



Feedback signals in visual cortex during episodic and schematic memory retrieval and their potential implications for aphantasia

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ABSTRACT

Recent findings indicate that visual feedback derived from episodic memory can be traced down to the earliest stages of visual processing, whereas feedback stemming from schema-related memories only reach intermediate levels in the visual processing hierarchy. In this opinion piece, we examine these differences in light of the 'what' and 'where' streams of visual perception. We build upon this new framework to propose that the memory deficits observed in aphantasics might be better understood as a difference in high-level feedback processing along the 'what' stream, rather than an episodic memory impairment.

Predictive processing accounts suggest that the brain works like a prediction engine, using the knowledge it has accumulated in the past to predict present and future sensory input. A wealth of studies has shown that perceptual expectations derived from such predictions could take the form of sensory templates in (early) sensory cortices that mimic and pre-empt the expected input (e.g., see Keller and Msrsc-Flogel, 2018). Both episodic and schema-related memories can form the basis of perceptual predictions (Bosch et al., 2014; Hindy et al., 2016; Ortiz-Tudela et al., 2023; Panichello et al., 2013). Episodic memory is the memory of specific events (instances) in space and time, whereas schematic memory is derived from regularities learned over multiple encounters, and hence captures general knowledge about the world (Tulving, 1972; Van Kesteren et al., 2012). The two types of memory are not completely separate and have shown to interact: for example, schematic memories are used to bolster fading episodic memory representations and can bias them (Tompary et al., 2020; Tompary and Thompson-Schill, 2021; Zeng et al., 2021). Despite this close interaction, a recent study shows that the access to the predicted sensory information – e.g., whether it is retrieved based on episodic or schema information – determines how far down predictions travel in the visual cortical hierarchy (Ortiz-Tudela et al., 2023). In the study, subjects were presented with images of different rooms (e.g., a kitchen or bathroom) and asked to retrieve and vividly imagine objects that were associated with these either episodically (via object-room associations learnt one day before; e.g. kitchen – bathtub) or semantically (based on schematic/world

knowledge; e.g. kitchen – stove). Interestingly, multivariate pattern classification of the associated neural activity patterns showed that mnemonic information during episodic retrieval was present in both mid-level lateral occipital cortex (LOC) and early visual cortices V1 and V2. In contrast, mnemonic information during schematic retrieval was only present in mid-level LOC.

From a conceptual perspective, this finding seems to make sense: Episodic memory is the memory of specific events, whereas schematic memory captures general world knowledge deprived of any episode-specific detail (Tulving, 1972; Van Kesteren et al., 2012). Early visual areas represent low-level visual features (e.g., the precise shape of an object), and hence a level of sensory granularity that schematic memory might not possess. Consequently, predictions drawn from schema memory would be visually less efficient (e.g., with poorer or slower reactivation of perceptual features) than those drawn from episodic memory. This reduced efficiency can explain why schematic predictions are only decodable in mid or higher-level visual regions which represent content with less sensory detail.

However, apart from this conceptual difference, there is another potentially crucial factor that could explain why object features from episodic memory are decodable in early visual regions but those from schematic memory are not. Namely, the different pathways that schematic and episodic feedback take when traveling down to visual regions (Fig. 1): Episodic memory retrieval is mediated by the medial temporal lobe (MTL; Preston and Eichenbaum, 2013; Van Kesteren et al., 2012),

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with the hippocampus potentially serving as an ‘index’ for memories that can be used to reconstruct sensory components of past events. Outputs from the hippocampus may return to the cortical regions from which they arose, travelling through feedback pathways in the perirhinal-lateral entorhinal cortex (belonging to the ‘what’ stream) and the parahippocampal-medial entorhinal cortex (the ‘where’ stream), and further on to association cortices (e.g., in temporal and parietal cortex) and sensory cortices (Preston and Eichenbaum, 2013). The idea that episodic memory delivers information through both the ‘what’ and ‘where’ streams of visual perception suggests that it can provide both spatial information (‘where’) and details about the object (‘what’). Although there are no direct anatomical connections between the hippocampus and the early visual cortex, the impact of hippocampal activity on early visual cortex during the reinstatement of memories is well documented (e.g., Hindy et al., 2016, Bosch et al., 2014, Aitken and Kok, 2022).

On the other hand, memory representations of schemas are assumed to be widely distributed over the cortex (Frisby et al., 2022). There is general agreement that the medial prefrontal cortex (mPFC) plays a crucial role in forming schematic memories and in making predictions based on schemas and contextual associations (Panichello et al., 2013, Van Kesteren et al., 2012; Gilboa and Marlatte, 2017; Robin and Moscovitch, 2017; Reagh and Ranganath, 2023). Interestingly, it has been suggested that the retrieval of schematic information and contextual predictions (such as bathroom → bathtub) recruits a distributed ‘context network’ that connects the mPFC with regions in the ‘where’ stream, namely the parahippocampal cortex (PHC) and the retrosplenial cortex (RSC). This network is also thought to influence LOC (Bar, 2004; Kveraga et al., 2011; Panichello et al., 2013) in which information retrieved based on schemas is still decodable (Ortiz-Tudela et al., 2023). The notion that schematic memory primarily recruits the ‘where’ stream could hence provide a functional explanation why low-level object

feature information cannot be decoded in V1 and V2 during schematic retrieval: the ‘where’ stream is thought to carry information about spatial relationships between objects, rather than the type of information that the ‘what’ stream and early visual regions V1 and V2 are specialised on (i.e., low-level visual features of objects, e.g. object shape; Ungerleider and Mishkin, 1982).

We hence argue that the visual feedback pathways used during episodic and schematic memory retrieval may differ in terms of the two streams of visual processing: episodic memory retrieval seems to rely on both the ‘what’ and ‘where’ streams, whereas schematic memory retrieval might primarily involve the ‘where’ stream (Fig. 2).

We believe this framework could also provide new insights for the study of mental imagery. The generation of mental images and memory retrieval rely on similar neural processes, and mental images and memories share representations in early visual cortex (e.g., Albers et al., 2013; Hassabis et al., 2007; Slotnick et al., 2012). Mental imagery capacities span a wide spectrum from very vivid imagination to a complete inability to form mental images (i.e., aphantasia). Interestingly, this inability to imagine is accompanied by a strong deficit in autobiographical memory, and episodic memory in general (Dawes et al., 2020). In contrast, schematic memory is less affected, at least when the knowledge can be represented in non-sensory ways, e.g., verbally (Monzel et al., 2022). This has led to the assumption that aphantasia may in fact be a cluster of episodic memory impairments (Blomkvist, 2022). Critically, however, it has also been found that individuals with aphantasia show specific deficits in object but not in spatial memory (Bainbridge et al., 2021).

This collection of findings indicates that spatial memory, as well as schematic memory, are relatively spared in aphantasia. As both of these appear to rely on the ‘where’ stream, this could suggest that processing in the ‘where’ stream is unaffected in aphantasia. Thus, we argue that describing aphantasia as a cluster of episodic memory impairments is

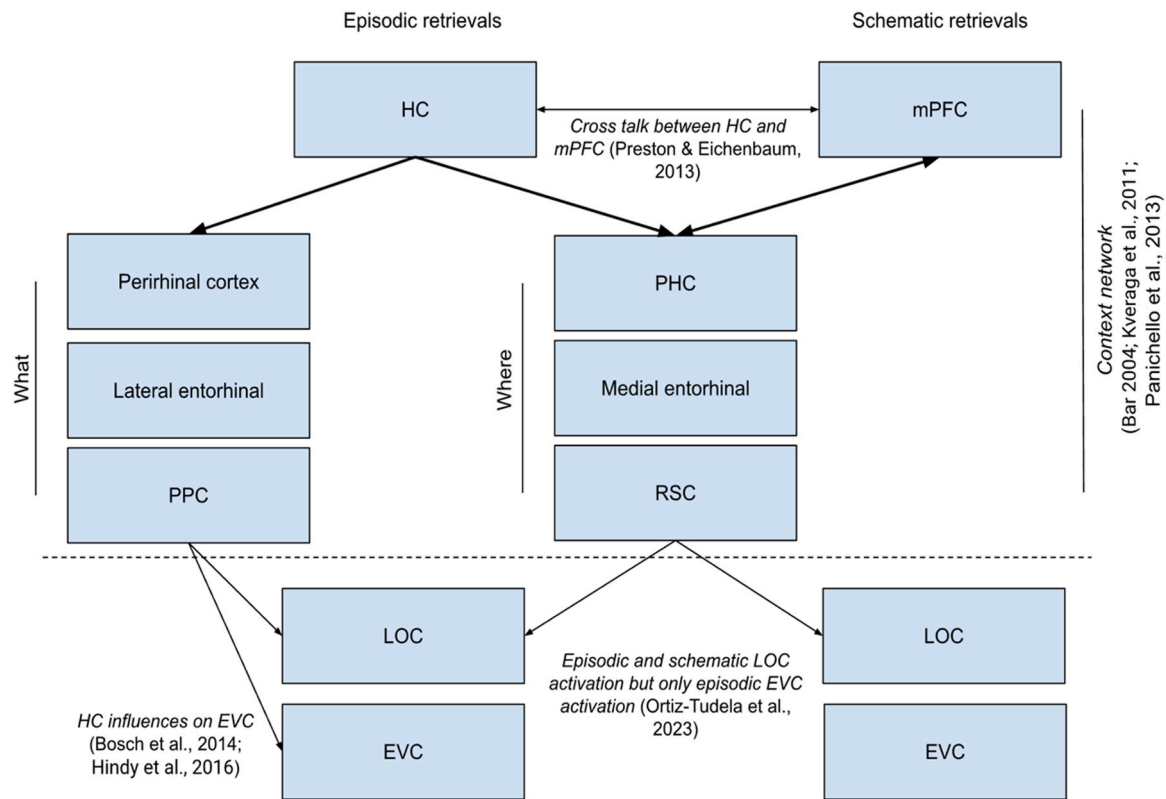


Fig. 1. Schematic representation of the proposed interaction between regions during episodic and schematic retrievals. Note that episodic and schematic retrievals are depicted as discrete scenarios for simplicity. The crosstalk between HC and mPFC allows for joint contributions of both retrieval routes to feature reinstatement (Preston and Eichenbaum, 2013).

Schematic of the proposed framework

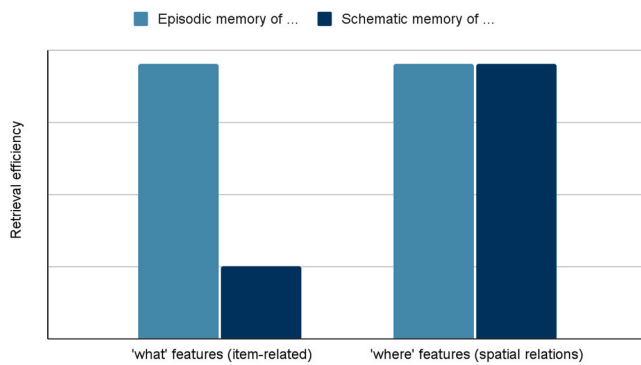


Fig. 2. Schematic depiction of the proposed framework. We argue that the efficiency with which features can be retrieved from memory depends on the interaction between the nature of the source memory and the recruited neural pathway. For example, a pure episodic retrieval can contain both high precision 'what'-dependent information (within item features) and high precision 'where'-dependent information (between item relations), whereas pure schematic retrievals would only be able to achieve this high level of precision for 'where'-dependent features. According to this framework and in light of recent findings on the memory deficits observed in aphantasia, we hypothesize that memory deficits in aphantasia would be better characterized as a specific impairment in the mnemonic retrieval of 'what'-dependent features regardless of whether they are accessed through an episodic or a semantic retrieval. Note that, as in Fig. 1, the episodic vs. schematic distinction is thought of as a continuum but displayed here as discrete entities for simplicity.

sub-optimal: rather than being an issue of episodic memory impairments per se, the pattern of memory deficits in aphantasia suggests that aphantasia may be due to specific differences in the feedback processes sent along the 'what' visual stream, where object-specific features are processed (see caption on Fig. 2). Individuals with aphantasia might hence lack the ability to reinstate visually precise object information from memory due to decreased or altered feedback signalling through the 'what' stream. This inability might be independent of whether the information is retrieved from episodic or schema memory and not caused by a specific 'faulty' brain region. This conceptualisation yields testable hypotheses for mnemonic processing and memory impairments in aphantasia and the corresponding neural correlates. For example, the comparison of the memory precision or capacity of different types of features could reveal whether decreased imagery in aphantasics is exclusively due to impaired high-level feedback signalling from the 'what' stream. If this is true, then the retrievals dependent on the 'what' stream (e.g., object features) should be less precise in aphantasia compared to non-aphantasic individuals than the retrievals dependent on the 'where' stream (e.g., spatial details), or the retrievals of details that rely neither on the 'what' nor 'where' stream (e.g., temporal details such as the temporal order of events where visual strategies are less likely). Moreover, such behavioural differences would be supported by differential patterns of brain activity: the neural reinstatement of 'what'-dependent features in early visual cortex would be impaired in aphantasics while the reinstatement of 'where'-dependent features would remain unaffected. These hypotheses, upon validation, would help to sharpen our understanding of the neural underpinnings of aphantasia.

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