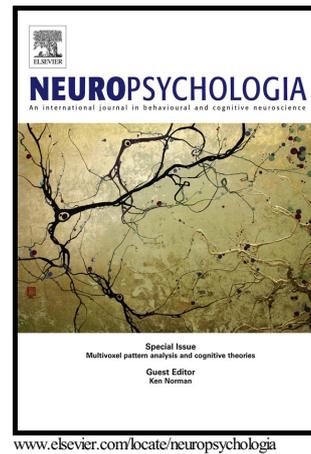


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False memories with age: neural and cognitive underpinnings

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Abstract

As we age we become increasingly susceptible to memory distortions and inaccuracies. Over the past decade numerous neuroimaging studies have attempted to illuminate the neural underpinnings of aging and false memory. Here we review these studies, and link their findings with those concerning the cognitive properties of age-related changes in memory accuracy. Collectively this evidence points towards a prominent role for age-related declines in medial temporal and prefrontal brain areas, and corresponding impairments in associative binding and strategic monitoring. A resulting cascade of cognitive changes contributes to the heightened vulnerability to false memories with age, including reduced recollective ability, a reliance on gist information and familiarity-based monitoring mechanisms, as well as a reduced ability to inhibit irrelevant information and erroneous binding of features between memory traces. We consider both theoretical and applied implications of research on aging and false memories, as well as questions remaining to be addressed in future research.

Key words: False memory; Memory distortion; Aging; Memory; Memory accuracy

1. Introduction

It is well-established that cognitive aging is associated with declines in the amount of material remembered across a range of encoding conditions, items, and retrieval tasks (Balota et al., 2000; Hoyer and Verhaeghen, 2006; Park et al., 2002). However, it is now also well known that what is remembered tends to be less accurate with age. Older adults exhibit an enhanced susceptibility to a wide range of memory errors and source misattributions, including familiarity-based errors (e.g., Jacoby, 1999), gist-based errors (e.g., Koutstaal & Schacter, 1997), conjunction errors (e.g., Castel & Craik, 2003), false memories for self-relevant information (Rosa and Gutchess, 2013), imagination inflation (e.g., McDaniel et al., 2008), and misinformation (Wylie et al., 2014). In recent years there has been great interest in elucidating the neural and cognitive underpinnings of this age-related increase in vulnerability to false memories.

There have been a number of previous reviews on the general topic of aging and false memory (cf., Jacoby & Rhodes, 2006; Koutstaal & Schacter, 2001; Pierce et al., 2004; Schacter et al., 1997), but none within the past decade, despite extensive research activity. Moreover, the earlier reviews of aging and false memory focused almost exclusively on evidence from cognitive/behavioral studies, in part because the preponderance of evidence available at the time these reviews were written came from such studies. However, during the past decade there has been a notable increase in neuroimaging studies of aging and false memory, allowing at least preliminary links to be made between the cognitive and neural processes associated with various kinds of age-related memory errors. The main purposes of the present paper are to review and link experimental evidence concerning the cognitive properties of changes in memory accuracy with age, and neuroimaging evidence concerning their neural underpinnings, focusing primarily on research from the past decade.

More specifically, we suggest that age-related increases in false memories are to a large extent attributable to changes in the medial temporal lobes (MTL) and prefrontal cortex (PFC), and corresponding impairments in recollection and executive functioning. Recent research has endeavored to link specific aspects of memory, executive functions, and related processes with specific subregions within the MTL and PFC (for reviews, see Passingham & Wise, 2012; Poppenk et al., 2013; Preston & Eichenbaum, 2013; Zeidman & Maguire, 2016). Thus, when we refer broadly to MTL and PFC in relation to age-related changes in memory, we are aware that we are referring to large brain regions containing multiple subregions that may serve distinct functions. In the course of the review, we consider evidence linking specific MTL and PFC regions with specific processes and functions associated with age-related increases in false memories, although as we note at the conclusion of the review, relatively little solid evidence currently exists regarding this important issue.

We begin by reviewing evidence linking changes in the MTL and PFC to age-related memory changes. Next, we consider how these neural changes produce an increased susceptibility to false memories, focusing on several candidate cognitive underpinnings: binding failures, gist-based processing, deficits in strategic retrieval, overreliance on familiarity, disinhibition and hyper-binding. Finally, we conclude by considering theoretical and applied implications of research on aging and false memory, as well as open questions and possible future research directions.

2. Medial temporal lobe and prefrontal cortex changes with aging

Converging evidence from lesion and neuroimaging studies has identified the MTL (particularly the hippocampus) and PFC as brain structures critical to episodic memory encoding and retrieval (e.g., Simons & Spiers, 2003). These two regions are also disproportionately affected by age-related structural and functional decline (Buckner, 2004; Buckner et al., 2006; Hedden and Gabrieli, 2004; Moscovitch and Winocur, 1995; Nugent et

al., 2014; Prull et al., 2000; Raz et al., 2005; West, 1996). The PFC is also thought to compensate for declines in cognitive resources elsewhere in the brain (such as the MTL), further taxing functioning of this region with age (Cabeza, 2002; Cabeza et al., 2002; Grady et al., 2003; Persson et al., 2006).

Both MTL and PFC dysfunction have been directly linked with memory impairments. Decreased hippocampal volume is associated with reduced memory performance both cross-sectionally (Driscoll et al., 2003) and longitudinally (Persson et al., 2012, 2006; Tisserand et al., 2004). Moreover, reduced functional activation of the hippocampus during memory encoding and retrieval is commonly observed with age (e.g., Dennis et al., 2007, 2008; Giovanello et al., 2010; Grady et al., 1995; Persson et al., 2012). Functional and structural decline in anterior, dorsolateral and ventrolateral PFC is also associated with reduced memory ability (Fandakova et al., 2014; Tisserand et al., 2004). Indeed, older adults often perform similarly to patients with lesions to lateral PFC, as well as other PFC subregions, on memory tests (cf., Janowsky et al., 1989; Schacter et al., 1991; Stuss et al., 1996; Swick et al., 2006).

Declines in MTL and PFC structure and function are also linked with an enhanced susceptibility to false memories. Younger and older adults with poor performance on behavioral tests reliant on MTL functioning are more likely to falsely identify lure items on the basis of semantic relatedness or familiarity with studied items (Fandakova et al., 2013b; Plancher et al., 2009; Rubin et al., 1999; see also Zhu et al., 2010), though the evidence for this relationship is mixed (McCabe et al., 2009). Likewise, performance on executive functioning tests sensitive to frontal functioning (particularly dorsolateral and superior medial PFC; see Stuss et al., 1998, 2000, 2001; Troyer et al., 1998) is associated with deficits in monitoring the source of incoming information for both younger and older adults (Chan & McDermott, 2007; Craik et al., 1990; Fandakova et al., 2013a; Glisky et al., 2001; Henkel et

al., 1998; Pansky et al., 2009; Plancher et al., 2009; Roediger & Geraci, 2007; Rubin et al., 1999; Sauz on et al., 2016). Highlighting the considerable heterogeneity in cognitive aging, older adults with preserved executive functioning are no more susceptible to false alarms than college students (Butler et al., 2004; Meade et al., 2012; though see Lindner & Davidson, 2014).

Neuroimaging studies substantiate the relationship between MTL and PFC integrity and false memory susceptibility. Older adults with a smaller hippocampal volume make more false alarms in an associative recognition task compared to older adults with a larger volume (Shing et al., 2011). During correct rejection of lure stimuli, older adults activate the hippocampus less than younger adults (Tsukiura et al., 2014). While dorsolateral PFC recruitment scales with retrieval monitoring demands for younger adults, older adults show greater recruitment of this region regardless of the amount of retrieval monitoring required, potentially reflecting a breakdown in the functional specialization of PFC activation (McDonough et al., 2013; see also Gutchess et al., 2007). Increased PFC activation may also be compensatory during memory monitoring; older adults performing highly on a memory test recruit additional right middle and medial superior frontal areas when making recognition judgments, compared to low-performing older adults (Gutchess et al., 2007). Moreover, those older adults displaying a younger adult-like pattern of activation during correct rejection of conjunction lures – specifically recruitment of a frontoparietal network – are less prone to false alarm to novel combinations of familiar elements (Fandakova et al., 2015).

In addition to regional declines, a reduction in the functional connectivity between PFC and MTL regions is observed with healthy aging (Andrews-Hanna et al., 2007; St. Jacques et al., 2012). An interactive and collaborative relationship between these regions exists to successfully store and recall an episode from memory (McClelland et al., 1995; Preston and Eichenbaum, 2013; Schlichting and Preston, 2015; Simons and Spiers, 2003). The MTL

system is thought to be reflexive, in that it encodes and retrieves without much control over the input or organization of information. As such, the frontal cortex provides encoding and retrieval support for the MTL, controlling the delivery and organization of information, guiding search attempts, and monitoring recalled information (cf. Working with Memory model; Moscovitch & Winocur, 2002). Thus the connective integrity of these two regions is vital for accurate memory encoding and retrieval. Indeed, Fandakova and colleagues (2015) demonstrated that older adults exhibiting strong functional connectivity of left anterior PFC and temporal areas (including the parahippocampus and middle temporal gyrus) perform better on tests of executive functioning, use strategic encoding mechanisms, and are less prone to memory distortions. Moreover, when correctly rejecting lure stimuli, older adults exhibit decreased interaction of PFC regions involved in source monitoring (specifically ventral PFC) and regions that cooperate with the hippocampus to aid recollection (supramarginal gyrus), implicating a disconnect in monitoring and recall processes with age (Tsukiura et al., 2014).

3. Mechanisms of false memory formation with age

While it is clear that MTL and PFC declines play a role in the age-related increase in memory errors, it is critical to understand *how* this dysfunction may result in enhanced susceptibility to false memories. Monitoring the source of memory output requires informative cues to be encoded and retrieved – processes reliant on hippocampal binding, as well as attention and memory organization mechanisms mediated by various PFC subregions. In this section we argue that declines in MTL and PFC contribute to binding and strategic monitoring deficits, creating a cascade of cognitive changes that increase opportunities for false memories to occur. More specifically, we suggest that:

1. Binding failures result in an impoverished memory trace devoid of distinctive source information, which may be misattributed to an incorrect source. Recollective declines

also increase phenomenological and neural overlap between memories of differing origins.

2. Unsuccessful separation of memory traces encourages source decisions based on gist, or the overall similarities of memory traces, rather than item-specific information.
3. Even when source information is encoded sufficiently, declines in strategic retrieval processes mean this information may not be effectively utilized to determine memory origin.
4. Reductions in recollective information and declines in strategic monitoring necessitate a reliance on misleading familiarity-based processes.
5. Declines in inhibitory processes may enhance distraction and formation of spurious associations between incoming information.

A more comprehensive discussion of each of these mechanisms follows.

3.1. Binding failures

The associative deficit hypothesis posits that age-related hippocampal decline results in a specific deficit in encoding and retrieving relations between items, more so than item information itself (Bender et al., 2010; Chalfonte and Johnson, 1996; Cohn et al., 2008; Kessels et al., 2007; Naveh-Benjamin, 2000; Naveh-Benjamin et al., 2003; Old and Naveh-Benjamin, 2008; Spencer and Raz, 1995). The hippocampus plays a vital role in associative memory, particularly in binding memory features during encoding (e.g., Davachi et al., 2003; Giovanello et al., 2004; Jackson & Schacter, 2004; Kirwan & Stark, 2004; Ranganath, 2010). This feature binding is critical for pattern completion, where activation of a subset of features comprising an event spreads to activate the remaining features at retrieval (McClelland et al., 1995; Nakazawa et al., 2002; Teyler & Rudy, 2007; see Schacter et al., 1998). Indeed, hippocampal damage results in deficits in both the formation and retrieval of memory relations (e.g., Hannula et al., 2006; Pertzov et al., 2013). In line with an associative-specific

deficit, age reductions in hippocampal recruitment are most prominent when feature binding is required (Dennis et al., 2008a; Mitchell et al., 2000).

The PFC also contributes to the strategic encoding of relational information (e.g., Cabeza, 2006). Associative declines have been linked to reduced dorsolateral and ventrolateral PFC volume (Becker et al., 2015; see also Blumenfeld et al., 2011), ventrolateral PFC dysfunction has been associated with impaired relational encoding in older adults (Addis et al., 2014), and age-related reductions in dorsolateral PFC recruitment are observed during successful encoding of associative, but not item information (Dennis et al., 2008a). Crucially, poor binding ability is linked with an enhanced susceptibility to false memories in both younger and older adults, including conjunction errors (Fandakova et al., 2013a) and gist-based errors (Henkel et al., 1998). As we discuss in detail below, inefficient binding of content and source, and a subsequent loss of distinctive information, may also contribute to source misattributions based on misinformation and imagination inflation.

3.1.1. Inefficient binding of content and source

The source monitoring framework suggests that specific characteristics of a mental experience are used to make an online judgment about the source of that experience at retrieval, based on the tendency for memories of different origins to have different characteristics (Johnson et al., 1993, 1988). For example, veridical events are typically rated higher in perceptual, emotional, temporal and spatial detail, while imagined events contain information about the cognitive operations involved in their generation (Johnson et al., 1988; Justice et al., 2013; McGinnis and Roberts, 1996). To be useful in determining the origin of an experience, information diagnostic of source must be bound at encoding and retrieved with the corresponding memory trace – processes which become less efficient with age. A result is that information is more likely to be misattributed to an incorrect source.

Lyle and colleagues (2006) demonstrated age-related deficits in binding source and content information. In their study younger and older adults perceived and imagined objects, and later made source and location judgments for objects that were studied (e.g., magnifying glass) and non-studied, but perceptually similar (e.g., lollipop). Older adults were more likely to make errors based on the perceptual similarity of objects (i.e., mistaking a lollipop as previously seen), replicating previous results (Henkel et al., 1998). However, older participants were less likely to claim that the falsely identified object was presented in the same location as the similar perceived object, suggesting that perceptual and contextual features of the studied stimuli are less tightly bound with age.

In line with this idea, older adults engage the hippocampus and lateral PFC areas less than younger adults during successful source encoding, reflective of decreased relational processing (Dennis et al., 2008a, 2007; Dulas and Duarte, 2014; Mitchell et al., 2006). During source retrieval, older adults also show reduced event-related potential (ERP) correlates of recollection (manifesting as a weaker parietal old-new effect, Dulas & Duarte, 2013). Moreover, providing older adults with relational memory support by encouraging careful consideration of the relationship between context and item at encoding eliminates age-related source memory deficits (Glisky et al., 2001; Naveh-Benjamin et al., 2007).

Loose binding of source information with a memory trace may explain why susceptibility to misinformation increases with age (Wylie et al., 2014). Misinformation-based errors arise when inaccurate post-event information becomes accepted as part of the original memory. For instance, when participants watch a video of a robbery, and are later misinformed that the item stolen was a ring rather than a necklace, older adults are more likely than younger adults to remember seeing a ring stolen in the original video (Cohen and Faulkner, 1989; Dodson and Krueger, 2006; Dodson et al., 2015). If contextual cues informing the source of either the original or misleading information are not fully bound with

the appropriate memory representation, there is a greater chance that the misinformation will be attributed to the incorrect source. Indeed, it has been shown in younger adults that acceptance of misinformation is associated with neural activation reflecting item encoding during the misinformation phase, coupled with source encoding during the original event (Baym and Gonsalves, 2012; Okado and Stark, 2005), though it remains to be seen whether this pattern of results holds in an older population.

Age-related declines in attention direction and conservation may also contribute to inefficient binding and reduced recollection, in that certain stimuli may never enter the encoding process in the first place (e.g., Gazzaley et al., 2005; Healey et al., 2008). The dorsolateral PFC is involved in directing and maintaining attention during episodic encoding (Cabeza et al., 2003; Iidaka et al., 2000; MacDonald et al., 2000; Uncapher and Rugg, 2005). Consistent with the idea that declines in attention mediated by this area contribute to false memory formation, when encoding items under conditions of divided attention younger adults perform at similar levels on subsequent memory tests as older adults under conditions of full attention (Attali and Dalla Barba, 2013; Castel and Craik, 2003; Jennings and Jacoby, 1993; Skinner and Fernandes, 2009). Disruption of parietal areas may also contribute to age-related attention deficits (Tisserand et al., 2004) and thus false memory susceptibility (Dennis et al., 2014; Duarte et al., 2010; Fandakova et al., 2015; Tsukiura et al., 2014).

3.1.2. *Dedifferentiation and distinctiveness*

Another consequence of reduced associative binding is that experiences from different sources are more similar in quality (dedifferentiated). If the enhanced phenomenological quality typically used to tag a memory as veridical (Johnson & Raye, 1981) is no longer available or reliable, people are less sensitive when discriminating between these and other experiences. Consistent with this proposal, older adults tend to rate authentic memories, imagined events and false memories as subjectively more similar than do younger adults

(Gallo et al., 2011; Henkel et al., 1998; Karpel et al., 2001; though see McGinnis & Roberts, 1996, for evidence against this claim).

The neural signatures associated with veridical and false memories are also less distinguishable with age. Using EEG, Gutchess and colleagues (2007) found that during encoding, a fronto-central ERP distinguished subsequent hits and misses for younger but not older adults. Likewise, during retrieval, hits and false alarms made by older adults were indistinguishable by their waveforms (see also Dywan et al., 2002; Swick et al., 2006). Corroborating findings have been reported using fMRI; unlike younger adults, older adults do not display differential activation for novel items conceptually similar to or different from studied information (Bowman and Dennis, 2015). Older adults also exhibit less specific activation patterns during recollection of true and false information (Duarte et al., 2010; Royet et al., 2011). The overlap in neural signatures with age suggests that older adults process information similarly regardless of novelty or authenticity, and are indicative of age-related difficulties in using distinctive item-specific information to make source decisions.

Experiential dedifferentiation of perceived and imagined events may contribute to the more prominent imagination inflation observed with age (Cohen and Faulkner, 1989; Henkel et al., 1998; Lyle et al., 2006; McDaniel et al., 2008; McDonough and Gallo, 2013; Thomas and Bulevich, 2006). Imagination inflation describes the phenomenon whereby imagining an event increases later belief that the event actually happened in the past (for a review, see Garry & Polaschek, 2000). For instance, people are more likely to claim they had actually performed an action if it was previously imagined, and this effect is larger for older adults (Cohen and Faulkner, 1989). Similarly, when asked to simulate counterfactual scenarios for events that have already taken place, older adults are more prone to mistaking the counterfactuals as the original occurrence (Gerlach et al., 2014). Inefficient binding means that distinctive perceptual and contextual information associated with memories, and

information on the cognitive operations involved in simulation, are less available with age (McDaniel et al., 2008). Therefore, internally-derived imaginations are less distinguishable from externally-generated memories, and are more likely to be confused as such. In line with this idea, older adults remember and imagine personal life events with less episodic detail (Addis et al., 2010, 2008, for review of these and related studies, see Schacter et al., 2013), and lower recruitment of neural areas involved episodic detail retrieval (Addis et al., 2011).

A shift in focus towards the emotional aspects of an experience may compound these recollective deficits. Affective information takes a more prominent role during encoding and retrieval with age due to changes in memory and communicative goals (Adams et al., 1997; Addis et al., 2008; Carstensen et al., 1999; Gaesser et al., 2011; Hashtroudi et al., 1990; James et al., 1998; Johnson, 2006). fMRI evidence reveals that when encoding the truthfulness of a statement, older adults engage areas involved in emotion processing (ventromedial PFC and insula) more than younger adults (Cassidy et al., 2014). Focusing on affective characteristics is thought to divert attention away from more source-informative perceptual qualities of an event (Hashtroudi et al., 1994, 1990), further contributing to the lowered discrimination between authentic and imagined memories (Rahhal et al., 2002; Suengas and Johnson, 1988). Furthermore, there is evidence that older adults are more susceptible to falsely recognizing and recalling positive relative to negative memories (Fernandes et al., 2008; Piguet et al., 2008; Werheid et al., 2010; see also Gallo et al., 2009), in line with an age-related positivity bias in memory (e.g., Mather & Carstensen, 2005).

If older adults are less effective at distinguishing between true and false memories, then it follows that age differences in false memory susceptibility can be mitigated by directing focus to distinctive information at encoding. Indeed, source monitoring is improved in both younger and older adults when information is presented in a distinctive manner (e.g., as pictures as opposed to words; Dodson & Schacter, 2002; Ferguson et al., 1992; Gallo et al.,

2007; Johnson et al., 1995; Pierce et al., 2008; Schacter et al., 1999; Smith et al., 2015). Age differences are also reduced by drawing attention to differentiating information at encoding or retrieval (e.g., Koutstaal et al., 1999; for a review see Koutstaal & Schacter, 2001). When attention is directed to source cues at study, both younger and older adults exhibit increased contextual binding related parahippocampal activity during encoding, and attenuated frontal post-retrieval monitoring effects (Dulas and Duarte, 2014, 2013). However, older adults require a greater disparity in the distinctiveness of presented stimuli to benefit memory, compared to that needed by younger adults, supportive of an inability to distinguish between related information with age (Smith et al., 2015). Moreover, directing focus to differentiating information during encoding or retrieval reduces, but does not eliminate age-differences in false recognition (Koutstaal et al., 1999), indicative of further cognitive mechanisms contributing to age increases in false memories.

3.2. *Gist-based processing*

Because encoding of distinctive information decreases with age, and memory traces become less differentiated, older adults tend to retrieve overall perceptual and conceptual similarities of stimuli, rather than item-specific information. While successful encoding involves integrating newly acquired information with existing relational memory networks, incoming information must also be encoded in a distinctive manner, so that the memory traces can be discriminated at retrieval (McClelland et al., 1995; O'Reilly and McClelland, 1994; Schacter et al., 1998). It has been proposed that the hippocampus becomes 'representationally rigid' with age. Subtle changes in hippocampal circuitry leads to a shift away from distinctive encoding of new information (pattern separation) and towards a reinstatement of already stored information (pattern completion; Wilson et al., 2006; Yassa, Mattfield, et al., 2011; Yassa, Lacy, et al., 2011). Age-related deterioration of ventrolateral PFC areas supervising pattern separation may also make this process less effective (Parkin et

al., 1999; Schacter et al., 1998). This shift toward pattern completion could be considered advantageous, in that we become more efficient at identifying familiar elements in new experiences, to better address novel future challenges (Wilson et al., 2006). However, extraction of information shared between events, rather than episode-specific information, increases overgeneralization and gist-based errors (Pidgeon and Morcom, 2014).

The Deese-Roediger-McDermott (DRM) paradigm (Deese, 1959; Roediger and McDermott, 1995) is commonly used to explore gist-based errors. In this paradigm, people who study lists of perceptually or conceptually related words (e.g., ‘sugar, candy, taste’), are likely to falsely remember studying an unseen yet semantically associated lure (e.g., ‘sweet’; see Gallo, 2006, for a review). Older adults are more susceptible to lure words than younger adults, suggestive of a reliance on memory for the general features of the studied stimuli, rather than specific item features (Balota et al., 1999; Gallo, 2006; Norman and Schacter, 1997; Schacter et al., 1997; Tun et al., 1998). Moreover, younger adults make fewer false alarms for repeatedly studied word lists, indicating an enhancement of item specific information; in contrast, older adults show no suppression of false alarms for repeatedly studied lists (Kensinger and Schacter, 1999). These findings are suggestive of a reduced ability to use recollection of the study list to oppose the build-up of gist (Kensinger and Schacter, 1999; Pierce et al., 2005). Similarly, increasing the category size of a studied list, and thus the strength of the gist trace, negatively influences memory accuracy more for older compared to younger adults (Koutstaal and Schacter, 1997; Pidgeon and Morcom, 2014). Furthermore, consistent with findings that focusing on emotional information diverts attention from more source-informative cues, emotional processing can increase conceptual similarity across studied items for older adults (Gallo et al., 2009).

Neuroimaging findings support these behavioral studies. During false recognition of perceptually related lures, Paige and colleagues (in press) observed greater hippocampal

activation for older relative to younger adults when gist was low, yet no age differences when gist was high. This result is thought to reflect older adults' shift away from pattern separation towards pattern completion as gist increases. Older adults also recruit areas involved in semantic processing and gist (namely lateral temporal regions) more than younger adults when encoding (Dennis et al., 2007) and retrieving falsely recognized semantically-related lures (Dennis et al., 2008b). When recollecting perceptually related lures, Dennis et al. (2014) found that older adults engage inferior frontal gyrus, anterior cingulate cortex, parahippocampus and occipitoparietal cortex to a lesser degree than younger adults, indicating a reduced reliance on reconstructive processes. Furthermore, an individual differences analysis in older adults demonstrated that higher false recollection predicted increased activity in temporal areas supporting semantic gist. These results indicate that false recollection in younger adults is attributable to erroneous reconstruction of studied event content, yet in older adults may be the result of gist trace retrieval.

3.3. Deficits in strategic retrieval

In addition to encoding deficits, impaired strategic retrieval also plays a role in age-related associative deficits (Cohn et al., 2008). Therefore, even when source information is successfully encoded, older adults may not use this information efficiently during retrieval to make monitoring decisions. Lateral PFC regions are pivotal to accurate retrieval monitoring, both in determining whether individual memory features pertain to the episode of interest, as well as whether the event as a whole is internally-derived or externally-experienced (Blumenfeld et al., 2011; Dobbins et al., 2002; Henson et al., 1999; Schacter et al., 1998; Slotnick et al., 2003). While lateral regions are most consistently associated with source monitoring (see Mitchell & Johnson, 2009 for a review), damage to other PFC regions (e.g., ventromedial, orbitofrontal) also results in source memory impairments and elevated false recognition (Melo et al., 1999; Parkin et al., 1996; Rapcsak et al., 1999; Schacter et al., 1996;

Simons et al., 2002). It is likely that age-related decline in lateral and other PFC regions contributes to retrieval source monitoring deficits.

To test whether retrieval monitoring difficulties contribute to age-related increases in false memories beyond encoding deficits, McDonough and Gallo (2013) had younger and older adults recall autobiographical memories and simulate personal future events. For half the events, elaboration instructions were used to increase the associated memory features. Participants were later asked to discriminate between the memories and future events. Despite successfully encoding and retrieving more features in the elaboration condition, older adults were not able to use these features to reduce source confusions to the level of younger adults. These results implicate age-related impairments in accurate retrieval monitoring processes above and beyond deficits in encoding or recollection. Further evidence shows that older adults use warnings given at retrieval about misleading information to reduce memory errors (Dodson et al., 2015; see also Coane et al., 2015; though see McCabe & Smith, 2002). Moreover, when older adults are provided with supportive instructions to focus on perceptual and contextual cues at retrieval, age-differences in imagination inflation are diminished (Henkel, 2008; Thomas and Bulevich, 2006). To be able to use these source informative cues they must be encoded in the first place, suggesting that older adults have difficulty spontaneously accessing or effectively using these cues during recall (Koutstaal, 2003).

Reduced efficiency of retrieval monitoring processes may necessitate a reliance on less effortful monitoring strategies. In a series of three DRM-based experiments, Thomas and McDaniel (2013) link an age-reduction in the effective use of source information at retrieval to declines in executive function. In their study, relational processing was manipulated during encoding of distinctive and non-distinctive items. Both younger and older adults were able to use distinctive information alone to reduce false alarms. However, older adults with lower executive functioning were unable to use distinctive information to overcome false memories

based on relational memory. It appears that when there are competing source cues, individuals with impoverished frontal functioning cannot effectively use strategic information to make recognition decisions, and so rely on less effortful relational information. Consistent with this theory, age-deficits in the use of source cues are particularly pronounced when multiple source cues are available (Ferguson et al., 1992; Gallo et al., 2006; Johnson et al., 1995).

3.4. Overreliance on familiarity

A repercussion of age-related reductions in memory encoding and retrieval is an increased reliance on automatic processes. The dual processing account theorizes two separable processes underlying recognition memory: familiarity and recollection (Hintzman & Curran, 1994; Jacoby, 1991; Yonelinas, 2002). Whereas recollection is an effortful retrieval of specific memory details, familiarity is a rapid process lacking conscious retrieval of context. In contrast to neural declines in hippocampally-mediated recollection, the neural substrates underlying familiarity (predominantly the parahippocampal and perirhinal cortices) are relatively spared with age (Daselaar et al., 2006; Dennis et al., 2008b; Insausti et al., 1998; Yonelinas et al., 2007). Thus, in the face of reductions in recollective memory, it is thought that older adults rely more on familiarity when making recognition judgments (Anderson et al., 2008; Craik & McDowd, 1987; Davidson & Glisky, 2002; Giovanello et al., 2010; Jennings & Jacoby, 1997; Parkin & Walter, 1992; Prull et al., 2006). Use of familiarity is a generally adaptive compensatory memory strategy; however, familiarity-based information without accompanying contextual details can be misleading, and therefore contributes to the enhanced rate of memory errors with age.

Consistent with an age-related reduction in recollection and increase in the use of familiarity, recall-to-reject mechanisms of source monitoring – where recollection of the original memory allows rejection of lure information – become less efficient with age (e.g.,

Gallo et al., 2006). Enhancing lure familiarity increases rates of false alarms in older but not younger adults (Edmonds et al., 2012; Fandakova et al., 2013a, 2013b; Jacoby, 1999; Jones & Jacoby, 2005; note, however, that age-differences are not always found for familiarity or fluency-based memory illusions; see Thapar & Westerman, 2009). When younger adults are placed under time pressure to reduce their ability to use recollective strategies, they respond similarly to older adults (Jones and Jacoby, 2005; Light et al., 2006). Older adults with poor associative memory or executive functioning are particularly reliant on familiarity when making recognition decisions (Fandakova et al., 2013a; Parkin and Walter, 1992), consistent with a reduced availability of recollective information due to MTL and PFC decline.

Familiarity in the absence of recollection is thought to underlie older adults' increased vulnerability to making memory conjunction errors. Conjunction errors occur when a lure comprised of features from studied stimuli is falsely recognized as being previously encountered (e.g., studied words = *snowball*, *sandman*; conjunction lure = *snowman*). Older adults are more susceptible to these errors across a range of stimuli types (word pairs, Castel & Craik, 2003; faces and names, Naveh-Benjamin et al., 2009; people and actions, Old & Naveh-Benjamin, 2008). An age-increase in conjunction errors is observed even when item memory is equivalent between age groups, implicating a specific relational deficit (Kersten and Earles, 2010). According to the associative deficit hypothesis, older adults are less able to remember relations between memory features, but memory for the individual features is preserved (see Naveh-Benjamin et al., 2003; Naveh-Benjamin, 2000). Therefore recognition decisions are based on familiarity with the component parts of the stimuli, which can be erroneously elicited by novel combinations of old features. Supporting this theory, older adults do not use strengthened associations between word pairs to the same degree as younger adults to avoid conjunction errors (Buchler et al., 2011; Jones and Jacoby, 2005). Older adults are also more likely to make conjunction errors between actors and actions regardless of the

original association between features (i.e., whether they are from the same or different events, Kersten et al., 2013).

Age-related increases in conjunction errors are associated with the functional and structural integrity of MTL regions. Specifically, structural decline in the dentate gyrus and CA3-4 subfield of the hippocampus is correlated with greater false alarms to conjunction lures (Shing et al., 2011). Giovanello and colleagues (2010) demonstrated that older adults recruit the right hippocampus less than younger adults during accurate retrieval of conjunction stimuli, reflective of recollective declines. Additionally, only older adults activate right parahippocampal activity more during false retrieval of conjunction lures compared with true, indicative of an overreliance on familiarity. In line with these findings, Fandakova et al. (2014) found that on an individual level, stronger hippocampal activation in response to associative novelty was related to fewer memory errors for both younger and older adults. However, overall the older group exhibited less hippocampal activation in response to conjunction lures, perhaps due to a lowered ability to detect novel associations of familiar stimuli.

Interestingly, study context influences the type of false memories produced in a similar manner for younger and older adults. Matzen and Benjamin (2013) combined the DRM and conjunction error paradigms, and asked participants to learn compound words (e.g. 'blackmail' and 'jailbird') in either a list or sentence context. Both younger and older adults were later more susceptible to semantic lures (e.g., 'criminal') rather than conjunction lures (e.g., 'blackbird') after studying the words in a sentence, whereas the opposite pattern was seen when the words were studied in a list. Presumably, in a sentence context participants encode the general gist of the word list, increasing vulnerability to conceptually related lures, but in a list context they rely on surface-level information, meaning conjunction errors can arise if associative information between word fragments is lost.

3.5. *Disinhibition and hyper-binding*

Relying on familiarity in the absence of recollection cannot entirely account for the increase in conjunction errors with age. Both younger adults and older adults claim to remember conjunction errors with a sense of recollection (Burt et al., 2004; Odegard and Lampinen, 2004; Pitarque et al., 2015; Reinitz et al., 1994, 1992), and these errors also occur in free recall (Reinitz and Hannigan, 2001). Moreover, recollection does not always allow rejection of conjunction lures (Jones and Bartlett, 2009). Additionally, across a number of studies it has been shown that effect sizes for age-related differences in false alarms are greater for ‘remember’ (characteristic of recollection, Tulving, 1985) than ‘know’ judgments (reflecting familiarity; McCabe et al., 2009). To account for this pattern of false alarms with age, Dodson, and colleagues (Dodson et al., 2007a, 2007b) proposed the misrecollection account, which argues that familiarity errors are the result of underbinding of memory elements, whereas recollection-based errors the result of excessive binding.

When tested on stimuli relevant to the memory task, older adults typically display associative deficits (Naveh-Benjamin, 2000). However, when tested on irrelevant information, older adults exhibit the opposite effect: forming too many associations, rather than too little (Campbell et al., 2012, 2010). This hyper-binding phenomenon is linked with age-related impairments in the inhibition of distracting information (e.g., Gazzaley et al., 2005; Hasher et al., 1999), a process dependent on various PFC subregions, including lateral and anterior cingulate cortices (Chao and Knight, 1995; Dillon and Pizzagalli, 2007; Elderkin-Thompson et al., 2008). Hyper-binding is more likely to occur when stimuli are presented close together in time, suggesting that older adults have difficulty suppressing recently learned but currently irrelevant information (Campbell et al., 2014, 2012, 2010). Conflicting information from these irrelevant associations disrupts the ability to form new associations between relevant stimuli, resulting in the associative deficits often observed with

age. Hyper-binding is thought to have some benefits, in that older adults are able to link more distant ideas together, and so are better able to see the ‘big picture’ (Campbell et al., 2014, 2012). However, hyper-binding may also contribute to deficits in pattern separation, allowing memory features to be erroneously incorporated across overlapping memory traces, thereby forming conjunction errors.

Campbell et al. (2014) explored the influence of hyper-binding on conjunction error formation by having younger and older adults learn word pairs. Memory for these pairs was tested using intact and conjunction stimuli; importantly, the conjunction stimuli were derived either from pairs occurring temporally close together or far apart on the study list. Older adults were particularly susceptible to making conjunction errors for pairs presented close together, whereas younger adults made about the same number of false alarms for near- and far-conjunctions. These results are consistent with the idea that older adults form erroneous associations between stimuli, especially if such stimuli occur within a close timeframe (see also Dodson et al., 2007a; Kroll et al., 1996; Shing et al., 2009). This age-increase in conjunction errors occurred for stimuli presented up to seven items apart; though because continuous spacing was not used, it remains to be determined how wide the ‘hyper-binding lens’ extends for older adults.

Age-related impairments in inhibitory ability can also contribute to familiarity-based distortions. Spreading activation between related memory constructs is preserved with age (Gallo & Roediger, 2003; Lee et al., 2012), yet older adults are less able to inhibit the sense of familiarity garnered by activated but irrelevant memory traces (Dehon and Brédart, 2004; Sommers and Huff, 2003). In line with this idea, poor executive functioning is associated with an increased susceptibility to familiarity for words as whole, as well as with the individual components (Fandakova et al., 2013a, 2013b). Neuroimaging studies also support this view; using EEG, Dywan et al. (2002) found greater amplitude ERP waveforms in frontal

areas for older compared to younger adults when false alarming to familiar words. This increased neural response is thought to reflect reduced suppression of the cortical response to the familiar non-target items. Yet in contrast to these findings, fMRI data show that older adults recruit the anterior PFC *less* than younger adults as lure word familiarity increases, despite false alarming to these lures more, suggestive of reduced efficiency of frontal monitoring processes (Fandakova et al., 2014). Differences in the timing and regional specificity of neural responses measured by EEG and fMRI likely reveal various aspects of the response to familiar lures.

Individual differences in inhibition ability also influences the effective use of retrieval monitoring strategies. Colombel et al. (2016) presented older adults with either typical DRM instructions to retrieve only studied items, or with inclusion instructions to recall all words thought of during study or recall regardless of accuracy. The inclusion condition removes the requirement of monitoring at retrieval, thus if faulty monitoring is to blame for errors in the typical DRM, participants should make a similar number of errors regardless of the instructions received. They found that inhibition ability was predictive of false alarms. Moreover, older adults with higher inhibition scores made more errors if they received the inclusion instructions, whereas those with lower inhibition scores had similar error rates following both typical and inclusion instructions, implicating ineffective use of monitoring processes with declining inhibition. However, as the authors note, this link is relatively fragile and further research is needed to disentangle the contribution of inhibition processes to memory distortions in both older and younger adults.

3.6. Summary

To summarize thus far, age-related increases in false memories result from interacting impairments in memory encoding, retrieval and monitoring mechanisms reliant on a number of regions within the MTL and PFC. Reduced associative binding means that memory traces

are less distinctive, allowing for source misattributions and gist-based errors to occur.

Additional declines in strategic monitoring processes are evident with age; in effect, older adults are reliant on less cognitively demanding, but also less accurate, monitoring mechanisms, such as making source decisions on the basis of familiarity. Older adults are also more likely to form spurious associations between incoming stimuli, and be distracted by cues that are not informative of source. Some of these cognitive processes – such as a reliance on familiarity in the absence of recollection, a shift towards pattern completion, and a tendency towards hyper-binding – could be considered adaptive changes with age, or at least strategies to compensate for limited memory resources. It has been argued that false memories in younger adults are the by-product of otherwise advantageous memory mechanisms (Schacter et al., 2011). In the same way, the cost of adopting more cognitively efficient memory processes with age may be increased opportunities for false memories to form.

4. Implications

In many circumstances memory authenticity is important; for instance, remembering whether one took their medication, turned the stove off, or locked the door before leaving, or only thought about doing so. A functional episodic memory system is vital for preserving a high quality of life with age, particularly with regards to maintaining independent living (Farias et al., 2009). Yet little is known about the impact of false memories on daily life in healthy older adults. It is evident that understanding the cognitive underpinnings of age-related increases in false memory susceptibility can inform strategies to improve memory accuracy in older adults. For instance, providing warnings of potential misinformation in memory accounts can reduce false alarms in older adults (Carmichael and Gutchess, 2015; Coane et al., 2015; Dodson et al., 2015; Watson et al., 2004). Moreover, directing attention towards differentiating information at encoding or retrieval (Dodson and Schacter, 2002;

Koutstaal et al., 1999; Schacter et al., 1999), or encouraging careful consideration of source during recall (Henkel, 2008), also reduces age differences in false memories. Training specific monitoring strategies can also benefit memory accuracy; Da Silva and Sunderland (2010) found that training older adults to detect repeated stimuli presentations reduces familiarity-based false memories, however this effect had limited generalizability to other memory tests. Development of a monitoring strategy that is effective across contexts would be a beneficial application of aging false memory research.

The increased susceptibility to false memories with age also has relevance for eyewitness testimony, which often serves as the primary form of evidence in legal cases (Buckhout, 1975; Howe and Knott, 2015; Loftus, 2003; Schacter and Loftus, 2013). Older adults are more likely than younger adults to report incorrect information after seeing a crime take place (Aizpurua et al., 2011, 2009; Cohen and Faulkner, 1989; Dodson and Krueger, 2006; Kersten et al., 2013) or identify the incorrect perpetrator in a suspect lineup (Memon et al., 2003). Moreover, older adults are poorly calibrated in determining the accuracy of their memories, in that they are more confident that these memory distortions represent reality (Cohen and Faulkner, 1989; Dehon and Brédart, 2004; Dodson and Krueger, 2006; Jacoby and Rhodes, 2006; Jacoby et al., 2010; Shing et al., 2009). Indeed, age differences in memory errors are greatest for decisions made with high confidence (Dodson et al., 2015; Fandakova et al., 2013b; Gallo et al., 2009; Tsukiura et al., 2014). Thus, it is important to understand the mechanisms underlying increased false memory with age, as even eyewitness testimony from older adults given with high confidence may not be a reliable indicator of genuine accuracy.

5. Further questions and considerations

A number of factors moderate the effect of age on false memory susceptibility, and should be taken into consideration both when exploring potential underlying cognitive and neural mechanisms, and when attempting to preserve memory accuracy.

First, “false memory” is a broad term that covers a range of errors. As discussed earlier, different types of false memories typically arise via separable mechanisms; for example, source misattribution can occur due to inefficient binding, whereas gist errors result from insufficient pattern separation. In some cases the same type of error may arise via multiple routes: for instance, conjunction errors can result from underbinding and a subsequent reliance on familiarity (Jones and Bartlett, 2009; Jones and Jacoby, 2001; Rubin et al., 1999), as well as excessive binding of memory features (Campbell et al., 2014; Dodson et al., 2007b; Kroll et al., 1996; Reinitz and Hannigan, 2001). Following from these observations, we must consider that individual heterogeneity in cognitive aging (e.g., Hultsch, Strauss, Hunter, & MacDonald, 2008) could be linked with variation in susceptibility to specific types of false memories. For younger adults, vulnerability to one type of memory error does not necessarily predict likelihood of falling prey to other types of errors (Calvillo & Parong, 2015; Ost et al., 2013; Zhu et al., 2013; though see Gallo, 2010). The question remains open whether age-related increases in false memory susceptibility are selective or generalizable across several types of memory errors at an individual level, and whether any differences can be linked to selective deficits in certain cognitive processes.

Related to this idea, while we have made progress in identifying neural correlates of false memories, we cannot yet draw firm conclusions regarding the role of specific MTL and PFC subregions in specific aspects of the age-related increase in false memories. In younger adults, a recent Activation Likelihood Estimation (ALE) meta-analysis of false memory neuroimaging studies sheds some light on PFC subregions consistently involved in memory distortions, identifying the medial superior PFC, ventromedial PFC and ventral anterior cingulate cortex as a critical components of the false memory network (Kurkela and Dennis, 2016). However, whether these regions are also implicated in the age-related false memory increase remains to be determined. Shing and colleagues (2011) provide another promising

lead on this front with regard to the MTL, identifying a link between structural decline in the dentate/CA3-4 subfield of the hippocampus and errors in an associative memory test in older adults. These findings dovetail nicely with those implicating changes in the dentate/CA3 subregion in the age-associated shift towards pattern completion (Wilson et al., 2006; Yassa et al., 2011a, 2011b). Future research should continue to address the subregional specificity of the processes contributing to false memories with age.

The recruitment of specific neural regions may be influenced by false memory strength or mode of memory retrieval. For instance, during false *recognition* of lure stimuli, older adults engage the parahippocampal gyrus more so than younger adults, potentially reflecting a reliance on familiarity in the absence of recollection (Giovanello et al., 2010). Yet when participants claim to *recollect* previously encountering a lure, by giving such stimuli a “remember” as opposed to a “know” response during recognition (Tulving, 1985), older adults show reduced parahippocampal recruitment compared to younger adults, perhaps due to a reduction in reconstructive processes with age (Dennis et al., 2014). These studies examined different types of false memories (conjunction errors and perceptually related distortions, respectively) which could account for the disparity in these findings. However, Paige et al. (in press) examined false recognition for perceptually related lures, and still report different activation patterns than Dennis et al. (see Section 3.2 above). It is therefore possible that the mode of false retrieval modulates MTL activity.

The nature of the testing environment can also moderate the age-related influence on false memory susceptibility. When older adults are tested at an optimal time of day (typically in the morning) age differences in memory accuracy are diminished (Hasher et al., 1999; Intons-Peterson et al., 1999). It has also recently been shown that invoking aging and memory stereotype threats before testing alters false memory rates. Invoking a stereotype threat explicitly, by providing participants with summaries of research supporting an age-

related memory decline, reduces false recall and recognition, potentially because older adults adopt a more conservative response criterion (Barber and Mather, 2013; Wong and Gallo, 2015). Interestingly, if the threat is invoked implicitly, by subliminally presenting negative age-related words (e.g., ‘feeble’), older adults are more likely to make false alarms, possibly because controlled monitoring processes are disrupted by anxiety over the testing situation (Krendl et al., 2015). The circumstances under which an elderly eyewitness is questioned is thus an important consideration to preserve accuracy of a memory.

Encoding and retrieval processes likely make different relative contributions to the increased false memories observed with aging. However, due to the inextricable links between encoding and retrieval, it is methodologically difficult to disentangle the independent influence of these two processes to false memory formation. For example, feature binding and pattern separation mechanisms at encoding influence the subsequent success of pattern completion procedures during retrieval. Often a false memory may arise at multiple points along the encoding and retrieval pipeline. For instance, misinformation errors may occur if the original information is not properly encoded, if source for the misleading information is not encoded, or if the misleading information is later retrieved along with the original memory trace. As such, delineating the independent contributions of encoding and retrieval to the generation of memory errors, particularly with regards to the aging process, is an ongoing endeavor (e.g., Abe et al., 2013; Huff et al., 2015; Kurkela & Dennis, 2016).

Finally, as noted briefly earlier, although the malleability of memory renders us susceptible to a range of memory distortions that become increasingly common with age, this property of episodic memory may also be adaptive (cf., Howe, 2011; Newman & Lindsay, 2009; Schacter et al., 2011; Schacter, 2001), in that it reflects the operation of a flexible system in which individual memory features can be rearranged to simulate future happenings (Schacter and Addis, 2007), imagine alternative past outcomes (De Brigard et al., 2013;

Gerlach et al., 2014), and creatively solve problems (Madore and Schacter, 2014; Madore et al., 2015; Sheldon et al., 2011). Recent studies of older adults have begun to examine adaptive uses of episodic memory in imagination (e.g., Addis et al., 2008), problem solving (Madore and Schacter, 2014; Sheldon et al., 2011), and creativity (Madore et al., 2016), but direct links between these adaptive processes and false memory in aging need to be explored.

In line with this general theme, the ability to update memory with newly acquired information is arguably an adaptive characteristic of the reconstructive memory system (Lee, 2009; Schacter et al., 2011). A consequence of the age-related reliance on reinstatement of previously encoded information is reduced memory updating (Attali and Dalla Barba, 2013). Somewhat paradoxically, a reduced capacity to update memory with new information may *prevent* the formation of false memories. While susceptibility to misinformation generally increases with age (Wylie et al., 2014), there are exceptions to this pattern. Umanath and Marsh (2012) demonstrated that, after reading stories containing factual inaccuracies, older adults reproduced fewer of these errors during retrieval, despite identifying them at an identical rate as younger adults during encoding (see also Umanath et al., 2014). Indeed, older adults exhibit a reduction in both the benefits and costs of memory reactivation (St. Jacques et al., 2015). These studies highlight the possibility that reliance on prior knowledge in the face of reduced memory updating can actually lower assimilation of misinformation. Of course, the flip side of reduced memory updating is that if an original memory is incorrect in some way, reliance on prior knowledge means that the inaccurate memory persists (Vannucci et al., 2012). It is also interesting that when information about the original event is sparse, older adults are less vulnerable to misinformation than younger adults, presumably due to lower memory for the misleading information (Marche et al., 2002). An intriguing prospect raised by these findings is that older adults with superior memory performance may in fact be more vulnerable to errors via misinformation than those with poorer memory.

6. Conclusion

In general, susceptibility to false memories increases with advancing age. In this review we highlight the complexity and heterogeneity of cognitive aging, demonstrating that the age increase in false memories can be attributed to a number of changes occurring at both encoding and retrieval. Broadly, the enhanced likelihood of memory errors can be linked to declines in a number of regions within MTL and PFC, leading to deficits in associative binding and strategic monitoring. Those impairments themselves result in a cascade of cognitive changes, including reduced recollective ability, a subsequent reliance on misleading monitoring mechanisms such as familiarity, incomplete pattern separation resulting in an overreliance on gist information, as well as a reduced ability to inhibit erroneous binding and irrelevant information. Elucidating the cognitive and neural underpinnings of enhanced false memories in older adults informs not only our understanding of typical memory changes with age, but also the functioning of the constructive memory system across the lifespan, and the way in which errors can take hold within this system.

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Highlights

- Review of behavioral and neuroimaging research on false memories and healthy aging
- Multifaceted cognitive changes contribute to false memory increase with age
- Age-related medial temporal and prefrontal decline play a prominent role
- Neural changes result in impaired associative memory and strategic monitoring