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Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev



Review

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

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ARTICLE INFO

Article history:

Received 26 September 2012
Received in revised form 7 April 2013
Accepted 17 April 2013

Keywords:

Episodic memory
Semantic memory
Cognitive development
Cognitive aging
Neuroimaging
Medial temporal lobe
MTL
Prefrontal cortex

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.

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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

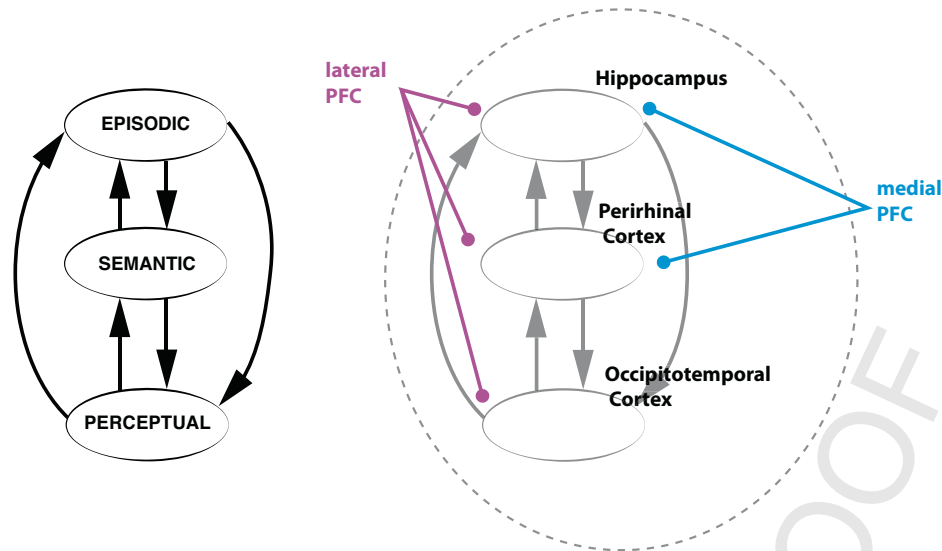


Fig. 1. Schematic representation of the predictive interactive multiple memory system framework (PIMMS) for encoding, storage and retrieval of memories (left panel) and the neural correlates proposed here that extend the original PIMMS model to include regions in the prefrontal cortex (right panel). Lateral and medial prefrontal cortex in proposed to contribute reciprocal connections that are modulated by information processing in occipital and temporal regions as well as top-down control over those regions. Medial prefrontal cortex is more strongly connected with MTL structures whereas lateral prefrontal is proposed to act more through a top down control of hippocampus, perirhinal and occipitotemporal cortex.

cortex (PFC). Across episodes, the hippocampus allows the integration, separation, and comparison of information from distributed brain regions, while the medial PFC integrates abstract representations across modalities with behavioral output (see also Roy et al., 2012) and represents semantic knowledge (Binder et al., 2009). With this, it is assumed that episodic memory gives rise to abstract knowledge that is akin to semantic memory. Such a notion converges with the complementary learning systems framework, which holds that the hippocampus learns rapidly using separated representations to encode the details of specific events, while the neocortex has a slow learning rate and uses overlapping distributed representations to extract the general statistical structure of the environment (McClelland et al., 1995). A recent extension of the complementary learning systems incorporates the role of the hippocampus in generalization (Kumaran and McClelland, 2012), achieved by incorporating recurrence flow within the hippocampal system and between the hippocampus and neocortex.

Therefore, the neural architecture of memory systems essentially includes the prefrontal cortex, both medial and lateral aspects. The prefrontal cortex has been implicated in memory functioning, through neuropsychological evidence of patients with lesions to the prefrontal cortex showing deficits in aspects of episodic memory (Janowsky et al., 1989; Schacter et al., 1984), and through its role in cognitive control. In particular the lateral PFC (including DLPFC, VLPFC, and anterior PFC) subserves goal-directed control functions that support the encoding of discrete memory traces, and the subsequent strategic retrieval and evaluation of stored representations (Simons and Spiers, 2003). More recently, van Kesteren et al. (2012) proposed a framework that relates the medial temporal lobe (MTL) and mPFC during memory processing of information as a function of its congruency with existing information represented in the neocortex (i.e., prior knowledge). This framework emphasizes the interaction between the MTL and mPFC, such that the mPFC detects the congruency of new information with existing information in neocortex. Only when there is low congruency will the MTL be involved in binding the elements of new information into a representation.

At this point we have summarized the guiding architecture and computational principles of the predictive memory systems model. With these in mind, we now turn to discuss the development of memory systems across child development, following by aging.

2. Memory systems' development from childhood to adulthood

Children's memory improves as they grow, and there is general agreement that some aspects develop throughout childhood to adulthood, while others show little developmental trends past early childhood (Brainerd et al., 2004; Ghetti and Angelini, 2008; Ofen et al., 2007; Picard et al., 2012; Shing et al., 2008). A common notion in characterizing dissociations in the development of memory is between developments of memory that is rich in details such as the one used in episodic memory and during recollection, compared to memory that is not rich in details and may rely more on semantic memory or familiarity. Changes in episodic memory functioning through development are also likely to reflect developmental trends in perception and semantic knowledge, and the interaction between these components. Below, we review evidence for the links between perceptual, semantic, and episodic systems during development and propose the adaptation of the PIMMS model to capture developmental trends in the three systems and their interaction.

2.1. Behavior - from perception to memory

Improvements in perceptual processing during development are protracted and influence memory functioning (Diamond and Carey, 1977; Mandler and Robinson, 1978; Mondloch et al., 2006; Skoczenski and Norcia, 2002). The interplay between perceptual and semantic systems during development is nicely illustrated by the rich literature on developmental trends in concept formation. Theorists have argued for a shift during development from reliance on concrete representations, to reliance on abstract knowledge (Vygotsky, 1986), in line with evidence that children, more than adults, tend to rely on perceptual features rather than abstract concepts (Jones and Smith, 1993; Tversky, 1985). Although

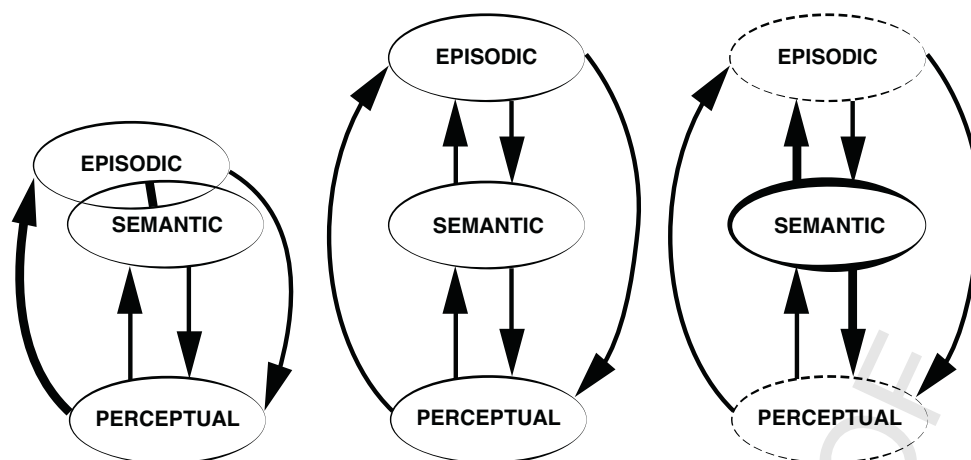


Fig. 2. The dynamic nature of architecture and interactions between memory systems across the lifespan. Episodic and semantic memory representations are gradually differentiated through development (left panel), whereas semantic representation becomes more dominant during aging (right panel).

children can use abstract concepts to override the tendency to rely on perceptual properties (Gelman and Markman, 1986; Keil et al., 1998), the evidence supports the notion that children weight perceptual information more than adults do. This differential tendency of children to rely on perceptual properties versus abstract concepts in categorization has implications for memory. Adults instructed to use an abstract 'gist' representation successfully use this instruction and fail to encode perceptual details that are irrelevant for the categorization. Children, compared to adults, are less likely to use abstract concepts in categorization, and as a result have better memory of specific exemplars (Sloutsky and Fisher, 2004). In sum, children seem to rely more on perceptual processing in early childhood, as semantic knowledge may be less developed at this stage, and that perceptual development may also contribute to improvement in semantic representations (Fig. 2).

2.2. Semantic and episodic knowledge: the chicken and the egg?

The episodic system is situated at the apex of the hierarchy within the PIMMS model (Henson and Gagnepain, 2010). Behavioral evidence of developmental trends in memory is in line with positioning the episodic system highest in the hierarchy as its developmental trajectory seems most protracted (Billingsley et al., 2002; Ghetti and Angelini, 2008). The influence of semantic knowledge on memory, however, dramatically increases with age (Brainerd et al., 2008; Ghatala et al., 1980). For example, when presented with a surprise recognition task, adults more so than children, would falsely recognize new items from studied categories (Brainerd et al., 2002; Koutstaal and Schacter, 1997). Thus, when considering the interplay between semantic and episodic systems it may be useful to revisit the notion of independence of episodic and semantic systems during development. Moreover, an influential framework in memory research suggest that semantic knowledge is created by a process in which episodic memories are being 'stripped' from their original context and become abstracted or 'semanticized' with time and over multiple repetitions (Moscovitch et al., 2006; Moscovitch et al., 2005). Such conceptualization would suggest that there would be more 'cross-talk' between the information represented in episodic and semantic systems and these systems may thus appear to be less differentiated in children compared to adults. We suggest that through development both systems are increasingly segregated and become progressively independent of one another (Fig. 2).

2.3. Neural correlates of memory development from childhood to adulthood

Childhood and adolescence are periods of robust change in the structure and function of the brain. Post-mortem and structural imaging evidence indicates that the brain continues to mature during development and that this maturation is most prolonged in prefrontal and parietal regions (Giedd et al., 1999; Gogtay et al., 2004; Gogtay et al., 2006; Huttenlocher, 1979; Sowell et al., 2003; Sowell et al., 2004). Structures in the MTL do not show robust structural changes with development, but some evidence suggests continued development of certain MTL regions in the human brain (Abraham et al., 2010; Giedd et al., 1996; Gogtay et al., 2006; Sowell and Jernigan, 1998; Sowell et al., 2002). Evidence of structural brain development is paralleled by changes in brain function from childhood through adolescence into adulthood (Bunge et al., 2002; Golarai et al., 2007; Luna et al., 2004; Schlaggar et al., 2002). The evidence for changes in memory systems with age is still limited but has grown steadily over the past few years (Chai et al., 2010; Chiu et al., 2006; Ghetti et al., 2010; Maril et al., 2011; Maril et al., 2010; Menon et al., 2005; Ofen et al., 2012; Ofen et al., 2007; Paz-Alonso et al., 2008; Wendelken et al., 2011).

2.3.1. Perception and memory development

Memory for high-level visual stimuli such as natural scenes and faces grows from childhood through adolescence into young adulthood (Diamond and Carey, 1977; Mandler and Robinson, 1978), and the development of this memory ability has been associated with the development of cortical areas that are specialized for visual perception of scenes and faces (Chai et al., 2010; Golarai et al., 2007). Specifically, functionally defined scene-selective posterior parahippocampal gyrus (PHG) known as the 'parahippocampal place area' (Epstein and Kanwisher, 1998) grows in size from childhood through adulthood, and this growth in size correlates with improved recognition memory for scenes (Golarai et al., 2007). Adults, compared to children, remember complex scenes better, and this development is linked to age-related increases in the functional representation of complex scenes in the posterior PHG. In linking functional development in perception and memory, Chai et al. (2010) have shown age-related increases in subsequent memory activations in the same posterior PHG region that show age-related increases in the activation for complex scene complexity. The relation between prolonged maturation of detailed memory for complex scenes and prolonged maturation of the posterior parahippocampal cortex representing scenes support the notion that

developmental trends in perception influence episodic memory. Attentional modulation of perception is also important in characterizing the influence of perception on memory. A recent study by Wendelken et al. (2011) shows that attentional modulation of activation in perceptual regions increases through development (between the age of 8 years and young adults) and is related to increases in successful memory encoding for studied stimuli.

2.3.2. Semantic knowledge and memory development

The influence of semantic knowledge on memory development is illustrated in a recent study by Maril et al. (2011), in which episodic memory formation was tested in the context of an encoding task tapping semantic decisions (whether an object and presented color match). Memory performance in this task was higher in adults, compared to children, and although both age groups showed a positive effect of congruency (when object and color did match, such as when a strawberry was presented with the color red) on memory, adults recruited regions primarily associated with semantic and conceptual processing (e.g., the left PFC and occipitotemporal cortices) when making a semantic color-object pair decision, whereas children recruited regions earlier in the processing stream that are more closely linked to perceptual processing (e.g., the right occipital cortex). These data provide initial evidence of a neural correlate supporting the notion of a developmental change in reliance on perceptual information to a reliance on semantic information (Section 2.1). Thus during childhood, episodic encoding may depend more on perceptual systems, whereas established representations of semantic knowledge as well as top-down frontal control systems become more prominent in the encoding process in adulthood.

Developmental changes in the prefrontal cortex are consistently found to support changes in memory encoding and retrieval with age. Changes within the MTL are less consistent and the fMRI data are only suggestive for when it comes to specificity in ascribing developmental trends to specific sub-regions within the MTL (Ofen, 2012). Structural evidence suggests local changes in the structures of the hippocampus (Gogtay et al., 2006), but there is currently little evidence of developmental change in the correlation of hippocampal structure and function (Ostby et al., 2012). Semantic knowledge in the PIMMS model is supported by representation in the perirhinal cortex (Henson and Gagnepain, 2010). Based on evidence that children recruit the MTL for successful memory formation (Maril et al., 2011), MTL processes that contribute to semantic memory may change little with age. As presented above, in the extension of the PIMMS model the mPFC is incorporated to support higher-level semantic knowledge, whereas basic semantic representations are thought to be supported by the perirhinal cortex in the MTL (Staresina et al., 2011). In line with the known protracted maturation of the prefrontal cortex, and relative constancy in both structural and functional development of the MTL, it is likely that in children, the semantic memory system may initially rely predominantly on MTL representations, specifically on the perirhinal cortex. Further studies that will be designed to address the specific contribution of the perirhinal cortex through development are needed to provide support for this notion.

A separate line of research, focusing on the development of memory retrieval using event-related potentials (ERP) lends additional support to the notion that changes in neural correlates linked to semantic processing may play a key role in developmental changes in memory. In contrast to behavioral evidence for age-invariance in familiarity-based memory, ERP studies examining memory development in children fail to find ERP components associated with familiarity-based processing (Czernochowski et al., 2005; Friedman et al., 2010; Van Strien et al., 2009; but see Cycowicz, 2000; de Chastelaine et al., 2007). These studies capitalize on known ERP components in adults that distinguish an early

mid-frontal component, associated with familiarity-based processes, and a later parietal component, associated with recollection. For example, Czernochowski et al. (2005) report parietal effects for source memory in both children and adults. In contrast, children's ERPs do not show the early mid-frontal effect. The difficulty in identifying familiarity component in children's ERP responses during retrieval may reflect protracted development of mPFC and in this structure's involvement in children's memory processes. Overall, ERP findings suggest that during memory retrieval, developmental effects may be more robust for components associated with familiarity, whereas little change is evident in components related to recollection. Such evidence is in contrast with the wealth of findings using behavioral paradigms that consistently show that developmental effects are more robust for recollection than for familiarity-based memory processes (Billingsley et al., 2002; Ghetti and Angelini, 2008). We suggest that this apparent inconsistency poses questions about the definition of recollection and familiarity in a developmental context and may have broader implications to understanding the changes in memory systems across the lifespan. These findings also point out that behavior alone is not sensitive enough to capture the dynamic between memory systems that support familiarity. They also pose a question about possible differences between encoding and retrieval and the development of processes that support these distinct stages in the life of a memory.

2.3.3. Gradual differentiation of episodic and semantic systems and the role of the hippocampus in memory development

As discussed above (Section 2.1.2), we proposed that episodic and semantic systems may be less differentiated early in development (Fig. 2). We based this notion on the idea that in adults, episodic memory is supported by the hippocampus, which is needed in detailed representations, and in supporting recollection of the past (Moscovitch et al., 2005). Once information is abstracted over time, it will become less dependent on the hippocampus. During development there may be a gradual change in the role the hippocampus is playing in memory representation, as knowledge is being progressively built up and becomes accessible in schematic hippocampal-independent form. Thus, in children the hippocampus may be involved in the encoding and retrieval of new information, including non-recollection based memory that, in adults, is relatively less dependent on the hippocampus. This notion is supported by a recent fMRI study that found that children aged 8-years old, but not adults, used the hippocampus similarly for the encoding of detailed information and information without specific details (Ghetti et al., 2010). Thus it is possible that during development, the memory system favors the hippocampus as a means of representation. In general, when considering developmental data it may be difficult to apply the same 'gold standards' of distinguishing between semantic and episodic memory in an adult-like manner.

2.4. Summarizing the developing memory system

The evidence reviewed above suggests a need for expanding models of memory systems to capture their development. The evidence suggests that systems continue to develop throughout childhood into adulthood, and children have somewhat rudimentary forms of perceptual system and of semantic knowledge. Furthermore, the evidence suggests that distinct systems in adults may be less differentiated in children. Finally, it is possible that the hierarchy and information flow between the systems is different in children and adults. For example, perceptual information takes front stage to semantic categorization in children. To fully characterize changes in memory across the life span, future work should be tuned to assessing developmental trends beyond considering a child as an immature version of an adult model.

3. Memory systems and aging

3.1. Behavior – from perception to memory

At the perceptual level, processing of basic visual and auditory attributes deteriorates with age (e.g., [Faubert, 2002](#)). Alterations in the central processing of visual and auditory information have been shown to account for age-related variance on a broad array of higher-order cognitive tests ([Baltes and Lindenberger, 1997](#); [Lindenberger and Baltes, 1997](#)). These findings suggest the importance of taking into consideration age alteration in basic perceptual processing when investigating higher-order cognition.

For semantic and episodic systems, longitudinal and cohort-sequential studies in adulthood show that verbal and visual episodic memory declines in old age, even in individuals who are healthy and show no signs of dementing illness (e.g., [Hultsch et al., 1998](#)). However, evidence on the age of onset of decline is mixed. The best estimates come from longitudinal studies that apply appropriate control for practice effects, which suggest onset of decline in episodic memory to be around 60–65 years of age. Tests of semantic memory, on the other hand, show relative maintenance in adulthood, declining only very late in life (e.g., [Rönnlund et al., 2005](#); [Schaie, 2005](#)). The maintenance of knowledge and knowledge access fueled theoretical distinctions on intelligence, as in the fluid-crystallized theory of Cattell ([Cattell, 1971](#)) and Horn (e.g., [Horn, 1968](#)), and Baltes and colleagues' emphasis on pragmatics versus mechanics from a lifespan perspective ([Baltes, 1987](#); [Lindenberger, 2001](#)). In a similar vein, cognitive mechanics have been shown to undergo earlier deterioration in aging, while cognitive pragmatics maintains its functioning until advanced aging ([Li et al., 2004](#)).

These findings suggest that knowledge and skills learned long ago persist, in at least partially accessible form, for long periods of time. For example, [Bahrck \(1984\)](#) demonstrated that middle-aged adults could, to some extent, recognize Spanish words they had studied years before in high school. With this, the concept of *permastore* was formulated, which is the idea that once information is entered in semantic memory, it stays there, with the only issue being the extent to which it could be accessed.

Increasing age, however, is indeed accompanied by changes in accessibility to information held in semantic memory ([Craik and Bialystok, 2006](#)). Deliberate search for information in semantic memory according to arbitrary rules, such as word fluency, declines with age ([Schaie, 2005](#)). Word finding problems increase with old age, and are particularly associated with some forms of dementia ([Laws et al., 2007](#)). Even when retrieval from semantic memory is successful, such as in comparative judgments of synonym meaning, access is often slowed (e.g., [Hertzog et al., 1986](#)), indicating a loss of control over memory. Taken together, aging individuals may retain representations for existing knowledge, but decline in control processes may produce impairments in direct access to this knowledge ([Craik and Bialystok, 2006](#)).

3.2. Changes in flexibility to switch between systems

Optimal remembering requires the flexible disposal of detailed recollection and recall of abstract or gist-based information, depending on changing goals. In line with a decline in control over memory, older adults show impairment in flexibility to switch between recalling fine-grained detail and gist information. For example, [Koutstaal \(2006\)](#) showed that older adults failed to resist endorsing lure items that shared semantic/lexical information with studied items. The “pull” toward responding on the basis of matching semantic information may be particularly strong in older adults, given their reduced item-specific memory. Therefore, such a deficit in resisting a positive recognition response in the face of semantic

matches may have resulted from a reduced distinctiveness of memory traces in combination with less efficient strategic control at retrieval.

3.3. Aging changes in neural regions of memory systems

In parallel to the behavioral evidence, age-related changes in neural regions of memory systems can be identified already at the perceptual level. Neural representations are postulated to become less distinctive in old age, a phenomenon known as *dedifferentiation* (e.g., [Li et al., 2001](#)). Using multi-voxel pattern analysis, [Carp et al. \(2011\)](#) found that age differences in neural distinctiveness extend beyond the ventral visual cortex, including early visual cortex, inferior parietal cortex, and medial and lateral prefrontal cortex (see also [Park et al., 2012](#)). Reduced uniqueness of stimulus representations, possibly due to individual differences in neural noise during the processing of visual information, plays an important role in age-related degradation of cognitive processing ([Park et al., 2004](#)).

3.3.1. The importance of MTL changes in aging

With respect to the core episodic memory network, age-related changes in the functional and structural integrity of the network are frequently observed in neuroimaging studies ([Cabeza et al., 2002](#); [Park and Gutchess, 2005](#); [Raz et al., 2005](#)). In old age, MTL gray and white matter exhibit profound decline ([Raz, 2005](#); [Raz et al., 2010](#); [Raz and Rodrigue, 2006](#)). Changes are especially pronounced in the hippocampus, and less so in the surrounding cortex ([Raz et al., 2005, 2004](#)). In a longitudinal fMRI study, [Persson et al. \(2011\)](#) examined the relationship between 6-year intraindividual change in fMRI activation for memory encoding and change in memory performance over 2 decades (participants aged 50–80). The results showed reduced activation and volume shrinkage in the hippocampus in participants with declining performance, while no change was found in stable individuals. These results demonstrate the detrimental effects of hippocampal senescence changes, and also the importance of taking into account individual differences in the progression of senescence in order to better understand brain-behavior changes.

Recent advances in neuroimaging have enabled research on differential age-related changes in hippocampus subfields, both in terms of its structural integrity and functional relevance. Aging-related volume reductions are found in the CA1 ([Mueller et al., 2008, 2007](#); [Shing et al., 2011](#)), in DG/CA3 ([Mueller et al., 2008](#); [Mueller and Weiner, 2009](#)) as well as in the subiculum ([La Joie et al., 2010](#)). A study by [Shing and colleagues \(Shing et al., 2011\)](#) demonstrated a negative relationship between the amount of memory conjunction errors and gray matter volume of CA3/DG in old age. According to [Wilson et al. \(2006\)](#), aging is associated with a diminished capacity for pattern separation (learning new information by decorrelating similar inputs to avoid interference) and an increased propensity for pattern completion (retrieval of previously stored information from a partial cue). This shift could be the result of a functional imbalance in the hippocampal dentate gyrus and CA3 network. Old age is also associated with changes in the structural integrity of the perforant path connecting the entorhinal cortex with DG ([Yassa et al., 2010](#)). This may result in a bias away from pattern separation toward pattern completion, such that older adults need greater dissimilarity between items in order to engage in DG/CA3-mediated pattern separation ([Yassa et al., 2011](#)). Taken together, the aging memory system shows weakened processing of new information and over-reliance on previously stored patterns.

3.3.2. PFC in aging

Prefrontal regions show linear declines in cortical volume beginning in the mid-20s ([Raz et al., 2005](#); [Sowell et al., 2003](#)). The

frontal-lobe hypothesis of cognitive aging suggests that many age-related changes in cognition, including episodic memory, reflect, to a large extent, senescent structural and neurochemical changes of the frontal lobes (Buckner, 2004; West, 1996). In terms of functional changes in episodic memory tasks, older adults have shown increased bilaterality in PFC activation during memory encoding and retrieval, sometimes resulting from increases in activation of the nondominant hemisphere, or reduced activation in the dominant hemisphere that is usually activated by the younger adults (see reviews in Cabeza, 2002; Park and Gutchess, 2005). These findings stand in contrast to a longitudinal study by Nyberg et al. (2010), which investigated change in brain structure and function (in a categorization task) over a period of 6 years. While the cross-sectional analysis revealed increased activation of dorsal PFC in the older adults, longitudinally activity in this region decreased. This finding challenges the notion of age-related re-organization of brain networks for functional compensation. Rather, it argues for brain maintenance as the primary determinant of successful memory aging (see also Nyberg et al., 2012) and highlights the importance of examining such developmental issues with longitudinal design.

3.4. Summarizing the aging memory system

Taken together, the evidence reviewed above sets the stage for several conclusions concerning aging changes in the memory systems. First, the system in the aging brain may become overly entrenched, such that there is a strong pull toward settling into a stable state driven by prediction generated from the semantic system (Fig. 2). This leads to a reduced capacity for generating new individual representations rich in unique details (i.e., weakening in contribution of the episodic and perceptual systems). Another consequence is that prediction-error-driven plasticity, as a general property of the brain, is reduced in aging (cf. Düzel et al., 2010). On the other hand, in face of reduction in efficiency of cognitive capacities and brain machineries, it may be adaptive for older adults to rely on prior knowledge and semantic memories that remain available even in old age.

4. Memory systems across the lifespan

In our review of the literature in development and aging, we compare each developmental stage to the adult conceptualization of the memory systems according to the PIMMS model. To summarize our extension of the model, we posit that young children rely on rudimentary forms of perceptual, semantic and episodic systems, supported by the posterior cortices and perirhinal cortex of the MTL. Through development, higher-level abstract knowledge as well as top-down control supported by the frontal regions become more prominent in guiding memory functions, which may lead to a better differentiation among the systems. In senescence, due to entrenchment in the aging system, there may be a tendency of the memory processes being driven by prediction generated from the semantic system, which lead to weakening in contribution of the episodic and perceptual systems. Weakened processing of new information and over-reliance on previously stored patterns may be driven by changes in the balance between pattern separation and pattern completion in the MTL. Aging difference in the medial PFC (which supports abstract knowledge) has not been demonstrated empirically but is plausible given the prominent senescent changes in PFC in general.

Only a few studies provide empirical evidence of developmental effects in memory functioning across the lifespan within a single experimental design. In general, lifespan studies find reduced memory performance in both children and older adults compared with young adults (e.g., Brehmer et al., 2007; Shing et al., 2008),

but the mechanisms underlying the age differences vary. Children's reduced performance is typically considered to reflect lower ability to engage in attentional and executive control processes, whereas older adults are additionally impaired in specific mnemonic functioning (e.g., binding) that supports correctly associating pairs of items (Fandakova et al., 2012). These notions have been captured by the two-component framework accounting for changes in memory across the lifespan (Shing et al., 2010) that focus on the associative and strategic components of memory. The framework we propose here with our extension of the PIMMS model, compliments this earlier framework of Shing and colleagues by being more explicit in postulating the changes in the memory systems and the processes they support. Our notion of enhanced reliance on semantic memory and reductions in episodic memory in older adults is consistent with impaired associative component, yet it may provide more specific explanation about the nature of age effects. In development our review of the literature brings us to postulate novel notions of rudimentary memory systems that provide testable hypotheses beyond the development of executive control. We note that the neural correlates accounting for memory decline with older age have, to date, been more extensively studied, and we look forward to new studies that will validate the framework we propose in this paper.

5. Questions for future research

In addition to the points we discussed above, there are further issues that are important to be considered in future research of lifespan changes in the memory systems. We now focus our discussion on two main issues, as presented in the following sections.

5.1. From discrete systems to network dynamics

Progress in the understanding of brain-behavior relations relies greatly on identifying functional networks, comprising discrete areas of the cerebral cortex that flexibly interact to support various cognitive functions. In the context of human memory, the role of the MTL in memory has been challenged in recent years as it was shown to support short-term processing and working-memory (Nichols et al., 2006; Ranganath and D'Esposito, 2001), and in perceptual matching (Barense et al., 2012), suggesting that the role of structures within the MTL is not limited to a dedicated memory system. These discoveries inspired calls for revision of the traditional conceptualization of memory systems and instead to consider memory processes and network interactions within brain regions that support memory (Henke, 2010; Nadel and Hardt, 2011; Nadel et al., 2012). In the PIMMS model and its extension, memory functions depend on spatial and temporal interactions among several widespread regions. Recent age-comparative studies suggest important age differences in the connectivity and organization of functional networks. For example, Davis et al. (2008) showed that, across memory and perceptual tasks and high and low confidence levels, older adults show reduction in occipital activity coupled with increased frontal activity. This suggests a posterior to anterior shift in neural recruitment in aging (see also Daselaar et al., 2006). At the child development side, functional connectivity between MTL and dorsolateral PFC increases with age during memory encoding, which may underlie the increasing importance of encoding strategies to successful memory formation (Menon et al., 2005). Similarly, functional connectivity between the MTL and inferior prefrontal cortex changes with age during retrieval, suggesting a change in the interplay between those structures during development (Ofen et al., 2012). At this point, we still know very little

about the dynamic links among structural connectivity, functional connectivity, and age-related memory changes. Future studies should combine diffusion tensor imaging and advanced connectivity techniques such as functional and effective connectivity to examine age-related alterations in network dynamics underlying the neural architecture of memory systems. Future research using effective connectivity (Friston et al., 2003) can be used to assess connections within a defined set of regions as proposed in our extension of the PIMMS framework (including the lateral and medial PFC) and their modulation during memory tasks across the lifespan.

5.2. Flexibility of systems through attentional modulation

A follow-up question on the issue of flexibility is to what extent top-down control processing can up- or down-regulate the different memory systems. Behaviorally, as reviewed above (Section 2.1), Sloutsky and Fisher (2004) show that after performing an induction task, young children (5-year olds) exhibit more accurate memory recognition on the stimuli than adults, due to their tendency to induce on the basis of perceptual similarity, which lead to accurate item-specific information. However, after being trained to perform induction in an adult-like category-based manner, children's memory accuracy dropped to the level of adults. This suggests that, with instruction, children can induce representations in a manner more in line with a priori conceptual assumption (see also Sloutsky and Spino, 2004). Furthermore, in memory systems focusing on skill acquisition, children may outperform adults demonstrating increased ability for flexibility (Dorfberger et al., 2007; Wilhelm et al., 2013), suggesting that flexibility in children is a term that needs better characterization. On the aging side, even with explicit instruction, older adults show impairment in flexibility to switch between recalling fine-grained detail and gist information (Koutstaal, 2006). Theoretically, representational systems are assumed to be organized hierarchically: general conceptual knowledge occupies the higher levels, and specific episodic instances occupy the lower levels (Craik, 2002). Initially in development, children may acquire information and knowledge about the world by specific instances of associations. Through development, they gradually acquire higher-level conceptual knowledge that increasingly affects subsequent learning. However, there seems to be flexibility and plasticity in children, through instruction and training, to switch between making and using representations from different levels. Older adults' system, on the other hand, may be more rigid and less susceptible to attentional modulation (cf. Craik and Bialystok, 2006). This lifespan conjecture needs to be corroborated with empirical evidence to better understand the boundary of flexibility in the memory systems.

6. Concluding remarks

In this review we take the challenge of incorporating behavioral and neuroimaging data from across the lifespan into current conceptualization of memory systems. In doing so we find that although memory functioning in children and older adults is impaired compared to young and middle aged adults, there is little symmetry in the likely causes of these differences. During development, memory systems may be less differentiated and the dynamics of their operation may prefer perceptual to semantic processes. In contrast, in old age, older adults rely more on prior knowledge and semantic memories that remain available, a change that may be adaptive in face of reduction in efficiency of cognitive capacities and brain machineries. Future findings may offer insights to clarify and constrain these notions and further our understanding of the change in memory across the lifespan.

Uncited references

Gazzaley et al., 2008 and Sander et al., 2011.

Acknowledgments

The authors wish to thank N. Raz, U. Lindenberger for productive discussions that informed the framework presented in this paper, and R. Serota for constructive comments on previous versions of the paper.

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