spatial stability across trial-pairs.

Trial	Trial-pair correlated with (Mean R)	Trial-pair comparison	*p*
A	B (0.31)	A-C	0.032*
		A-D	1.00
		A-E	1.00
		A-F	1.00
		A-G	1.00
		B-C	1.00
		B-D	0.053
		B-E	1.00
		B-F	1.00
		B-G	1.00
		C-D	0.11
		C-E	0.033*
		C-F	1.00
		C-G	1.00
		D-E	1.00
		D-F	0.84
		D-G	1.00
		E-F	1.00
		E-G	1.00
		F-G	1.00
		A-D	0.002**

		A-E	1.00
		A-F	0.32
		A-G	1.00
		B-C	1.00
		B-D	< 0.001**
		B-E	1.00
		B-F	1.00
		B-G	1.00
		C-D	< 0.001**
	C (0.54)	C-E	1.00
		C-F	1.00
		C-G	1.00
		D-E	< 0.001**
		D-F	0.001**
		D-G	0.017*
		E-F	1.00
		E-G	1.00
		F-G	1.00
		A-E	0.04*
		A-F	1.00
		A-G	0.009**
		B-C	0.13
	D (0.05)	B-D	1.00
		B-E	0.66
		B-F	< 0.001**
		B-G	0.35
		C-D	1.00

		C-E	< 0.001**
		C-F	0.34
		C-G	0.004**
		D-E	1.00
		D-F	1.00
		D-G	1.00
		E-F	0.37
		E-G	0.003**
		F-G	0.017*
	E (0.46)	A-F	1.00
		A-G	1.00
		B-C	1.00
		B-D	< 0.001**
		B-E	1.00
		B-F	1.00
		B-G	1.00
		C-D	< 0.001**
		C-E	0.47
		C-F	1.00
		C-G	1.00
		D-E	0.004**
		D-F	0.006**
		D-G	0.28
		E-F	1.00
		E-G	1.00
		F-G	1.00
		A-G	1.00

	F (0.27)	B-C	1.00
		B-D	0.09
		B-E	1.00
		B-F	0.21
		B-G	1.00
		C-D	0.07
		C-E	0.001**
		C-F	1.00
		C-G	0.33
		D-E	0.97
		D-F	0.13
		D-G	1.00
		E-F	1.00
		E-G	0.37
		F-G	0.09
	G (0.41)	B-C	1.00
		B-D	0.005**
		B-E	1.00
		B-F	1.00
		B-G	1.00
		C-D	< 0.001**
		C-E	0.85
		C-F	1.00
		C-G	1.00
		D-E	0.006**
		D-F	0.003**
		D-G	0.09

		E-F	1.00
		E-G	1.00
		F-G	1.00
B	C (0.47)	B-D	0.004**
		B-E	1.00
		B-F	1.00
		B-G	1.00
		C-D	0.015*
		C-E	1.00
		C-F	1.00
		C-G	1.00
		D-E	0.15
		D-F	0.09
		D-G	1.00
		E-F	1.00
		E-G	1.00
		F-G	1.00
	D (-0.002)	B-E	0.019*
		B-F	< 0.001**
		B-G	0.006**
		C-D	1.00
		C-E	< 0.001**
		C-F	0.023*
		C-G	< 0.001**
		D-E	1.00
		D-F	1.00
		D-G	1.00

		E-F	0.007**
		E-G	< 0.001**
		F-G	< 0.001**
	E (0.34)	B-F	1.00
		B-G	1.00
		C-D	0.07
		C-E	0.026*
		C-F	1.00
		C-G	1.00
		D-E	0.66
		D-F	0.32
		D-G	1.00
		E-F	1.00
		E-G	0.97
		F-G	1.00
	F (0.52)	B-G	1.00
		C-D	< 0.001**
		C-E	1.00
		C-F	1.00
		C-G	1.00
		D-E	< 0.001**
		D-F	< 0.001**
		D-G	0.003**
		E-F	1.00
		E-G	1.00
		F-G	1.00
		C-D	0.02*

	G (0.37)	C-E	0.17
		C-F	1.00
		C-G	1.00
		D-E	0.33
		D-F	0.14
		D-G	1.00
		E-F	1.00
		E-G	1.00
		F-G	1.00
C	D (0.03)	C-E	< 0.001**
		C-F	0.038*
		C-G	< 0.001**
		D-E	1.00
		D-F	1.00
		D-G	1.00
		E-F	0.039*
		E-G	< 0.001**
		F-G	< 0.001**
	E (0.64)	C-F	1.00
		C-G	0.15
		D-E	< 0.001**
		D-F	< 0.001**
		D-G	< 0.001**
		E-F	1.00
		E-G	1.00
		F-G	1.00
		C-G	1.00

	F (0.40)	D-E	0.27
		D-F	0.07
		D-G	1.00
		E-F	1.00
		E-G	1.00
		F-G	1.00
	G (0.49)	D-E	< 0.001**
		D-F	< 0.001**
		D-G	0.002**
		E-F	1.00
		E-G	1.00
		F-G	1.00
D	E (0.08)	D-F	1.00
		D-G	1.00
		E-F	0.30
		E-G	< 0.001**
		F-G	0.001**
	F (0.02)	D-G	0.48
		E-F	0.044*
		E-G	< 0.001**
		F-G	< 0.001**
	G (0.14)	E-F	1.00
		E-G	0.004**
		F-G	0.046*
E	F (0.42)	E-G	1.00
		F-G	1.00

	G (0.56)	F-G	1.00
F	G (0.52)	-	

* $p < 0.005$ ** $p < 0.001$

Table 2
Post-hoc comparisons for the probability distributions of inter-spike-intervals across trials.

Trial	Trial comparison	*p*
A	B	< 0.001
	C	1.00
	D	< 0.001
	E	1.00
	F	0.44
	G	< 0.001
B	C	< 0.001
	D	< 0.001
	E	< 0.001
	F	< 0.001
	G	1.00
C	D	< 0.001
	E	1.00
	F	1.00
	G	< 0.001
D	E	< 0.001
	F	< 0.001
	G	< 0.001
E	F	0.54
	G	< 0.001
F	G	< 0.001

7. General discussion

The overarching question of the current thesis asked does comparable segmentation of continuous experience (event segmentation processes) occur for episodic-like memory in non-human animals? To this end, the main results of the thesis relevant to this question can be summarised as four-fold, and they will be further discussed in the context of wider literature, before drawing a comparison between episodic-like memory and episodic memory.

I) Rats can use top-down like prediction-error processing facilitating segmentation for mnemonic-guided behaviour in an episodic-like task (chapter two).

II) Mice readily incorporate conspecific-contextual information using episodic-like memory processing, suggestive that conspecific may act as potential segmentation cue in non-human animals (chapter three).

III) Humans and rodents similarly segment continuous experience at turns made around spatial boundaries (chapter four).

IV) Individual place cells in mice can represent simultaneously integrated object-place-spatial-context associations i.e., content of episodic nature (chapter five).

7.1. Event segmentation in non-human animals

One dominant theory explaining why humans segment is event segmentation theory reliant on the error of one's predictions (Zacks et al., 2007; chapter 1, section 1.1.). In chapter 2 this was tested using the episodic-like object-place-context task in rats (Eacott & Norman, 2004). Rats could form associations between floor-tone cue pairings in an incidental manner which could serve as 'context' to separate and distinguish certain events in memory. Probe trials aimed to perturb these floor-tone contextual associations. This was realised by presenting a previously stable contextual cue by pairing it with unexpected cue (that was previously habituated). For example, in a probe trial the floor cue could remain stable, but it was now paired with white noise instead of 1kHz tone. While before probe trials it was found that rats behaved variably, after probe trials rats had changed their recognition behavioural

pattern in a way that was ignorant to the contextual cues and reliant on an object in place recency-based strategy (chapter 2, section 3.2.1.; Tam et al., 2015). One interpretation, which is the current view, is that probe trials cued event boundaries for rats driven by their prediction-error. This would explain why mnemonic-guided behaviour changed to a recency-based strategy after probe trials (and not chance-level variability) because the contextual cues may have no longer become an effective way for rats to separate and distinguish events in memory due to prediction-error of probe trials (Honey & Good, 2000). Another behavioural study supports prediction-error bounding mechanisms for subsequent memory in great apes. Kano and Hirata (2015) exposed apes to passively watch a video stimulus where a 'King Kong' dressed actor appeared through one of two doors (a target door and a distractor door) and proceeded to 'attack' a human actor. The room, actor and doors were familiar to the apes, but the lighting and Kong actor was novel. Hence, it was likely that this would have been an unexpected moment for the Kong actor to appear through the door (prediction-error). After just a single viewing on day 1, the apes gazed significantly longer at the target door opposed to the distractor door in the moments leading up to the Kong actor appearance ~24 hours later. This would suggest that apes successfully retrieved what had occurred in the movie stimuli on day 1 by anticipating the Kong appearance on day 2. Thus, one can argue that the Kong appearance on day 1 cued segmentation due to prediction-error mechanisms in a manner similarly to what has been observed in human studies (Zacks et al., 2007; Sargent et al., 2013).

In chapter 3 of this thesis, it was shown that mice were able to use conspecific presence/absence as a contextual information to separate and distinguish specific events in memory (chapter 3, section 4.2.1.). Yet, this was not the case when an additional local object could act as context specifier (chapter 3, section 4.2.2.). The results from these experiments in spontaneous recognition paradigms highlight important points regarding segmentation in non-human animals. Firstly, the presence/absence of conspecifics may equally act as a segmentation cue during continuous experience in an environment (as similarly suggested in humans, Zwaan et al., 1995; Milivojevic et al., 2016). Secondly, some changing aspects in ongoing experience may not effectively cue segmentation or act as context specifiers in

memory, and in combination to the former and latter points, not all segmentations act equally for mnemonic processing in non-human animals. For example, Qiao and colleagues (2023) recently report a variation of a serial novel object recognition task in female mice, where the environment was comprised of 4 quadrants separated by moveable doors. During habituation mice explored pairs of objects in each quadrant for ~5-minutes led in a specific sequence by experimenters, and importantly each quadrant was distinctly contextually specified. It was found that mice could discriminate the novel object in up to 3 out of 4 quadrants, observing a strong primacy but weaker recency effect after an 80-minute delay. Interestingly, however, recognition performance was significantly worse in the 3rd quadrant as opposed to all the other quadrants. Yet exploration time was comparable to the 2nd and 4th quadrant. The experimenters interpret such findings from a capacity issue, but this does not solely explain why performance was worse specifically in the 3rd quadrant. An alternative interpretation from a segmentation perspective would argue that transitions between quadrants could prompt event bounding, as each quadrant was distinctly contextually specified (c.f. chapter 1, section 2.4.3.). In this way, an interpretation where salience of the event boundaries decreases over the quadrant sequence (some resurgence after the 4th quadrant as mice were likely handled out of the environment i.e., different segmentation) could also explain the overall behavioural pattern. Together, such work suggests that not all event boundaries are processed equally in non-human animals which is again similar to humans (e.g., Radvandsky, 2012).

One limitation of the aforementioned spontaneous recognition experiments (chapters 2 and 3), was that potential segmentation cues (probe trials and conspecifics, respectively) were accompanied by spatiotemporal shifts imposed by the experimenter, which likely also influenced event bounding (bridging of chapter 3 and 4). However, this was rectified in chapter 4, where an event segmentation paradigm showed that humans were more likely to segment around turns at spatial boundaries (and positioning around spatial boundaries influences memory, appendix A). Importantly, previous work with rats has shown that turns made around spatial boundaries modulated the activity of grid and place cells by resetting the activity at turns into a new part of a familiarised environment (Derdikman et al., 2009).

Together, this supports the notion that non-human animals also segment their experience during turns around spatial boundaries similarly to humans.

The evidence reported in the general introduction and chapter 1 demonstrates that non-human animals not only perceptually construct events similarly to humans (chapter 1, section 2.3), but also behaviourally express the capability of episodic-like memory (general introduction, section 1.2.). Naturally, this would infer that segmentation-like processing which bridges perception and episodic-like memory (potentially considered as an extension of perceptual processes) also occurs in non-human animals, as it does in humans for episodic memory). Collectively, the results from chapter 2 to 4 and re-interpretation of existing evidence from a segmentation perspective (e.g., chapter 1, section 2.4.3), would argue that non-human animals do similarly segment their continuous experience for episodic-like memory, like humans segment their experience for episodic memory.

7.2. Episodic indexing: discrete versus gradated coding?

Hippocampal indexing theory, as introduced in chapter 5, seeks to explain why episodic(-like) memory is critically dependent on the hippocampus (Teyler & Rudy, 2007; Goode et al., 2020). As mentioned in chapter 5, section 6.4.4., Kolibius and colleagues (2023) recently presented evidence that single hippocampal cells in human participants increase their firing during specific formulated episodes and show a reinstated increase in firing when shown a partial cue of that initial integrated episode. They argue that these termed episode specific neurons (ESNs; and potential indexing cells in general) show no initial tuning and are allocated to a specific episode during memory formation (some neurons did show activity to the onset of a visual stimulus, but their activity was maximal during the episodic formation). Here, this will be referred to as ‘discrete’ index coding by individual cells.

It is necessary to contextualise such findings with the task that participants were asked to complete. Participants were first shown an animal image stimulus and were then asked to vividly create a mental story consisting of the animal image with one or two associate images (faces or places), rating their plausibility after. This encoding period spanned over seconds, and this was the timeframe used to detect

potential episode specific neurons (an encoding block contained around 20 episodes). After an encoding block and a distractor phase, the animal image was shown again, and participants were asked to retrieve the associated images. Again, a window of 2-3 seconds after, the animal cue onset was used to detect episode specific neurons and importantly, each episode was learned and retrieved once.

If one considers such a paradigm through the lens of event segmentation, the onset of the stimuli and the goal change of being asked to create and imagine the story from the associative cues could arguably be interpreted as the bounding of an event. Hence, one could speculate that these ESNs were also sensitive to event boundaries (c.f. Zheng et al., 2022). Therefore, could one expect discrete index coding by these episode specific neurons for all segmentations, no matter how coarse or fine? It seems unlikely that every event boundary could evoke discrete index coding as this mechanism alone would be biologically and computationally taxing (Laughlin et al., 1998). Estimates yielded from the supplementary tables reported by Kolibius et al., (2023) show that on average ~26% of all recorded hippocampal single units were ESNs, with average trial number being ~61. Thus, only ~16% of trials recruited discrete index coding despite all trials being perceptually eligible as unique episodes. Moreover, Trouche and colleagues (2016) report discrete-like coding in mice, where repetitive opto-silencing of tagged active CA1 place cells in spatial context led to the emergence of another ensemble of place cells that were markedly silent previously. Similarly, Radvansky and colleagues (2021) show that CA1 place cells discretely remapped when mice change between engaging in a visual-based task versus an odour-based task in otherwise the same virtual environment (arguably a goal-change driven event boundary, Clewett et al., 2019). Hence, the argument here does not aim to question the existence of discrete index coding, but it does highlight the limits if this were to be the only coding mechanism in place.

The preliminary results reported in chapter 5 offer an alternative view and complementary coding mechanism. In contrast to discrete index coding, the place cells recorded from mice in chapter 5 were already active in baseline trial A and then seemingly formed a simultaneously integrated episodic representation (specific object-context association) in trial B. Here, one can argue for a gradated indexing

code in which some active cells (in this case those that exhibited place tuning) readily assimilate new input in forming an episodic index. This echoes the associative activity by human hippocampal formation units by Ison and colleagues (2015), where units initially had a preferred stimulus (e.g., person) versus a non-preferred stimulus (e.g., place) as indicated by higher firing rates for the preferred stimulus. After exposing participants to a composite stimuli (i.e., person in place) some cells were seen to respond with higher firing to the initially non-preferred stimulus (e.g., the place) after this learnt association (but not to other place stimuli). Additionally, Cai and colleagues (2016) showed in mice that CA1 ensembles activate in different spatial contexts were more overlapping when separated by 5 hours as opposed to 7 days (in accordance with intrinsic excitability playing a role, see also chapter 5, section 6.4.1.). Indeed, accumulating evidence demonstrates how task-responsive single units in the hippocampal formation exhibit mixed selectivity (Ledergerber et al., 2021; Jercog et al., 2019; Gulli et al., 2020). In this way, rapid hippocampal plasticity mechanisms allow for already active cells to incorporate associative information, with some of these associations reflecting content of episodic nature, hence formalising episodic indices without a need for significant recruitment of more cells.

Why would discrete versus gradated mechanisms have evolved in animals? Discrete indexing by the hippocampus may be more associated with reducing interference for learning and memory of salient experiences (e.g., valanced and or novel). This is supported for example, by the rodent contextual fear conditioning literature (e.g., Tonegawa et al., 2015), where Bonapersona and colleagues (2022) report that aversive shocks can activate subsets of cells in over 95% of brain regions and the activity changes in a region-dependent manner. And Roy and colleagues (2022) observed that many brain regions are activated by retrieval of a single fear memory. In this way, a discrete indexing mechanism may not be unique to the hippocampus, but as Goode and colleagues (2020) argue, the hippocampus may be in a unique position to orchestrate such indexing. At the same time, however, this is not to say that gradated indexing does not also support salient experiences such as foot shocks (Schuette et al., 2020), just that the probability of discrete indexing being utilised increases with salience. Another reason, specifically necessary of gradated

indexing, is to always allow a certain proportion of cells to be 'in reserve' for potential allocation to future (salient) experiences (Frankland & Josselyn, 2018). For instance, Thompson and Best, (1989) report that only 36.8% of units in rats were reliable active CA1 place cells in any of the recorded spatial context, whereas Eliav and colleagues (2021) state that 83.4% of units were active CA1 place cells in bats flying in a large 200m space. Thus, even with the latter study exhibiting a ~2.3-fold greater proportion than the former, a proportion of cells were still markedly silent. Finally, while these hypotheses are attractive from a cognitive standpoint, one should note that balance of hippocampal excitability and inhibition are not only important for indexing (chapter 5, section 6.4.1.), but an abnormal balance can result in epileptic pathology (Cavazos & Cross, 2006) and regulate non-cognitive functions (Tingley et al., 2021; Buzsáki, 2015).

To summarise, the discrete versus gradated coding mechanisms highlighted here have been long discussed in relation to cognitive mapping with some starting relations to episodic memory (O'Keefe & Nadel, 1979; Jeffery et al., 2004; Leutgeb et al., 2005; Kubie et al., 2020). However, in explicitly linking these mechanisms to indexing and event segmentation (see Fig. 1), they can form part of the working

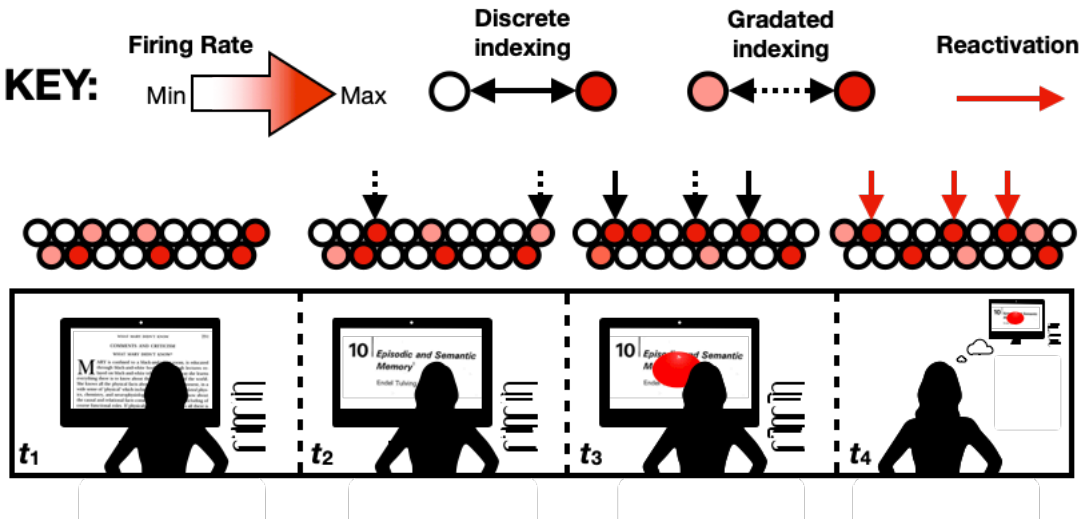

Figure 1. Schematic of indexing and event segmentation using the Mary's room thought experiment. Left to right: At t_1 Mary is reading a paper and once she finishes, begins reading another paper at t_2 (middle-left). The upper schematic shows that some cells (red-circles) which were active at t_1 have become more active in t_2 via gradated coding (or in the case of place cells, have developed a new firing field, c.f. chapter 5, section 6). At t_3 the red stimulus suddenly appears (middle-right), this salient change affords indexing in a discrete and gradated manner. Finally, at t_4 (right) later when Mary recalls the event of t_3 these indexing cells (of t_3) become reactivated. Notably, the transition from t_1 to t_2 is a finer-grained segmentation relative to the transition between t_2 and t_3 which is a coarser-grained segmentation (see general introduction, Fig. 1).

hypotheses to explain, at least on the cellular and meso-circuit level, how and why episodic memory is critically dependent on the hippocampal formation. Yet, one cannot ignore the roles of other regions beyond the hippocampal formation.

7.3. Beyond the hippocampal formation

The present thesis has focussed upon the hippocampal formation as this region is critically associated with the success of episodic recollection and there is an extensive literature upon the neural correlates of content representation in the hippocampus. However, converging evidence highlights that the medial diencephalon with regions such as the anterior thalamic nuclei and mammillary bodies are also critically involved with episodic memory (Aggleton & O'Mara, 2022). In line with hippocampal episodic indexing theory, some possibilities arise as to how to reconcile the hippocampal formation stream and medial diencephalic steam (Aggleton & O'Mara, 2022). Place-like units have been reported in the dorsal subiculum and anterior thalamus (Jankowski et al., 2015) and anterior thalamic lesions disrupt spatially-modulated firing in the dorsal subiculum (Frost et al., 2021). Thus, an attractive hypothesis as alluded to earlier, is that output of the hippocampal index forms critical indices in the subiculum and anterior thalamus that are also required for successful recall (with place-like units potentially playing an indexing role, Kitanishi et al., 2021). In support of such a view, Roy and colleagues (2022) showed that both the antero-medial and antero-ventral nuclei are strongly activated during perception of a shock and retrieval of that contextual fear memory in mice. On the other hand, the medial diencephalon may contribute to the formalisation of a functional hippocampal index (McNaughton & Vann, 2022). For example, Ito et al., (2018) reported that opto-inhibition of neurons in the supramammillary nucleus reduced the coordination of firing between CA1-nucleus reuniens-medial prefrontal circuit in the theta range when rats were at the choice point of a T maze.

To reiterate indexing mechanisms are not unique to the hippocampal formation (Goode et al., 2020) and exist in numerous regions such as the thalamus, amygdala, and medial prefrontal cortex (Roy et al., 2022; Auguste et al., 2023; Kitamura et al., 2017; Weible et al., 2012). However, converging evidence from

various neuroscience literatures demonstrate that the hippocampal formation and medial diencephalic regions are indispensable for successful episodic memory recall likely due to indexing functions of these regions (Vargha-Khadem et al., 1997; Aggleton & O'Mara, 2022; Ferguson et al., 2019; Maguire & Mullally, 2013; Aggleton & Brown, 1999; Elward et al., 2021; Ryan et al., 2015; Teyler & Rudy, 2007; Goode et al., 2020; chapter 1, section 2.6.2.).

7.4. Is episodic-like memory simply episodic memory?

Event segmentation provides a lens for episodic processing in terms of recent experience. Based on the research of this thesis and existing literature it seems reasonable to conclude that:

I) Non-human animals perceive scenes similarly to humans (monitored over time this describes event perception).

II) Non-human animals segment their experience similarly to humans.

III) They also display the biocomputational means to support the formalisation of episodic representations via indexing.

IV) Accumulating evidence also suggests that these indices are reactivated during mnemonic retrieval.

V) Non-human animals display appropriate behaviour in tasks that are solved using episodic-like memory.

Despite there not being an explicit link (currently available) between III-V, i.e., episodic indices and behaviour in an episodic-like memory task (chapter 5, section 6.4.3.), one certainly could make the argument that episodic-like memory is episodic memory (Eichenbaum et al., 2005). However, reluctance to do so may be due to the phenomenological aspect concomitant with human episodic memory (Tulving, 2002; Klein, 2015).

There is no clear scientific consensus as to how phenomenological consciousness arises in biological systems (LeDoux et al., 2023), yet, it has been used to develop memory taxonomy (e.g., declarative and non-declarative memory, Squire & Zola-Morgan, 1991) and remains an integral part of human episodic memory (Klein, 2015; Rugg & Renoult, 2020). The present issue at the time of

writing, is that one cannot ignore the introspective evidence from humans (Zaman & Russell, 2022) nor can one test in a falsifiable manner phenomenological consciousness in non-human animals. However, researchers have tried drawn parallels with humans by considering various behavioural dimensions in the context of an animal's habitat (e.g., Birch et al., 2020; Templer & Hampton, 2013).

A hypothesis stemming from the ability of episodic memory is that of mental time travel (MTT; Corballis & Suddendorf, 1997; Buonomano, 2017). The cognitive process of MTT is also based in phenomenology and describes the mental projection of oneself into past experiences, but also projection of oneself into imaginary and or hypothetical future events (allowing foresight, Cheng et al., 2016). The activity of place cell sequences in the rodent hippocampus shows such representation of awake replay experience and prospective coding on the scale of seconds (e.g., Diba & Buzsaki, 2007; Kay et al., 2020, respectively). And recently, Lai and colleagues (2023) reported that rats could volitionally use their hippocampal activity relating to places in a virtual environment to be 'jumped' there or move virtual objects there in a goal-directed manner. Moreover, work has also shown that non-human animals are capable of meta-cognition about their memory confidence of previous experiences (Hampton, 2001; Joo et al., 2021). However, because there is 'no traveller' (i.e., autonoesis, Tulving, 2002), human MTT is considered distinct (Cheng et al., 2016; Redshaw, 2014) and such a debate will likely continue for a long time (e.g., LeDoux et al., 2023; Crystal & Suddendorf, 2019; Solms, 2021). Yet, if the preliminary finding that place cells can represent episodic content is upheld and that they casually influence behavioural expression of episodic-like memory, perhaps it is necessary to clarify what is meant by episodic memory. For example, some authors have attempted to disambiguate event memory from autonoetic-dependent episodic memory.

In the account of Keven (2016) some of the features of event memory include retention of temporal slices as determined by event boundaries, represent predominately as visual images with high accuracy, with encoding being unconscious and recall being rapid and cue driven. On the other hand, episodic memory retains narrative binding over longer timescales determined by one's goal or attempted outcome structures. Additionally, episodes are represented in the form of

narratives with lower accuracy and encoding is conscious with recall being cue driven or voluntary (Keven, 2016). In Rubin and Umanath's (2015) view event memory is "the mental construction of a scene, real or imagined, for the past or the future. The scene can be experience as happening to the person recalling it or imagined as happening to another person." (Rubin & Umanath, 2015, p. 1). Here, autonoesis is not a necessary component of event memory but event memory also lacks a uniqueness in this view. Both of the aforementioned conceptualisations of event memory offer key insights relevant to whether episodic-like memory is episodic memory relevant to the conclusions of this present thesis.

The view here concludes that episodic-like memory is not episodic memory. The introspective evidence in humans (e.g., Zaman & Russel, 2021; Perrin et al., 2020) cannot be ignored and as previously stated there are no current methods available to access introspection in non-human animals. What can be argued based on I-V (earlier of this section 7.4.) is that in some ways episodic-like memory can be considered as event memory. Like episodic memory, event memory is equally uniquely specified by event segmentation, but lacks the autonoesis and yet, importantly, the biocomputational mechanisms involved in event memory are similarly necessary for successful episodic memory (i.e., indexing, section 7.2.). In this way, humans likely also experience various forms of episodic cognition including event memory as non-human animals may experience it (c.f., Rubin, 2022; Gilboa & Moscovitch, 2021; Palombo et al., 2018; Manning, 2021; Tanguay et al., 2023). For example, Vargha-Khadem and collegues (1994) report the case of an adolescent boy Neil, who had damage to his hippocampal formational of the left hemisphere (including other regions). Neil had impaired episodic memory but could arguably retrieve event details implicitly. He could write briefly about specific spatiotemporally contexts he had visited with the clinician during the day, although he could not recognise his own writing. The clinicians confirmed that most information he wrote was accurate, but when asked whether one of the events had really happened, he replied "I just have a slight feeling inside me". (Vargha-Khadem et al., 1994, p. 693). One can wonder whether this is like the subjective experience of episodic-like memory for a non-human animal.

7.5. Conclusion

The evidence gathered in this thesis has suggested that non-human animals similarly segment their continuous experience for subsequent episodic-like (event) memory, like humans segment their experience for episodic memory. While it strengthens the view that there are overlapping biocomputational cognitive mechanisms shared between humans and non-humans in the processing of events, there is still reservation to the claim that episodic-like memory is simply episodic memory. This is due to the phenomenological aspect of episodic memory that is not fully understood in any species. But notably, 'absence of evidence is not evidence of absence'. Future work may further bridge the gap between humans and non-human animals to ultimately understand how the brain via episodic recollection, as Tulving put it: "violates the law of the irreversibility of the flow of time…in the reality of the mind [of course]" (Tulving, 2002, p. 2). Thus, episodic memory remains one of evolution's enigma, but substantial progress in the scientific understanding of it has been made and one should be confident that steady progress will continue.

7.6. References

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8. Appendix A: Memory experiment in the corridor arm maze of chapter 4 (preliminary evidence that word position in the maze affects word recall)

8.1. Methods

This present work describes the methods and results from one trial of a word recall experiment in the corridor arm maze (see chapter 4, section 5). For these present analyses, one participant (of the original 40 participants) was excluded for failure to recall any words. Thus, the data from 39 participants were analysed (29 female, 18-30 years, M_{age} = 19.84, SD_{age} = 2.52).

Words were positioned along every corridor at the start, middle and end, once the agent had made its first turn in the maze (see Fig. 1; always placed upon the boundary facing west, relative to the agent's starting position regarded as north). Words were of 3-5 letters, 1 or 2 syllables and never begun with the same letter (Table 1). The length of word was counterbalanced across positions within corridors. Details of the participant recruitment, materials and experimental procedure of the entire experiment are provided in (chapter 4, section 5). Briefly, participants were

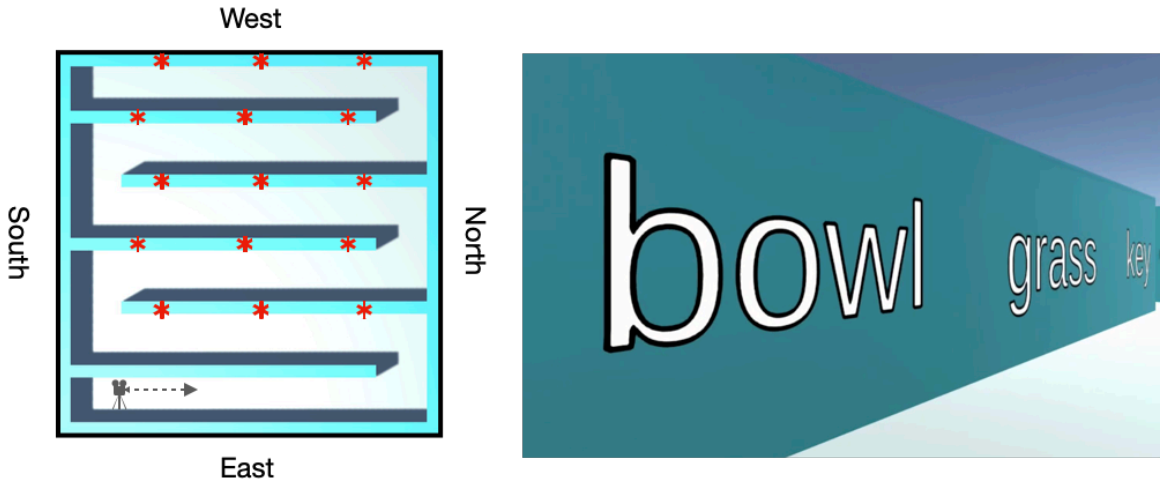

Figure 1. Schematic of the virtual corridor arm maze with word stimuli. Left: In experiment 1, participants passively viewed the agent traversing a fixed path from a first-person perspective in the corridor arm environment with words placed along the start, middle and end within a corridor, once the agent had made its first turn (all placed along the west boundary, relative to the agent's starting position being north). Right: example video frame once the agent had made a right turn into a new corridor.

aware that the purpose of the study involved memory from the information provided before consent, however preceding the word video stimulus participants were just informed that “another video will begin next”, and to click the screen to continue to the video. Immediately after the video ended participants were asked to “recall as many words as possible, in order that you like”, typing their responses (in ~60s) before being debriefed and the experiment ending.

Given that participants were not reminded of a possible memory test immediately before the trial, and that they did not have an unlimited amount of time we tolerated some error in spelling for the words being considered as correctly recalled. The addition, omission, or a replacement of a letter were acceptable when the actual word was not in the recall list. For example, ‘glass’ instead of grass (replacement), but only if grass was not recalled. ‘Cane’ instead of canoe (omission example), ‘dinner’ or keys instead of diner or key (two addition examples, respectively). The only exception to these rules was one case of an incorrect spelling but phonetically correct, ‘canno’ instead of canoe, all other listed words were considered incorrect. To analyse the potential effect of corridor order (1-5) and word position (i.e., start, middle and end within corridors) the data was scored in binary, 0 no/incorrect recall and 1 correctly recalled in that corridor/ position, before being subjected to analysis of variance (ANOVA). Reported post-hoc tests were Bonferroni corrected for multiple comparisons.

Table 1
Word list used in the recall trial by corridor and position.

Corridor	Start word	Middle word	End word
1	sap	yard	diner
2	bowl	grass	key
3	fence	limb	rod
4	opera	tile	ant
5	wick	mat	canoe

8.2. Results

The mean proportion of words correctly recalled from the absolute total was 33% (Md = 26.7% SD = 18.1%). With the proportion of total words listed to those being correctly recalled target words being 81% (Md = 85.7%, SD = 20.1%), significantly differing from 100% ($Z = -4.30$, $p < 0.001$, $r = 0.79$, one-sample Wilcoxon signed rank test, see methods for tolerance of spelling errors). This suggested that some participants had falsely remembered words, consistent with previous memory research using word lists (Roediger & McDermott, 1995).

To assess the potential effect of corridor order and word position a repeated measures ANOVA was conducted. There was no significant main effect of 'corridor' (i.e., the order of the corridor in the maze; $F_{(4,152)} = 0.24$, $p = 0.92$, $\eta_p^2 = 0.006$), but a significant main effect of 'word position' (i.e., word positions within corridors, 'start', after an agent had made its turn, 'middle' and 'end', before an agent made its turn; $F_{(2,76)} = 5.02$, $p = 0.009$, $\eta_p^2 = 0.12$). There was also an overall significant interaction between corridor and word position ($F_{(8,304)} = 2.28$, $p = 0.02$, $\eta_p^2 = 0.06$). Interestingly, post-hoc test showed that there was comparable amount of recall across corridors (Fig. 2A, all $p = 1.00$). However, end words (M = 0.37) were recalled significantly more than middle words (M = 0.27, $p = 0.012$; Fig. 2B). There was a comparable level of recall between start (M = 0.36) and end, and start and middle words ($p = 1.00$, $p = 0.06$; respectively). For the interaction, post-hoc tests yielded no differences within word positions across corridors (all $p \geq 0.18$). However, within corridor (see Table 2), there was evidence of a primacy effect within the 4th corridor, with the start word (M = 0.41) being recalled significantly more than the middle word (M = 0.21, $p = 0.029$). Also, there was evidence of a recency effect in the last corridor with the end word (M = 0.51) being recalled significantly more than the start and middle words (M = 0.23, M = 0.21, $p = 0.029$, $p = 0.017$).

To summarise, this evidence suggested that 1) contrary to classic word recall list experiments where there are typically primacy and recency effects found (e.g., Jahnke, 1965) this was not seen at the corridor-level. That is, recall level was consistent across corridors (Fig. 2A), whereas one would have predicted better recall in the first and last corridor if expecting a primacy and recency effect, respectively.

However, 2) there was evidence of some within corridor primacy and recency effects at the penultimate and last corridors, respectively. 3) Across corridors, words at the

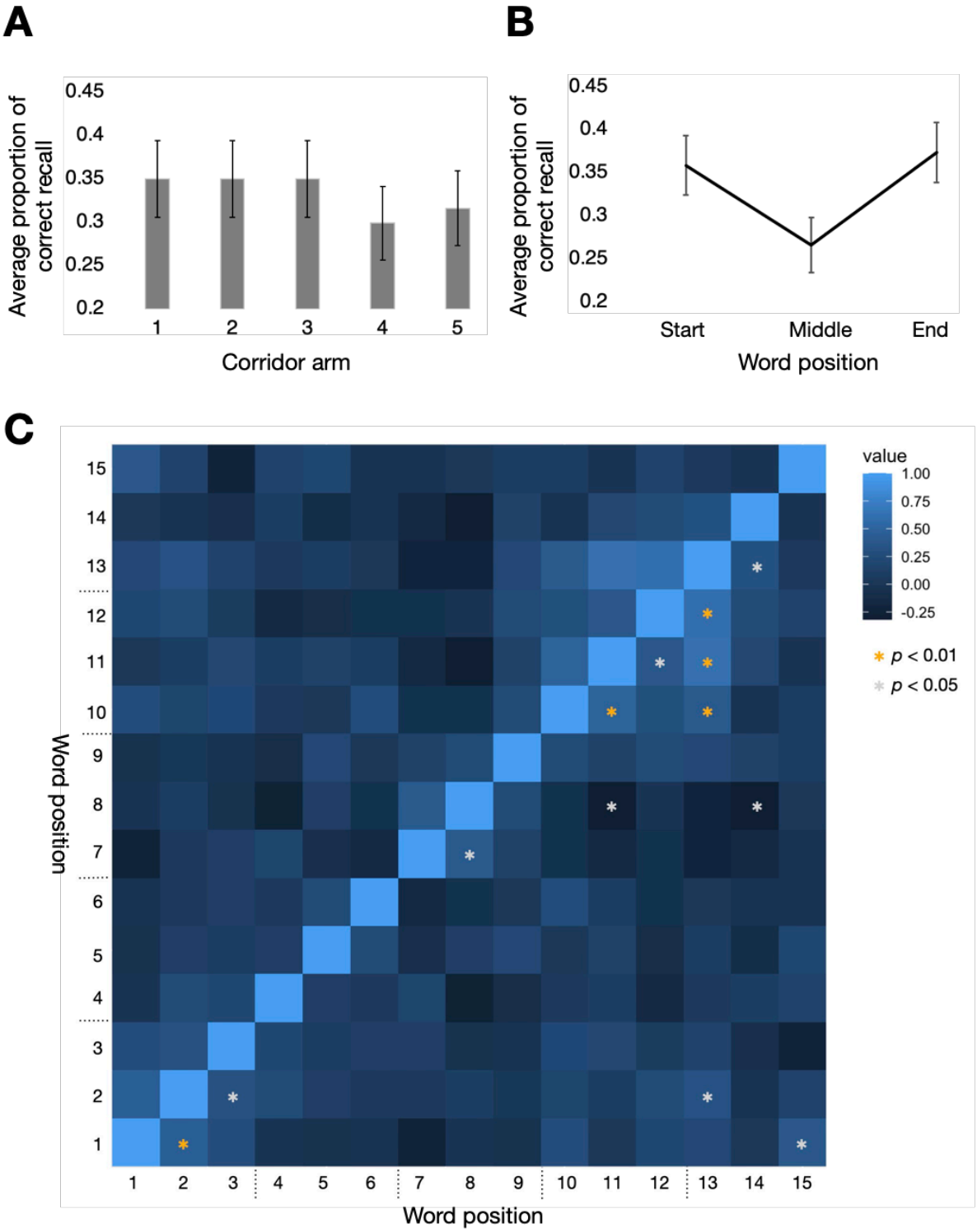

Figure 2. Word position influences memory in the corridor arm maze. **(A)** The average proportion of correct recall by corridor arm. **(B)** The average proportion of correct recall by word position. **(C)** Correlation matrix representing the relationship of recall between pairs of words by word position across participants (Spearman's rank correlations). Silver asterisks denote $p < 0.05$. Gold asterisks denote $p < 0.01$.

end of the corridor were better remembered more than words in the middle of the corridor (Fig. 2B). Given this latter finding, we lastly sought to ask what was the relationship between recalling a given word and another given word. We found evidence of 'chained' recall, significantly positive correlations between positions of words that tended to be sequentially perceived within corridors (e.g., 1st, 3rd, 4th and 5th corridors, $p < 0.05$; see Fig. 2C,). Interestingly, there was also evidence of some paired-recall across the penultimate and last corridors, suggesting stronger evidence of a recency effect when considering recall beyond single words. Thus, we preliminarily conclude that word position and corridor position influences memory recall in the corridor arm maze. This further suggests that using such stimuli (e.g., the corridor arm maze) is a potential way to better understand the relationship event segmentation behaviour and episodic memory (see Chapter 4, section 5).

Table 2

Post-hoc comparisons within corridor for the interaction between corridor and word position.

Corridor	Position (Mean)	Position comparison	*p*
1	Start (0.46)	Middle	0.10
		End	0.33
	Middle (0.28)	End	1.00
	End (0.31)	-	-
2	Start (0.28)	Middle	1.00
		End	0.69
	Middle (0.36)	End	1.00
	End (0.41)	-	-
3	Start (0.41)	Middle	0.40
		End	1.00
	Middle (0.28)	End	1.00
	End (0.36)	-	-
4	Start (0.41)	Middle	0.029*
		End	0.51
	Middle (0.21)	End	0.97
	End (0.28)	-	-
5	Start (0.23)	Middle	1.00
		End	0.029*
	Middle (0.21)	End	0.017*
	End (0.51)	-	-

* $p < 0.05$

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