

Multivoxel pattern similarity suggests the integration of temporal duration in hippocampal event sequence representations



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ABSTRACT

Recent rodent work suggests the hippocampus may provide a temporal representation of event sequences, in which the order of events and the interval durations between them are encoded. There is, however, limited human evidence for the latter, in particular whether the hippocampus processes duration information pertaining to the passage of time rather than qualitative or quantitative changes in event content. We scanned participants while they made match-mismatch judgements on each trial between a study sequence of events and a subsequent test sequence. Participants explicitly remembered event order or interval duration information (Experiment 1), or monitored order only, with duration being manipulated implicitly (Experiment 2). Hippocampal study-test pattern similarity was significantly reduced by changes to order or duration in mismatch trials, even when duration was processed implicitly. Our findings suggest the human hippocampus processes short intervals within sequences and support the idea that duration information is integrated into hippocampal mnemonic representations.

Introduction

A fundamental property of episodic memory is that it is organized in time, enabling us to remember when past events took place (Tulving, 1972). Given its importance to episodic memory, there has been significant interest in how the medial temporal lobe (MTL), in particular the hippocampus (HC), contributes to the temporal organization of memory. Two potential frameworks by which the HC may structure memories are ordinal representation and temporal representation (Howard and Eichenbaum, 2013). In the former, the temporal order of events is preserved while the actual durations of intervals between events are discarded, whereas in the latter, both order and durations are encoded, leading to temporally richer mnemonic representations.

Much evidence points clearly towards a role for the HC in supporting the ordinal structure of memories. In rodents, lesion and electrophysiological work has implicated the HC in processing the sequential order of events (Fortin et al., 2002; Kesner et al., 2002; Manns et al., 2007). Similarly, patients with HC damage possess impaired temporal order memory (Mayes et al., 2001; Shimamura et al., 1990) and functional MRI (fMRI) research has revealed that HC activity can reflect subsequent memory for sequence order, the disambiguation of overlapping event

sequences, and the temporal position of individual items within a sequence (Hsieh et al., 2014; Kumaran and Maguire, 2006; Lehn et al., 2009; Tubridy and Davachi, 2011).

Beyond an ordinal framework, there is also evidence to suggest that the HC may process a temporal representation of events, although its precise role remains uncertain. For example, while there is a general consensus that HC dysfunction can impact performance on tasks in which there is an explicit requirement to process temporal duration (e.g. prospective timing) (MacDonald, 2014), there are discrepancies across studies regarding the extent to which the HC is involved. Rodents with HC or fornix damage demonstrate poorer timing compared to controls when they are required to respond to a stimulus after a specified interval of seconds (Meck et al., 1984; Olton et al., 1987; Yin and Meck, 2014). In contrast, human patients with selective HC damage can be impaired when asked to estimate or reproduce a temporal duration but critically, only when durations are relatively long and not on the order of seconds (Noulhiane et al., 2007; Palombo et al., 2016; Richards, 1973; Shaw and Aggleton, 1994). Similarly, functional neuroimaging studies have typically not observed HC involvement in interval judgment tasks involving short durations (Bueti et al., 2012; Coull et al., 2008), with the exception, to our knowledge, of one report of HC activity during the encoding of

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intervals less than 2s (Harrington et al., 2004). Notably, the relative lack of evidence for human HC involvement in processing short durations may be explained, at least in part, by the nature of the paradigms that have been employed, and the use of stimuli that are not typically associated with HC involvement. For instance, the majority of human prospective timing tasks have examined the processing of single durations, in many cases, demarcated by basic sensory stimuli, which contrasts with the rich sequence information that is associated with HC-dependent memories. Suggestive of the possibility that the HC is involved in processing short durations in the context of sequences, we previously found using fMRI that HC activity is sensitive to explicit changes in the durations of intervals within sequences of spatial scene stimuli (Barnett et al., 2014). Critically, however, only the overall magnitude of HC activity was examined in this study, rendering it unclear as to whether duration information is itself encoded into HC representations.

Additional evidence for a role of the HC in processing a temporal representation of events comes from studies that have investigated the implicit processing of duration information (e.g. retrospective timing). Since temporal information is often encoded implicitly and our appraisal of the temporal structure of past events is typically retrospective in nature, this distinction between prospective and retrospective timing is a crucial one. Perhaps the most striking rodent evidence, to date, comes from studies that have demonstrated the existence of CA1 neurons that fire during the empty delay period between two discrete events (MacDonald et al., 2011). Since different neurons are active at different time points and their activity cannot be explained by HC-dependent spatial

processing (Kraus et al., 2013; MacDonald et al., 2013), these ‘time cells’ are suggested to bridge the gap between events by encoding duration information and signalling the passage of time.

In humans, the role of the HC in retrospective timing has been examined by exploring the impact of temporal distance on neural activity (Deuker et al., 2016; Ezzayat and Davachi, 2014; Lositsky et al., 2016). Recent work has reported more similar multivoxel patterns of fMRI activity in the HC for events that are subsequently judged to have occurred close in time as compared to those judged to have occurred far apart, suggesting that such information may be integrated into HC mnemonic representations (Deuker et al., 2016; Ezzayat and Davachi, 2014). It is important to highlight, however, that judgements of temporal distance in these studies were not based simply on the passage of time but the nature and quantity of intervening event information, for instance, whether an event boundary was traversed or the number of elapsed events between two stimuli. It remains to be seen, therefore, whether human HC activity reflects the actual durations of implicitly processed intervals within event sequences, in a manner akin to that observed in the rodent HC during an empty interval between two events.

Across two experiments (Fig. 1a–b), we used fMRI in conjunction with multivoxel pattern similarity analysis (Kriegeskorte, 2009; Kriegeskorte et al., 2008), to explore HC processing of temporal information during sequences of events. To address the aforementioned gaps in the literature pertaining to temporal representation, we examined how HC event sequence representations were impacted by changes to the durations of intervals separating events, in the context of explicit and implicit

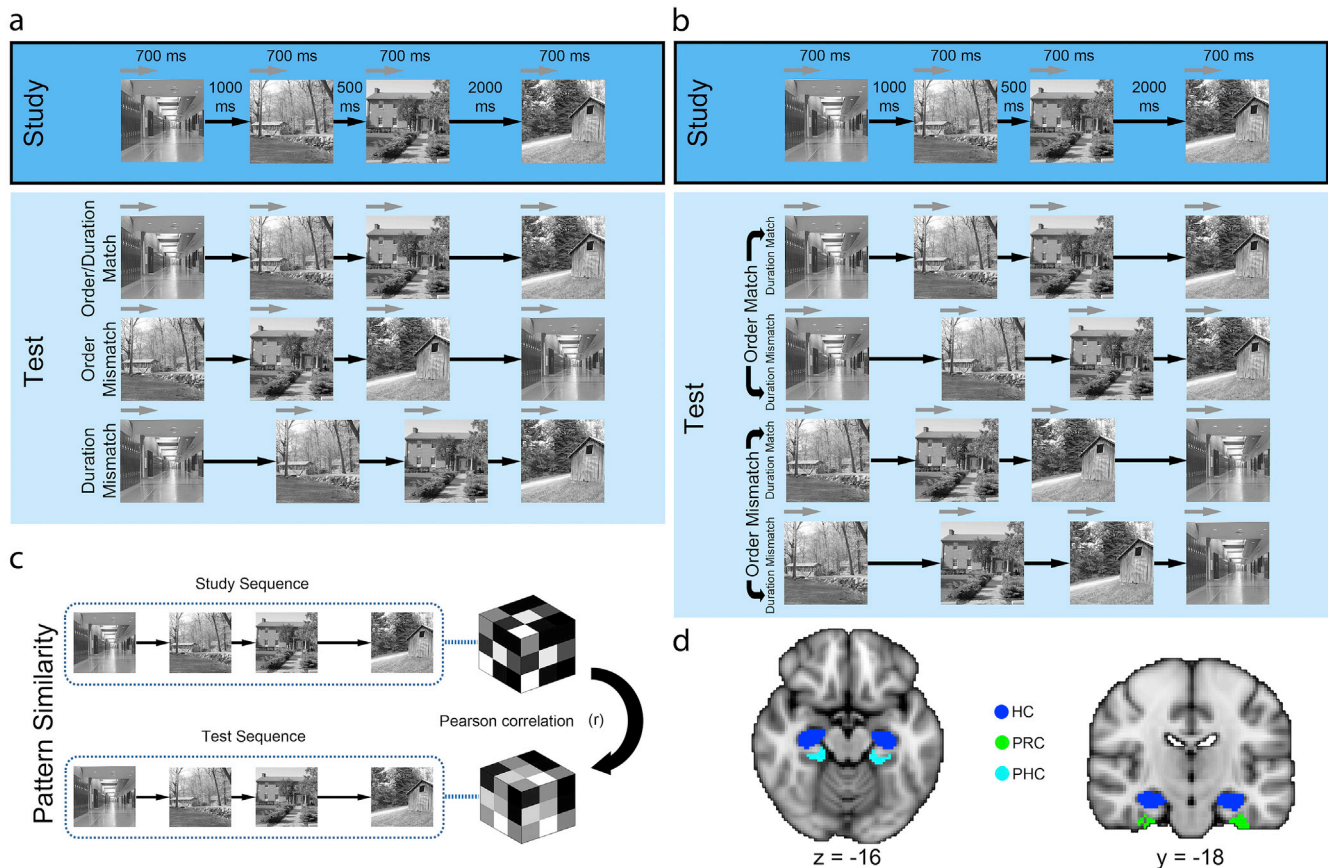


Fig. 1. Schematic of the study and test phases of the different trial types in (a) Experiment 1; and (b) Experiment 2. In Experiment 1, participants were instructed to remember either the order of the scene images or the durations of the inter-stimulus intervals (ISIs). In Experiment 2, participants were asked to remember the order of the scenes only, with ISI durations being manipulated implicitly. The study and test phases were separated by a jittered 3500 ms fixation cross, and participants were asked to indicate their response during a 2500 ms response screen at the end of each test phase. ISIs were trial unique, with the mean ISI values shown in the figure. (c) Activation patterns for each study and test sequence were compared using a Pearson correlation, resulting in an estimate of study-test pattern similarity for every trial. Correlation values (r) were transformed using Fisher's r -to- z transformation and then averaged by condition before being entered into nonparametric statistical tests. (d) A priori regions of interest (ROI) that were examined.

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