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How older adults remember the world depends on how they see it

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Abstract

Age-related changes in visual exploration and memory have typically been studied separately. However, recent evidence suggests that mnemonic processes both affect and are affected by eye movements. By relating older adults' memory deficits to age-specific visual exploration patterns, we can improve upon models of cognitive aging.

Keywords

aging; memory; eye movements

Understanding age-related memory decline: A role for visual exploration

One of the hallmarks of cognitive aging is a decline in the ability to remember the past. This deficit is thought to result primarily from age-related alterations in brain regions supporting memory, including the hippocampus and broader medial temporal lobe network, that change the way older adults encode and retrieve memories [1]. Researchers have also acknowledged a role for impaired cognitive control and associated changes in prefrontal function that contribute to increased memory problems with aging [2]. Here, we consider a related hypothesis, that age-related memory declines are also the result of changes in visual exploration, resulting from and reflecting age-related changes in cognition. In short, older adults remember differently because they see differently.

Whereas traditional models of memory and visual exploration have remained largely separate, the past few years have seen a surge of evidence demonstrating that the neural regions supporting memory (e.g., hippocampus) and oculomotor control (e.g., frontal eye fields) are both anatomically and functionally connected (see Box 1). These findings raise the intriguing possibility that age-related changes in gaze behavior might, at least partly, account for age differences in memory. Accordingly, we propose that understanding and measuring age-related changes in visual exploration is critical for understanding and characterizing age-related changes in memory.

Age differences in visual sampling and memory encoding

Eye movements (EMs) are the primary way in which humans gather information from the surrounding visual environment. Accordingly, where we look largely dictates what information gets encoded into memory and is subsequently available for retrieval.

Converging evidence indicates that older adults sample the visual world differently than younger adults both during memory formation and retrieval (see Box 2). For example, compared with younger adults, older adults are more likely to have their attention captured by the sudden onset of an exogenously salient (e.g., bright or moving) cue, even when explicitly instructed to ignore it or given advance knowledge of its appearance [3]. This failure is thought to result from an age-related deficit in controlled inhibition, which is required to suppress unwanted, reflexive saccades. Accordingly, in laboratory studies in which participants are required to override the natural tendency to look at an abruptly presented peripheral cue by instead generating a gaze shift or *antisaccade* in the opposite direction, older adults make more errors (erroneous looks or *prosaccades* to the sudden onset cue) than younger adults [3]. Although attentional capture by salient, irrelevant cues can be adaptive, such as when those cues signal reward or threat, in everyday tasks like visual search for a target or studying the layout of a new environment, involuntary exogenous orienting may detract EMs from viewing task-relevant features and instead increase processing and subsequent memory for, task-irrelevant features.

Just as salient exogenous cues are a strong driver of visual attention in older adults, endogenous cues like knowledge and expectations about where and when items are likely to appear also show strong age-related viewing effects. During naturalistic visual search, for example, older adults (probably as a result of reduced inhibitory processing) are more likely than younger adults to direct their fixations to regions of a scene in which a target object would be most expected based on prior knowledge or *schemas* (e.g., searching for a kettle on the stove) [4]. This is the case even when predictive cues indicate that the expected location does not contain the target. Preferential viewing of expected (i.e., schema-congruent) locations is also associated with increased search times and decreased memory accuracy (collapsed across both age groups) when targets are located in unexpected (i.e., schema-incongruent) locations [4]. Thus, increased biasing of visual attention based on endogenous cues can have critical negative consequences for older adults' behavior and memory (see next section).

Partly as a result of changes in exogenous and endogenous orienting, older adults consistently make more fixations than younger adults [e.g., 5,6]. However, recent work suggests that the relationship between fixations and memory may change as a function of age. During face viewing, for example, older adults' make more fixations and fewer transitions between facial features (particularly the eyes) than younger adults, consistent with a more "holistic" scanning pattern, and this pattern is associated with poor recognition memory and low overall cognitive ability (i.e., scores on the Montreal Cognitive Assessment (MoCA)) [5]. Extending this work, recent research using functional magnetic resonance imaging (fMRI) demonstrates that visual sampling (i.e., number of fixations) during face viewing predicts encoding-related hippocampal activity and retrieval-related suppression of

hippocampal activity in younger adults, but less so in older adults [6]. Thus, the ability to use EMs to build up lasting memory representations may be impaired with age. More broadly, these findings suggest that age differences in gaze behavior may reflect or contribute to age differences in encoding processes.

Visual exploration shapes mnemonic representations

While age differences in viewing behavior are generally considered to be indicative of broader changes in cognition, they may also contribute to them. Specifically, age-related changes in visual exploration, resulting from changes in cognition, might change the nature of mnemonic representations formed by older adults, and thus might help to explain some of their more commonly seen memory impairments. For example, research indicates that older adults show increased processing of distractors, leading to cluttered memory representations containing both target and non-target information [7]. While these findings are generally considered to reflect age-related declines in cognitive control and inhibition, these same factors are thought to underlie increased exogenous orienting by older adults [4]. Thus, increased viewing of exogenously salient cues, as a result of reduced inhibition, might contribute to cluttered memory representations by biasing older adults to involuntarily look at and encode salient distracting information.

In a similar vein, associations between schema-congruency of encoded information and mnemonic performance in older adults [e.g., 8] might be partly attributed to increased guidance of viewing by endogenous cues. In line with this proposal, recent work demonstrates that increased viewing of endogenously cued (i.e., schema-congruent) scene regions by older adults during target search is associated with poorer memory-guided search performance and subsequent memory for target locations [4]. Specifically, older adults whose search is more constrained by prior knowledge are marginally more likely to incorrectly report a previously detected target as having been located in an expected (schema-congruent) location, suggesting that age-related gaze biases influence not only what, but also how accurately older adults remember.

Although changes in gaze behavior with age are often the result of changes in attention and other cognitive processes, emerging research suggests that EMs may affect memory independently of attention. For example, research with both younger and older adults suggests that EMs during free viewing might benefit memory by reinstating the encoding context [e.g., 11, 12]. Specifically, the extent to which gaze patterns made during encoding are reinstated during retrieval is associated with memory success (see Box 2). Importantly, recent research in young adults has demonstrated that memory retrieval is significantly impaired when participants must maintain fixation (a demand that does not increase working memory load [9]), compared to when they can freely move their eyes, even in the absence of visual input [10]. Taken together with evidence of age-related changes in exogenous and endogenous viewing, these findings make a strong case for utilizing EM monitoring in aging and memory research to measure and predict age-related changes in memory.

Concluding Remarks

When we consider age-related memory deficits, rarely do we consider gaze behavior. Yet, decades of research on visual exploration, advanced by recent work, suggest that EMs and memory are intimately related. Considered together, these two seemingly disparate lines of work converge on a critical conclusion: fundamental differences in the way younger and older adults explore the visual environment via gaze shifts might not only reveal, but also account for, or contribute to, age-related changes in memory encoding and retrieval.

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Box 1:**Brain mechanisms support interactions between visual exploration and memory**

Although the vision and memory literatures have largely developed in parallel, research from the past decade suggests that these fields are closer than previously thought. For example, research indicates that theta rhythms in the hippocampus, which are critical for memory formation, are aligned to saccades during visual exploration, and this alignment is predictive of subsequent memory [10], suggesting that the coordination of hippocampal activity and EMs may be important for optimizing memory encoding. Indeed, network analyses suggest that there are several anatomical pathways through which the memory and oculomotor networks can share information [13]. Accordingly, stimulation of memory regions in a virtual network results in observable responses in oculomotor regions, supporting a role for hippocampally-mediated memories in guiding EMs. Moreover, subsequent feedback activity (observed following responses in oculomotor regions) in regions involved in internally directed cognition further suggests that information attained from EMs might affect mnemonic representations via cortical updating [13]. Taken together, evidence from multiple methodologies therefore suggests that EMs can both be modulated by and modulate hippocampal memory functions.

Box 2:**Do eye movements influence retrieval processes?**

Evidence that EMs are involuntarily and preferentially directed towards regions of a stimulus that (a) have changed from encoding, or (b) reflect a previously learned association, suggests that EMs can reflect the contents of memory [10]. Yet, recent work suggests that EMs may also play a more active role in memory retrieval. For example, when explicitly instructed to retrieve an encoded stimulus from memory, younger adults spontaneously move their eyes to regions of the screen that they had viewed during encoding (i.e., regions where the stimulus was originally presented), even when there is no stimulus on the screen (i.e., *looking at nothing*), suggesting that EMs might facilitate reinstatement of the encoding context [10, 11]. Moreover, this pattern of EM-based reinstatement is associated with memory success, suggesting that EMs may be functionally involved in memory retrieval. Notably, older adults show an increase in EM-based reinstatement relative to younger adults, and this reinstatement is associated with age-equivalent mnemonic performance, suggesting that EMs may play a compensatory role in older adults [12]. While this research is still ongoing, preliminary findings provide a promising avenue for assessing and potentially influencing memory retrieval in older adults using EMs.