

Prior knowledge influences on hippocampus and medial prefrontal cortex interactions in subsequent memory



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ABSTRACT

Prior knowledge is known to influence the encoding of new events. Specifically, recent theoretical frameworks suggest that positively correlated hippocampus (HC)–medial prefrontal cortex (mPFC) activity is involved in creating enduring traces of events inconsistent with our prior knowledge. Events that are consistent with our schemas are suggested to be encoded via mPFC–cortical interactions. Previous studies examined differences in functional connectivity between subsequently remembered and forgotten items, but the source of these differences was not addressed. Therefore, the involvement of the inter-regions functional connectivity in subsequent remembering or subsequent forgetting of events is unknown. In this study, in addition to probing for a remembered–forgotten difference in functional connectivity, we also examined how connectivity differed from baseline in each of the memory conditions. At encoding, the participants were presented with pairs of semantically related (schema-consistent) and semantically unrelated (schema-inconsistent) words. A surprise recognition test was administered, and a subsequent memory analysis evaluating potential interactions with the HC and mPFC was conducted. Consistent with the suggested frameworks, subsequent memory modulated HC–mPFC connectivity only in schema-inconsistent events. Importantly, the HC and mPFC were positively correlated with respect to subsequently remembered schema-inconsistent items, whereas the subsequently forgotten schema-inconsistent events did not differ from baseline. We also found that positively correlated activity of the mPFC with visual and parietal regions mediated subsequent memory of schema-inconsistent items. Therefore, inconsistent events may be encoded by a network of cortical and medial temporal lobe regions.

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1. Introduction

One of the fundamental questions in cognitive neuroscience is how the brain creates and maintains a memory trace of a novel event. Typically, new events are not encoded in a vacuum; instead, they are processed in relation to already existing knowledge. In the cognitive literature, the influence of prior knowledge on the memory of new events has been widely documented (e.g., [Alba and Hasher, 1983](#); [Bransford and Johnson, 1972](#); [Craik and Tulving, 1975](#); [Schulman, 1974](#)). Recently, this issue became a topic of intense interest in the field of neuroscience (in rodents: [Tse et al., 2007, 2011](#); in humans: [Ghosh and Gilboa, 2014](#); [Kumaran et al., 2009](#); [Preston and Eichenbaum, 2013](#); [van Kesteren et al., 2013, 2010a, 2010b](#); [Zeithamova et al.,](#)

[2012](#)). Importantly, these studies identified the hippocampus (HC) and the medial prefrontal cortex (mPFC) as key regions mediating the influence of existing schemas¹ on encoding, consolidation, and retrieval processes.

A proposed framework for the involvement of the HC and mPFC in schema influences on encoding suggests that events that are consistent with our existing knowledge structures can be rapidly assimilated in these cortical knowledge structures via mPFC–cortical interactions. However, if events are inconsistent with existing knowledge, the HC–mPFC interaction mediates the construction of a new knowledge structure or the maintenance of a separate representation of the inconsistent event until it can be gradually

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¹ We use the term ‘schema’ in order to be consistent with current neurocognitive literature in the field (e.g., [Tse et al., 2007](#); [McClelland, 2013](#)). ‘Schema’ is used here interchangeably with “prior knowledge” or “existing knowledge”. While the selection of stimuli for this experiment is consistent with the core attributes of ‘schema’ as defined and described in a recent review ([Ghosh and Gilboa, 2014](#)), we are not specifically committed to one structural form of prior knowledge.

incorporated into our schemas (van Kesteren et al., 2013, 2010a, 2010b, see also van Kesteren et al. (2012)). Another framework suggests that upon encountering an inconsistent event, a conflict with prior knowledge arises, and the HC–mPFC interaction summons the retrieval of relevant information to facilitate the resolution of the conflict and incorporate the conflicting event into our knowledge (Preston and Eichenbaum, 2013). Both frameworks associate a *positive correlation* between the HC and mPFC with later memory of non-schema events.

A key prediction of these theoretical frameworks is that the HC–mPFC interaction predicts the successful establishment of memory traces of non-schema items. A recent subsequent memory (DM, difference in memory; Brewer et al., 1998; Wagner et al., 1998) study reported an approximate linear trend in which a DM effect on HC–mPFC connectivity increased as inconsistency with prior knowledge increased (van Kesteren et al., 2013). However, because *differences* in activation are ambiguous, the reported increase in the DM effect as inconsistency increases may result from divergent patterns of results, some of which are inconsistent with the notion that positively correlated activity of the HC and mPFC mediates later memory of non-schema events. For example, a pattern of results whereby the DM effect in HC–mPFC connectivity is negative for schema events but not different from baseline for non-schema events would yield the reported linear effect but may result from a negative interaction between the HC and mPFC for later remembered schema items, whereas the HC–mPFC interaction is irrelevant to later memory of non-schema items (Fig. 1A). Another possibility is that the DM effect on connectivity for schema items is not different from baseline, whereas the DM effect on non-schema items results from mediation of the later forgetting of non-schema events by negative connectivity, with base-line connectivity for later remembered non-schema items. This pattern of results indicates that the HC–mPFC interaction mediates later forgetting, rather than later memory, of non-schema items (Fig. 1B).

Similar logic also applies to mPFC–cortical interactions. Van Kesteren and her colleagues suggest that positively correlated activity between the mPFC and task-related cortical regions mediates later memory of schema events. Consistent with this suggestion, the involvement of mPFC–cortical correlated activity in subsequent memory increased as the congruency of items increased (van Kesteren et al., 2013). Nevertheless, as was mentioned, this relationship could reflect different patterns of results, and some may not support the suggested framework (e.g., negative mPFC–cortex correlation for later forgotten schema items, with baseline correlation for later remembered items).

Therefore, to provide a full examination of HC–mPFC and mPFC–cortex interactions in subsequent memory of schema and non-schema items, the investigation should not be limited to subsequent memory

differences in connectivity but should also examine the connectivity of the specific conditions, namely, subsequently remembered and subsequently forgotten schema and non-schema items. The current study attempted to pursue this aim. Based on the current frameworks (Preston and Eichenbaum, 2013; van Kesteren et al., 2010a, 2010b), we predicted a larger subsequent memory difference in HC–mPFC connectivity for non-schema items than for schema items. We also predicted that this difference would result from positively correlated activity for subsequently remembered non-schema items, which would be higher than the correlation for later-forgotten non-schema items. In contrast, for mPFC–cortical interactions, we predicted a larger subsequent memory difference for schema items than for non-schema items. This interaction was predicted to reflect positively correlated activity for subsequently remembered schema items, which would be higher than the correlation for later-forgotten schema items.

Finally, whereas the theoretical frameworks consider schema effects in a rather broad and general manner (Preston and Eichenbaum, 2013; van Kesteren et al., 2010a, 2010b, 2012), empirical studies have primarily used visual stimuli (Kumaran et al., 2009; van Kesteren et al., 2013, 2010a; Zeithamova et al., 2012) in an intentional learning paradigm (van Kesteren et al., 2013, 2010a; Zeithamova et al., 2012). In contrast, the majority of the behavioral literature regarding schema influences on encoding has utilized verbal stimuli in an incidental learning task (e.g., Alba and Hasher, 1983; Craik and Tulving, 1975; Moscovitch and Craik, 1976; Schulman, 1974). Therefore, in the current study, we attempted to extend neuroscientific research to be more similar to the behavioral investigations of prior knowledge effects (see also Maril et al., 2011; Staresina et al., 2009, who used a similar design but did not address HC–mPFC connectivity). A target item (e.g., BIKINI) was presented, accompanied by either a schema-related item (e.g., beach; schema condition) or a schema-unrelated item (e.g., eggplant; no-schema condition). Subsequently, recognition memory for the target items was tested. Functional connectivity during encoding was then examined for schema and non-schema items that were later remembered vs. later forgotten. The functional connectivity with the HC and mPFC in subsequent memory of schema and non-schema items could therefore be fully addressed.

2. Materials and methods

2.1. Participants

20 subjects (9 females; aged 22–30 years, mean age: 26 years) participated in the experiment. Data from two additional participants were excluded from the analysis; one subject was excluded because of movement exceeding 6 mm, and one subject was removed because of too few responses (responded to 61% of the trials, which was not within 3 SD of the average response rate). All of the participants

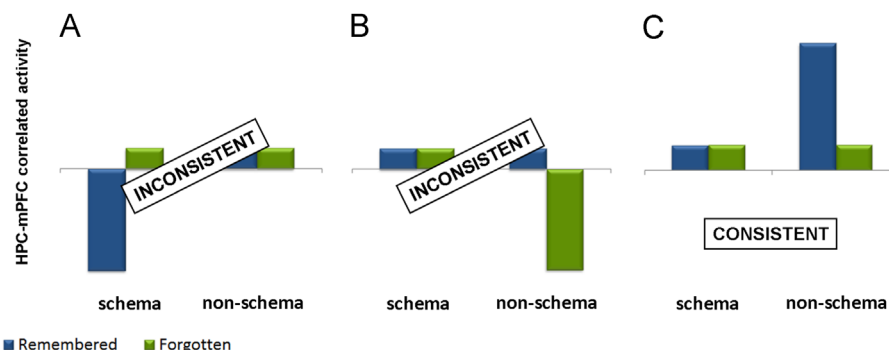


Fig. 1. Illustration of possible result patterns. All patterns yield a linear trend of the DM effect, which increases as inconsistency with schema increases. Panel A: the trend results from a negative correlation mediating subsequent memory of schema items. Panel B: the trend results from a negative correlation mediating subsequent forgetting of non-schema items. Panel C: the trend results from a positive correlation mediating subsequently remembered non-schema items. Only panel C is consistent with the suggested frameworks (see Section 1).

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