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Review

From perception to memory: Changes in memory systems across the lifespan

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ABSTRACT

Human memory is not a unitary entity; rather it is thought to arise out of a complex architecture involving interactions between distinct representational systems that specialize in perceptual, semantic, and episodic representations. Neuropsychological and neuroimaging evidence are combined in support of models of memory systems, however most models only capture a 'mature' state of human memory and there is little attempt to incorporate evidence of the contribution of developmental and senescence changes in various processes involved in memory across the lifespan. Here we review behavioral and neuroimaging evidence for changes in memory functioning across the lifespan and propose specific principles that may be used to extend models of human memory across the lifespan. In contrast to a simplistic reduced version of the adult model, we suggest that the architecture and dynamics of memory systems become gradually differentiated during development and that a dynamic shift toward favoring semantic memory occurs during aging. Characterizing transformations in memory systems across the lifespan can illustrate and inform us about the plasticity of human memory systems.

Contents

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1. Introduction

The notion that there are multiple memory systems in the human brain is widely accepted and supported by neuropsychological, computational, and neuroimaging data (see reviews in Schacter and Tulving, 1994; Squire, 2009). Just as memory is not a single faculty of the mind, the developmental and senescence changes in various processes involved in memory are also not uniform. In this paper we aimed to apply and extend a framework that captures the complex architecture and interactions between memory systems (PIMMS; Henson and Gagnepain, 2010) to the human lifespan. The PIMMS framework follows earlier accounts of memory in proposing three memory systems: perceptual, semantic, and episodic. However, it diverges from earlier accounts by highlighting the predictive interactions between systems as the general principle of operation between (and within each of) the systems.

In this paper we argue that the framework suggested by Henson and Gagnepain (2010) is useful for guiding a life-span perspective on memory, as it incorporates behavioral data and points to likely candidates for the corresponding neural architecture. We focus on explicit forms of memory, including encoding, recognizing, and recalling aspects of past experience in a conscious manner. In doing so, we acknowledge that we are leaving out important developmental changes in implicit forms of memory (Thomas et al., 2004). It is also beyond the scope of this review concerning potential differences during encoding and retrieval in the interaction between multiple memory systems. We review findings from age-comparative studies on encoding or retrieval by describing which process they focus on but without making further differentiation in developmental effects for encoding and retrieval.

We adopt the premise that memory serves a predictive function (cf. Schacter and Addis, 2007), a notion that is rarely examined within memory development and aging. Within the PIMMS model, the 'predictive' function refers more specifically to the idea that higher-level systems predict the activity in lower-level systems for basic perception. Later on, we discuss how the notion of 'prediction' can be extended to include more abstract conceptual knowledge that serves to guide behavior over time. In general, prediction-error-driven plasticity is a property of the brain that likely undergoes changes across the lifespan and may have broad implications for cognitive functioning. Research in recent years have capitalized on advancement in neuroimaging methodologies and yielded a growing evidence of changes in memory systems during development and in aging. This paper takes the viewpoint of the framework of interactive memory systems for organizing this wealth of evidence. We aimed to extend the notions of this framework to capture the dynamics and plasticity of changes in memory processes that occur during child development and aging. A unified framework across the life span, we believe, will not only help understanding the changes during development and aging, but will have implications for better characterization of the framework as applied to the more 'stable' form of the network during adulthood.

The perceptual, semantic, and episodic systems within the PIMMS framework are distinguished primarily by their representational content and assumed computational principles (see Fig. 1, middle panel). At the lowest level, the perceptual system extracts and represents features of incoming information from the environment. The semantic system records combinations of perceptually defined features that repeatedly co-occur in the environment and supports familiarity as a retrieval mechanism (Cowell et al., 2010; Murray et al., 2007; Rogers et al., 2004). At the apex of the hierarchy, the episodic system records events defined by a feature at a given context (i.e., background where the feature occurred), or co-occurrence of two or more unrelated features. It is assumed that the hippocampus is a key region of the episodic system and supports recollection as a retrieval mechanism, given its central role in binding mechanisms. In contrast, it is assumed that the perirhinal cortex is a key region of the semantic system (see extension of the semantic system in Section 2.3.2), whereas the more posterior cortices (e.g., the ventral visual pathway in the occipitotemporal cortex or the auditory pathway in the lateral temporal cortex) are key regions of the perceptual system. The proposed role of the perirhinal cortex as a key region in the semantic system is supported by its involvement in familiarity-based processes (Ranganath et al., 2004) and its apparent content-specificity for mnemonic processing of objects compared to scenes (Staresina et al., 2011; Watson and Lee, 2013).

The PIMMS framework fosters the notion that there is a high degree of recurrent interaction across memory systems and neural regions. It is assumed that feedback from one system predicts the activity in lower systems in the hierarchy. Feed-forward flow of information, on the other hand, transmits the difference between such top-down predictions and the current bottom-up input. For example, a representation of the current spatial context in the hippocampal system (e.g., entering a bathroom) may predict items that are likely to appear in that context. This is carried out by providing feedback to the semantic system and activating representations for certain familiar items (e.g., toothbrush, towel, etc.), which in turn guides activity in the ventral visual and auditory pathway. The purpose of such recurrent interactions is to minimize prediction error (cf. Bar, 2009; Friston, 2010). The difference between the feedback predictions and the forward transmission of sensory evidence is eventually minimized, while the system settles into perception of a specific object. In line with the Bayesian brain hypothesis (Knill and Pouget, 2004), the PIMMS framework assumes that the brain operates with the inherent tendency to attempt to predict its surrounding environment. Prediction errors are generated when there is a mismatch between the prediction and the immediate context, and serve to update the internal system to help improve predictions in the future. Larger residual prediction errors (after perception/retrieval has occurred) entail greater synaptic change, which will also lead to more successful encoding. Prediction error thus serves as a general process enabling the operation of memory systems and interaction between systems.

1.1. From basic perception to abstract knowledge

The PIMMS model focuses on interactions between the hippocampus, perirhinal cortex, and the ventral visual system for the purpose of predictive memory for item categories. Kroes and Fernandez (2012) advanced the notion of predictive memory to higher conceptual abstract knowledge, which arises from extracting regularities across diverse experiences. This process is assumed to achieve through dynamic interactions between the hippocampus and neocortex, including the medial prefrontal cortex (PFC).