Modifying memory for a museum tour in older adults: Reactivation-related updating that enhances and distorts memory is reduced in ageing

Peggy L. St. Jacques^{1,2}, Daniel Montgomery^{1,2}, and Daniel L. Schacter^{1,2}

¹Department of Psychology, Harvard University, Cambridge, MA, USA ²Center for Brain Science, Harvard University, Cambridge, MA, USA

(Received 23 January 2014; accepted 3 June 2014)

Memory reactivation, the activation of a latent memory trace when we are reminded of a past experience, strengthens memory but can also contribute to distortions if new information present during reactivation is integrated with existing memory. In a previous study in young adults we found that the quality of memory reactivation, manipulated using the principle of encoding specificity and indexed by recollection ratings, modulated subsequent true and false memories for events experienced during a museum tour. Here in this study, we examined age-related changes in the quality of memory reactivated and then immediately followed by the presentation of a novel lure photo from an alternate tour version (i.e., reactivation plus new information). There was an increase in subsequent true memories for reactivated targets and for subsequent false memories for lures that followed reactivated targets, when compared to baseline target and lure photos. However, the influence of reactivation on subsequent memories was reduced in older adults. These data reveal that ageing alters reactivation, on subsequently reducing memory distortions in older adults compared to young adults.

Keywords: Autobiographical memory; Ageing; Reactivation; False memory; Episodic memory.

Updating memory to strengthen existing memory representations and to incorporate relevant new information is critical for maintaining the relevance of our past experiences (Bjork, 1978; Lee, 2009). This adaptive function of memory, however, can contribute to distortions or false memories if novel information is integrated with old information (Hardt, Einarsson, & Nader, 2010; Schacter, Guerin, & St. Jacques, 2011). Memory reactivation, or the activation of a latent memory trace when we remember a past experience, is a component process of memory that enables memories to be updated with new information (Johnson & Chalfonte, 1994; Johnson & Johnson, 2009), and later retained via reconsolidation processes (for reviews, see Hardt et al., 2010; Nadel, Hupbach, Gomez, & Newman-Smith, 2012). For example, Hupbach, Gomez, Hardt, and Nadel (2007)

Address correspondence to: Peggy L. St. Jacques, Department of Psychology, Harvard University, 864 William James Hall, Cambridge, MA 02138, USA. E-mail: pstjacques@fas.harvard.edu

We thank Justin Kim and Sally Justus for their helpful assistance and the Natural History Museum and Peabody Museum of Archaeology and Ethnology at Harvard University for their cooperation.

This work was supported by National Institute on Aging Grant [grant number AG08441], awarded to DLS; and by National Institute on Aging Grant [grant number NRSA AG038079], awarded to PLS.

investigated the influence of reactivating a memory prior to learning new information. Participants were asked to encode a set of objects (set 1), and then a second set of objects (set 2) 48 hours later. Prior to learning set 2, one group of participants was reminded about learning the first set of objects by asking them to describe the procedure in the previous session, while another group was not reminded. Finally, 48 hours later, participants were asked to recall set 1 or set 2 objects. When asked to recall set 1 objects, participants in the reminder group experienced more intrusions of set 2 objects compared to participants in the noreminder group. However, there was a similar level of intrusions of set 1 objects across the groups when recalling set 2 objects (i.e., asymmetrical pattern of intrusions). Hupbach et al. (2007) interpreted this pattern of findings as evidence that reactivation enabled the incorporation of new information from set 1 into existing memory for set 2 (but also see Sederberg, Gershman, Polyn, & Norman, 2011), rather than more generally increasing source confusion between set 1 and set 2. Although a number of studies have shown that reactivation affects subsequent memories (Chan & LaPaglia, 2013; Forcato, Rodriguez, Pedreira, & Maldonado, 2010; Schiller et al., 2010), including autobiographical memories (Schwabe & Wolf, 2010), less is known regarding how reactivation contributes to both enhancement and distortion effects in memory, which has both theoretical implications (e.g., Hardt et al., 2010; Schacter et al., 2011) and important practical implications for such issues as understanding evewitness memory (Lacy & Stark, 2013; Schacter & Loftus, 2013).

In a previous study with young adults, we examined the influence of memory reactivation for naturalistic events on both subsequent true and false memories (St. Jacques & Schacter, 2013). Participants first encoded events they experienced during a guided museum tour. They then returned to the lab 48 hours later and were shown photos from stops they visited during the tour, in order to reactivate their memories; these old (target) photos were paired with new (lure) photos of museum stops from an alternate version of the tour that were not previously seen. We predicted that reactivation would strengthen memory for the target photos, but would also facilitate encoding of the novel lures that followed. In order to test these predications, participants were brought back 48 hours later for a recognition memory test for stops they visited during the museum tour, which consisted of reactivated targets and lures that were

previously shown or baseline targets and lures that were not previously shown. Consistent with our predictions, we found an increase in subsequent hit rates for reactivated targets (i.e., true memories) and in subsequent false alarm rates for lures that were paired with reactivated targets (i.e., false memories), when compared to baseline target and lure photos that were not previously shown. Additionally, subsequent true and false memories were influenced by the quality of memory reactivation. There was an increase in both kinds of subsequent memory effects in high reactivation conditions (i.e., retrieval cues during reactivation matched the encoding experience) compared to low reactivation conditions (i.e., retrieval cues during reactivation mismatched the encoding experience). Subjective ratings of the amount of recollection during memory reactivation also modulated these recognition memory increases, such that the effects of reactivation on subsequent memory were maximal when participants indicated strong recollective experience during reactivation. Thus, we found that reactivating a memory influences how new information present during memory retrieval will be encoded and retained at a later time, which we linked to memory-updating processes (see also St. Jacques, Olm, & Schacter, 2013). We thus refer to this effect as *reactivation-related updating*.

These findings provide a basis for raising questions about the effects of reactivation on memory in older adults. Previous studies have shown that older adults recall less accurate memories and are more susceptible to various errors and distortions in memory (for reviews, see Fandakova, Shing, & Lindenberger, 2013; Jacoby & Rhodes, 2006; Koutstaal & Schacter, 2001; Schacter, Koutstaal, & Norman, 1997). Ageing also impairs subjective recollection processes and contextual recall (for reviews, see Spencer & Raz, 1995; Yonelinas, 2002), which contribute to the quality of memory reactivation. However, it remains unknown how age-related changes in reactivation quality during retrieval potentially contribute to changes in subsequent true and false memories. In the current study, we examined age-related changes in reactivation-induced memory updating that enhance and distort subsequent memories.

Many studies have examined the influence of retrieval or rehearsal on memory in ageing. Although young adults show beneficial effects of rehearsal on memory (e.g., Linton, 1975; Nadel, Campbell, & Ryan, 2007; Roediger & Karpicke, 2006), the findings are mixed in older adults. Ageing has been associated with both similar benefits (Bluck, Levine, & Laulhere, 1999; Meyer & Logan, 2013; Rabinowitz & Craik, 1986; Schacter, Koutstaal, Johnson, Gross, & Angell, 1997) and age-related reductions (Henkel, 2007; Koutstaal, Schacter, Johnson, Angell, & Gross, 1998; Widner, Otani, & Smith, 2000) in memory following rehearsal. Additionally, memory retrieval can increase distortions and errors in subsequent memory in older adults (e.g., Henkel, 2007; Jacoby, 1999; Kensinger & Schacter, 1999; Schacter, Koutstaal, Johnson, et al., 1997; but also see Chan, Thomas, & Bulevich, 2009). Better understanding the influence of reactivation quality during memory retrieval/rehearsal could provide insight into how retrieval differentially influences subsequent memory in young and older adults.

In the current study, we investigated agerelated changes in reactivation-related updating that contributes to subsequent true and false memories for real-world events experienced during a museum tour. Young and older adult participants encoded events they experienced during an audio-guided museum tour that was adapted from our original study (see Figure 1). The museum paradigm allowed us to verify the accuracy of memories for subsequent memory analysis while exerting control over the encoding of real-world events. Participants returned to the lab 48 hours later and reactivated memories for the museum tour cued by photos from stops they visited; on some trials, reactivated memories were followed by a novel lure photo from an alternate museum tour. A recognition memory test occurred 48 hours later in which participants were shown target and lure photos that were previously presented (i.e., reactivation) or not previously presented (i.e., baseline). Given the typical pattern of age-related decreases in true memories and increases in false memories, we predicted that when subsequent true and false memories were collapsed across reactivation and baseline conditions, we would find a similar age-related pattern in recognition memory performance. However, because older adults exhibit reductions in recollection processes and contextual recall, which contribute to the quality of reactivation (Sederberg et al., 2011; St. Jacques & Schacter, 2013; St. Jacques et al., 2013), we also predicted that age-related reductions in reactivation quality would lead to a reduction in these enhancement and distortion effects in subsequent memories. Thus, compared to young adults, we predicted that older adults will show a decrease in subsequent true and false memories in the reactivated versus baseline conditions.

METHODS

Participants

Participants included 16 young [8 women; mean age in years (M) = 21.68, SD = 2.96] and 16 older adults (9 women: M = 73.00, SD = 5.81), who reported no history of neurological or psychiatric impairment, were not taking any medications known to affect cognitive function and reported no hearing or non-corrected vision impairments. Older adults scored high on the mini-mental state examination (M = 29.19, SD = 0.91; all older adults scored > 28 out of a maximum of 30). There were no significant differences in years of education in young adults (M = 15.08, SD = 2.40) compared to older adults (M = 16.69, SD = 3.98). Participants provided written informed consent for a protocol approved by the Harvard Institutional Review Board. Participants were excluded if they had previously visited the museums used in the study (Peabody Museum of Archaeology and Ethnology and Harvard Museum of Natural History) in the last 10 years.

Procedure

Participants completed three sessions, each separated by 48 hours. In Session 1, participants went on an audio-guided tour of the Harvard Peabody and Natural History Museums accompanied by the experimenter. During the museum tour, participants visited 68 stops and listened to a short audio narrative presented on an iTouch. The audio narratives were approximately 45 seconds long and participants moved to the next stop immediately after listening to the audio. Participants were instructed to stand directly in front of each item at the museum so that it was unobstructed by other people and to attend to the relevant items in front of them that were described in the audio narrative. There were two versions of the museum tour with the alternate tour showing similar stops to be used as lure images in later sessions (see Figure 1). We minimized the possibility that participants would view or walk directly past items in the alternative version of the tour by selecting stops in each tour so that they were separated by barriers and/or on opposites sides of the room. Additionally, the experimenter 'tour guide' ensured that participants did not attend to items in the alternative version of the tour when directing them through



Figure 1. Experimental design. The study took place in three sessions separated by 48 hours. In Session 1, participants went on one of two audio-guided museum tours accompanied by the experimenter. In Session 2, they were shown photographs from stops they visited and asked to make reliving ratings (target-only trial). On some trials (target and lure trial), the target was followed by a photograph taken from the alternate museum tour (lure), after a 0.5- or 6-second delay, and participants were asked to judge the amount of visual detail. In Session 3, participants were shown reactivated targets and lures (i.e., shown during Session 2) or baseline targets and lures (i.e., not shown during Session 2) and asked to indicate whether the photograph showed a stop they had visited during the museum tour. A reliving rating followed 'yes' and 'no' responses during recognition memory.

the museums. In Session 2, participants were shown colored digital photos of a subset of museum stops from the tours. The photos were taken by the experimenter during a separate trip to the museum. The photos captured items in the museum stop (display case, sign, etc.) from a centered and horizontal perspective and excluded people. Photos were selected so that they were similar to ones taken in our previous studies using the museum tour paradigm (St. Jacques & Schacter, 2013; St. Jacques et al., 2013), in which participants wore a sensor-based camera that automatically takes photos. Thus, the photos were very similar to how participants would have viewed the item during their museum tour. On each trial participants were shown target photos of museum stops they had visited during the tour and asked to rate the degree of reliving, or subjection recollection, on a 5-point scale (from 1 = low to 5 = high) within 6 seconds (target-only trial) to provide a measure of the quality of memory reactivation. Following some targets, participants viewed the corresponding lure photo from the alternate tour and were asked to rate the amount of detail, or visual information, depicted in the photo on a 5-point scale (from 1 = low to 5 = high) within 6 seconds (target and lure trial). Lure photos were shown after a 0.5- or 6-second delay. The differential delay was included in order to test predictions regarding the timing of the modulatory influence of reactivation on processing of the lure photo (e.g., Duncan, Sadanand, & Davachi, 2012). However, because preliminary analysis revealed no differences as a function of delay, we combined the data from the separate delays. We will refer to targets presented in Session 2 as 'reactivated targets' and to lures that were paired with these targets as 'reactivated lures'. In Session 3, participants were shown reactivated target photos (15 trials) and reactivated lure photos (24 trials), or baseline target photos (i.e., not shown in Session 2; 15 trials) and baseline lure photos (14 trials) and were asked to a make yes/no recognition memory decision regarding whether they had visited the depicted stop during their museum tour. Participants were warned that the lure photos would look very similar to stops that they actually visited during the museum tour and to look carefully at each photo before making their response. For 'yes' responses participants additionally rated reliving on a 5-point scale (from 1 = low to 5 = high). No time limit was given, although participants were asked to respond as soon as the answer came to mind.

RESULTS

Recognition memory

In order to examine age-related differences in whether reactivating a memory strengthened and distorted subsequent memories we conducted a 2 (retrieval cue: target, lure) $\times 2$ (condition: reactivated, baseline) \times 2 (age group: young, older) analysis of variance (ANOVA) on the proportion of 'yes' responses in recognition memory, with cue and condition as within-participants measures and age group as a between-participants factor (see Table 1). There was a main effect of age group, F(1,30) = 4.01, p = .05, MSE = .03, $\eta_p^2 = .12$, with older adults (M = 0.57, SD = 0.10) showing a greater overall proportion of 'yes' responses than young adults (M = 0.51, SD = 0.07). Thus, older adults were more likely overall to endorse a photo as a stop on their museum tour. Further, there was also a main effect of retrieval cue, $F(1,30) = 234.28, p < .0001, MSE = .03, \eta_p^2 = .89,$ reflecting an increase in 'yes' responses to target photos (i.e., hits; M = 0.78, SD = 0.11) than lure photos (i.e., false alarms; M = 0.29, SD = 0.16). However, there was a significant retrieval cue × age-group interaction, F(1,30) = 11.02, p = .002,

 TABLE 1

 Recognition memory performance

	Hit		False alarm	
	Reactivation	Baseline	Reactivation	Baseline
Young Old	$0.90 (0.14) \\ 0.80 (0.11)$	0.71 (0.16) 0.72 (0.15)	0.32 (0.15) 0.45 (0.15)	0.14 (.15) 0.30 (.21)

Mean (standard deviation).

MSE = .03, $\eta_p^2 = .27$, which showed that older adults had a significant increase in the proportion of 'yes' responses to lures, or false alarms, t(30) =3.41, p = .002, and a non-significant decrease in the proportion of 'yes' responses to targets, or hits, when compared to young adults (see Figure 2A). Thus, older adults showed the predicted increase in false alarms when compared to young adults, but we did not observe the typical decrease in hits.

There was also a main effect of condition, $F(1,30) = 97.86, p < .0001, MSE = .01, \eta_p^2 = .77,$ reflecting an overall increase in 'yes' responses in the reactivated (M = 0.62, SD = 0.09) versus baseline (M = 0.46, SD = 0.11) conditions. However, as predicted, this main effect was qualified by a condition \times age-group interaction, $F(1,30) = 6.00, p = .02, MSE = .01, \eta_p^2 = .17.$ Compared to young adults (reactivated: $\dot{M} = 0.61$, SD = 0.09; baseline: M = 0.41, SD = 0.08), older adults (reactivated: M = 0.63, SD = 0.09; baseline: M = 0.51, SD = 0.11) showed a smaller difference between reactivated and baseline conditions. t(30) = 2.50, p = .02 (see Figure 2B). Whereas young adults had a 20% boost in the reactivated versus baseline conditions, older adults only had a 10% difference between these conditions. Thus, ageing reduced the influence of reactivation on subsequent true and false memories. There were no other significant interactions.

To investigate age-related differences in reaction time (RT) during recognition memory in Session 3, we conducted a similar 2 (retrieval cue: target, lure) × 2 (condition: reactivated, baseline) × 2 (age group: young, older) ANOVA. We found a main effect of age group, $F(1,25^1) = 4.62$, p = .04, MSE = 21.07, $\eta_p^2 = .16$, with older adults (M = 6.28 s, SD = 3.26 s) having slower RTs than young adults (M = 4.00 s, SD = 0.82 s). There was also a main effect of condition, F(1,25) = 15.36, p = .001,

¹Here and elsewhere, difference in degrees of freedom reflects lack of responses for reactivated misses or baseline false alarms.



Figure 2. Age-related changes in subsequent recognition memory. (A) Collapsed across reactivation and baseline conditions, we observed the typical pattern of age-related increase in false memories and a non-significant decrease in true memories. (B) There was an age-related reduction in the influence of reactivation on subsequent memories. Error bars indicated \pm SEM, *p < .05, **p < .005.

 $MSE = .97, \eta_p^2 = .38$, reflecting faster RTs in the reactivated (M = 4.78 s, SD = 2.75 s) versus baseline (M = 5.56 s, SD = 2.56 s) conditions. Additionally, the condition × age-group interaction approached significance, $F(1,25) = 4.07, p = .06, MSE = .97, \eta_p^2 = .14$. Post-hoc analyses indicated that the interaction was related to slower RTs in the reactivated condition in older adults (reactivated: M = 6.10 s, SD = 3.38 s; baseline: M = 6.12 s, SD = 3.05 s) when compared to young adults (reactivated: M = 3.47 s, SD = 0.70 s; baseline: M = 4.60 s, SD = 1.15 s), t(30) = 3.04, p = .005. There were no other significant effects.

Subjective ratings: Session 2

To investigate age-related differences in reliving ratings for target photos in Session 2 we conducted a 2 (subsequent memory response: 'yes', 'no') \times 2 (retrieval cue: target, lure) $\times 2$ (age group: young, older) ANOVA on mean reliving ratings and RT, with subsequent memory response and retrieval cue as within-participants measures and age group as a between-participants factor. First, turning to mean reliving ratings, we found a main effect of age group, F(1,30) = 19.83, p = .0001, MSE = 1.49, $\eta_{\rm p}^2$ = .40, with older adults (*M* = 3.89, *SD* = 0.71) showing higher reliving ratings than young adults (M = 3.05, SD = 0.45). There was a main effect of subsequent memory response, F(1,30) = 26.84, $p = .00001, MSE = .44, \eta_p^2 = .47$, reflecting higher reliving ratings for 'yes' (i.e., hits plus false alarms;

M = 3.58, SD = 0.79) than 'no' (i.e., misses plus correct rejections; M = 2.97, SD = 0.89) responses, and a main effect of retrieval cue, F(1,30) = 6.74, $p = .01, MSE = .46, \eta_p^2 = .18$, which reflected higher reliving ratings for lures (M = 3.43, SD = 0.80) than targets (M = 3.12, SD = 0.89). We also found a significant subsequent memory response × retrieval cue interaction, F(1, 30) = 20.74, p =.00008, MSE = .30, $\eta_p^2 = .41$, reflecting a greater difference in reliving between target 'yes' responses (i.e., hits; M = 3.64, SD = 0.76) and target 'no' responses (i.e., misses; M = 2.60, SD = 1.23) compared to lure 'yes' responses (i.e., false alarms; M = 3.51, SD = 0.96) and lure 'no' responses (i.e., correct rejections; M = 3.35, SD = 0.78). Post-hoc analyses revealed that this interaction was driven by a significant difference in reliving for 'yes' responses to targets (i.e., hits) compared to 'no' responses to targets (i.e., misses), t(31) = 5.85, p = .000002. Finally, there was a subsequent memory response × retrieval cue × age-group interaction, F(1, 30) = 5.32, p = .03, $MSE = .30, \eta_p^2 = .15$. Simple effects analyses revealed that the difference in reliving between 'yes' and 'no' responses to targets (i.e., hits versus misses) compared to lures (i.e., false alarms versus correct rejections) was significant, F(1, 15) = 24.23, $p = .0002, MSE = .29, \eta_p^2 = .62$, in young adults (hit: M = 3.27, SD = 0.44; miss: M = 1.91, SD = 0.75;false alarm: M = 3.01, SD = 0.92; correct rejection: M = 2.99, SD = 0.66), but not in older adults (hit: M = 4.02, SD = 0.84; miss: M = 3.27, SD = 1.26;false alarm: M = 4.02, SD = 0.72; correct rejection: M = 3.70, SD = 0.74). There were no other significant interactions. Thus, these results are generally consistent with our previous reports suggesting that the quality of reactivation, here indexed by reliving ratings, influences subsequent memory effects such that memories reactivated more strongly are more likely to be associated with subsequent hits and false alarms (St. Jacques et al., 2013; St. Jacques & Schacter, 2013). That is, the quality with which a target memory is reactivated in Session 2 influences whether the lure that follows will be integrated with existing memory for the museum tour, leading to a subsequent false alarm in Session 3.

Second, turning to RT for reliving ratings in Session 2, there was a significant main effect of age group, F(1, 30) = 4.83, p = .04, MSE = 6.47, $\eta_{\rm p}^2$ = .14, with slower RT for older adults (M = 3.56 s, SD = 0.54 s) compared to young adults (M = 3.11 s, SD = 0.62 s). We found a main effect of subsequent memory response, F(1, 30) = 4.89, $p = .04, MSE = .69, \eta_p^2 = .14$, with slower RT for 'yes' responses (M = 3.50 s, SD = 0.61 s) than 'no' responses (M = 3.17 s, SD = 0.91 s). However, a subsequent memory response \times age-group interaction, F(1, 30) = 10.59, p = .003, MSE = .69, η_p^2 = .26, revealed that the difference in RT for 'yes' versus 'no' responses was greater in young adults ('yes': M = 3.51 s, SD = 0.68 s; 'no': M = 2.71 s, SD = 0.94 s) than older adults ('yes': M = 3.48 s, SD = 0.56 s; 'no': M = 3.63 s, SD =0.61 s). Post-hoc analyses revealed that the subsequent memory response × age-group interaction was the result of slower RTs for 'no' responses in older adults than young adults, t(30) = 3.31, p = .002. There was also a main effect of retrieval cue, F(1, 30) = 10.74, p = .003, MSE = .44, $\eta_p^2 = .26$, reflecting slower RTs for lures (M = 3.53 s, SD = 0.59 s) than targets (M = 3.14 s, SD = 0.82 s), but a retrieval cue \times age-group interaction, F(1, 30) = 8.96, p = .005, $MSE = .44, \eta_p^2 = .23$, showed that the difference in RT for lures versus targets was greater in young adults (true: M = 2.74 s, SD = 0.84 s; false: M = 3.48 s, SD = 0.65 s) than older adults (true: M = 3.54 s, SD = 0.59 s; false: M = 3.58 s, SD = 0.54 s). Post-hoc analyses showed that this interaction was driven by slower RTs for reliving ratings made for targets in older adults compared to young adults, t(30) = 3.12, p = .004. Finally, there was a subsequent memory response \times retrieval cue \times age-group interaction, F(1, 30) =5.17, p = .03, MSE = .75, $\eta_p^2 = .15$. Post-hoc analyses showed that the three-way interaction

was the result of a greater difference in reliving RT for hits versus misses, F(1,15) = 4.23, p = .058, in young adults (hit: M = 4.02, SD = 0.84; miss: M = 3.27, SD = 1.26; false alarm: M = 4.02, SD = 0.72; correct rejection: M = 3.70, SD = 0.74) but not in older adults (hit: M = 4.02, SD = 0.84; miss: M = 3.27, SD = 1.26; false alarm: M = 4.02, SD = 0.74); correct rejection: M = 3.70, SD = 0.84; miss: M = 3.27, SD = 1.26; false alarm: M = 4.02, SD = 0.72; correct rejection: M = 3.70, SD = 0.74).

To investigate age-related differences in detail ratings made to the lure photos in Session 2 we conducted a 2 (response: false alarm, correct rejection) ×2 (age group: young, older) ANOVA on mean ratings and RT, with response as a within-participants measure and age group as a between-participants factor. First, turning to mean detail ratings, we found a main effect of group, F(1, 30) = 12.54, p = .001, MSE = .59, $\eta_{\rm p}^2$ = .30, reflecting lower detail ratings in older adults (M = 3.10, SD = 0.58) compared to young adults (M = 3.78, SD = 0.51). There was also a main effect of response, F(1, 30) = 6.27, p = .02, $MSE = .20, \eta_p^2 = .17$, reflecting higher detail ratings for photos associated with subsequent false alarms (M = 3.58, SD = 0.78) than correct rejections (M = 3.30, SD = 0.66). There was also a response \times age-group interaction, F(1, 30) = 6.75, p = .01, MSE = .20, $\eta_p^2 = .18$, reflecting a greater difference in detail ratings for subsequent false alarms than correct rejections in young (false alarm: M = 4.07, SD = 0.45; correct rejection: M = 3.50, SD = 0.71) versus older (false alarm: M = 3.10, SD = 0.75; correct rejection: M = 3.11, SD = 0.56) adults. Post-hoc analyses indicated that this interaction was primarily due to higher detail ratings for false alarms in young than older adults, t(30) = 4.44, p = .0001. There were no significant main effects or interactions in RT for detail ratings (young: M = 3.43 s, SD = 0.62; older: M = 3.57 s, SD = 0.55 s).

Subjective ratings: Session 3

To investigate age-related differences in reliving ratings made to 'yes' responses during recognition memory in Session 3 we conducted a 2 (retrieval cue: target, lure) × 2 (condition: reactivated, baseline) × 2 (age group: young, older) mixed design ANOVA on mean ratings and RT. First, for mean reliving ratings, there was a main effect of retrieval cue, F(1, 25) = 35.92, p = .000003, MSE = .21, $\eta_p^2 = .59$, reflecting higher reliving ratings for targets (i.e., hits; M = 3.42, SD = 0.56) than lures (i.e., false alarms; M = 2.85, SD = 0.74). There was also a main effect of condition, F(1, 25) = 5.15, p = .03, MSE = .24, $\eta_p^2 = .17$, which revealed higher reliving ratings for the reactivated (M = 3.24, SD = 0.63) versus baseline (M = 3.10, SD = 0.66) conditions. There were no other significant main effects or interactions. Second, for reliving RT, we found a main effect of age group, F(1, 25) = 4.82, MSE = 1.35, p = .04, $\eta_p^2 = .16$, reflecting slower RT in older adults (M = 1.95 s, SD = 0.69 s) than in young adults (M = 1.48 s, SD = 0.36 s). There were no other significant main effects or interactions.

DISCUSSION

The current study shows that ageing reduces the extent of reactivation-related updating in memory for naturalistic events. Consistent with our previous finding in young adults (St. Jacques & Schacter, 2013), reactivation influenced subsequent retrieval by enhancing and distorting memory, particularly for memories that were highly reactivated. In both age groups, we found an increase in subsequent true and false memories in the reactivated versus baseline conditions. Additionally, linking these effects to the quality of memory reactivation, we also found higher reliving ratings during reactivation for photos associated with 'yes' responses (i.e., hits and false alarms) than 'no' responses (i.e., misses and critical rejections) during subsequent recognition memory. However, here we show that the magnitude of reactivation-related memory effects is reduced in older adults. Despite an overall age-related increase in subsequent false memories, older adults had a smaller boost in subsequent true and false memories due to reactivation when compared to young adults.

Our research contributes to the growing literature on memory distortions in ageing (e.g., Balota et al., 1999; Dennis, Kim, & Cabeza, 2008; Dodson & Krueger, 2006; Dodson & Schacter, 2002; Fandakova et al., 2013; Giovanello, Kensinger, Wong, & Schacter, 2010; Jacoby, Bishara, Hessels, & Toth, 2005; Koutstaal & Schacter, 1997; Rosa & Gutchess, 2013; Schacter, Israel, & Racine, 1999; Tun, Wingfield, Rosen, & Blanchard, 1998), particularly on tasks involving false memories for information presented after study. For example, in the post-event misinformation paradigm (for review, see Loftus, 2005), older adults are generally more susceptible to falsely recalling erroneous information presented during misinformation on a subsequent memory test (e.g., Cohen & Faulkner, 1989; Karpel, Hoyer, & Toglia, 2001; Loftus, Levidow, & Duensing, 1992; but also see Coxon & Valentine, 1997). Similarly, Schacter, Koutstaal, Johnson, et al. (1997) showed that older adults are more likely to claim that they saw an event during a video recording when it had only occurred in a photo. Age-related increases in distortions in these types of studies have been linked to a source-monitoring impairment (Mitchell, Johnson, & Mather, 2003; Roediger, & Geraci, 2007). In contrast, the reactivation-related effects that contributed to false memories in the current study cannot be easily explained due to a simple source confusion account (e.g., Chan & LaPaglia, 2013; Hupbach et al., 2007; St. Jacques & Schacter, 2013). For example, in our previous study (St. Jacques & Schacter, 2013) we controlled for source confusion by presenting post-event misinformation in both our high and low reactivation conditions and examined the differences in the false alarm rate in these two conditions rather than the presence or absence of a lure in one condition than another. Thus, source confusion should have been equivalent in our high and low reactivation conditions, yet we still observed an increase in subsequent memories in the high- compared to the low reactivation conditions. Consistent with these findings, here we show an age-related reduction in reactivation processes that contribute to false memories in young adults. If the reactivation memory effects were simply due to source confusion, then age-related impairments in source monitoring should have led to an increase in subsequent false memories for lures presented during reactivation when compared to young adults. However, what we observed in the current study was an age-related decrease in subsequent memory effects due to reactivation.

In previous research we found that the quality of memory reactivation and its relationship with contextual recall supports memory updating (St. Jacques & Schacter, 2013; St. Jacques et al., 2013). In the current study we also observed that reactivation quality contributes to updating, such that higher reliving ratings were associated with 'yes' (hits and false alarms) versus 'no' (misses and correct rejections) responses in subsequent memories, and also higher reliving ratings in the reactivated condition compared to baseline. These findings provide support for theoretical and neurobiological models of memory that have linked reactivation to the ability to strengthen existing memory and contribute to the incorporation of new information in memory (Hardt et al., 2010; Johnson & Chalfonte, 1994). We originally predicted that older adults' impairments in subjective recollection (Yonelinas, 2002) would contribute to age-related reductions in reactivation-related updating. However, older adults had inflated subjective ratings, for both reliving and detail, which have sometimes been observed in other studies (e.g., Janssen, Rubin, & St. Jacques, 2011; Rubin & Schulkind, 1997). Thus, it is unclear whether older adults' reliving ratings are truly representative of the quality of memory retrieval. One possibility is that the phenomenological experience is decoupled from the actual contextual recall of memories in ageing. Future research examining age-related declines in contextual recall during memory reactivation could help to better understand this issue.

Two other factors that could contribute to the age-related reduction in memory reactivation should also be considered. First, older adults may have encoded the memories more poorly during the museum tour, which could lead to a reduction in reactivation and its effects on subsequent memory. However, weaker encoding typically increases misinformation errors (e.g., Ecker, Lewandowsky, Swire, & Chang, 2011), whereas here we show decreases in memory distortions due to reactivation in older adults. Second, there may be important age-related changes in the extent to which memory is updated and encoded during reactivation. In a neuroimaging study using a similar design in a separate group of young adults (St. Jacques et al., 2013) we found that subsequent false memories were supported by additional neural mechanisms during reactivation that allow for the integration of separable episodes via relational memory processes. It is well known that ageing impairs such associative and relational memory processes that bind items together (Chalfonte & Johnson, 1996; Naveh-Benjamin, 2000). Thus, age-related reductions in binding could also contribute to the overall reduction in reactivationrelated updating (i.e., inability to bind lure with target memory). Better understanding the boundary conditions and the component processes during memory reactivation that contribute to agerelated changes in subsequent memories will be an important avenue for future research.

Remembering events from our personal past is a frequent occurrence in daily life (Rubin & Berntsen, 2009) that shapes the subsequent expression of those memories in young adults (Hirst & Echterhoff, 2012; Marsh, 2007). The current study reveals that reactivation-related effects on subsequent memory are reduced in ageing. Our findings fit with an adaptive perspective on memory distortions (Howe, 2011; Newman & Lindsay, 2009; Schacter et al., 2011) in which such apparent flaws are the outcome of beneficial cognitive processes that support the normal functioning of memory. Thus, reactivation allows for memories to be updated with relevant new information that is essential for the operation of a dynamic and flexible memory system. From this perspective, the distortions we found due to reactivation in the current study could also be seen as successful encoding of new information relevant to the museum tour. Our findings showed, however, that such adaptive memory updating processes are reduced in older adults. Decline in memory reactivation in ageing has the potential benefit of reducing these types of distortions in older adults, but it comes at the cost of a reduction in the ability to update memory. The locus of these age-related changes remains to be determined, but we suggest that age-related changes in contextual recall and binding of new information with old may be candidate processes. Such age-related changes in memory updating could underlie many typical memory complaints in daily life, such as forgetting where the car is parked or misplacing items (e.g., Bjork, 1978). These age-related reductions in memory reactivation might be improved using techniques that bolster older adults' memory retrieval (e.g., Dornburg & McDaniel, 2006; Madore, Gaesser, & Schacter, 2014), and thus perhaps attenuate age-related declines in memory updating.

REFERENCES

- Balota, D. A., Cortese, M. J., Duchek, J. M., Adams, D., Roediger III, H. L., McDermott, K. B., & Yerys, B. E. (1999). Veridical and false memories in healthy older adults and in dementia of the Alzheimer's type. *Cognitive Neuropsychology*, *16*, 361–384. doi:10.1080/026432999380834
- Bjork, R. A. (1978). The updating of human memory. In G. H. Bower (Ed.), *The psychology of learning* and motivation (Vol. 12, pp. 235–259). New York, NY: Academic Press.
- Bluck, S., Levine, L. J., & Laulhere, T. M. (1999). Autobiographical remembering and hypermnesia: A comparison of older and younger adults. *Psychology* & *Aging*, 14, 671–682. doi:10.1037/0882-7974.14. 4.671
- Chalfonte, B. L., & Johnson, M. K. (1996). Feature memory and binding in young and older adults.

Memory & Cognition, 24, 403–416. doi:10.3758/ BF03200930

- Chan, J. C., & LaPaglia, J. A. (2013). Impairing existing declarative memory in humans by disrupting reconsolidation. *Proceedings of the National Academy of Sciences USA*, 110, 9309–9313. doi:10.1073/pnas. 1218472110
- Chan, J. C., Thomas, A. K., & Bulevich, J. B. (2009). Recalling a witnessed event increases eyewitness suggestibility: The reversed testing effect. *Psychological Science*, 20(1), 66–73. doi:10.1111/j.1467-9280. 2008.02245.x
- Cohen, G., & Faulkner, D. (1989). Age differences in source forgetting: Effects on reality monitoring and on eyewitness testimony. *Psychology & Aging*, 4(1), 10–17. doi:10.1037/0882-7974.4.1.10
- Coxon, P., & Valentine, T. (1997). The effects of the age of eyewitnesses on the accuracy and suggestibility of their testimony. *Applied Cognitive Psychology*, *11*, 415–430. doi:10.1002/(SICI)1099-0720(199710)11:5< 415::AID-ACP469>3.0.CO;2-A
- Dennis, N. A., Kim, H., & Cabeza, R. (2008). Agerelated differences in brain activity during true and false memory retrieval. *Journal of Cognitive Neuroscience*, 20, 1390–1402. doi:10.1037/0882-7974.19. 3.379
- Dodson, C. S., & Krueger, L. E. (2006). I misremember it well: Why older adults are unreliable eyewitnesses. *Psychonomic Bulletin & Review*, 13, 770–775.
- Dodson, C. S, & Schacter, D. L. (2002). Aging and strategic retrieval processes: Reducing false memories with a distinctiveness heuristic. *Psychology and Aging*, 17, 405–415. doi:10.1037/0882-7974.17.3.405
- Dornburg, C. C., & McDaniel, M. A. (2006). The Cognitive Interview enhances long-term free recall of older adults. *Psychology & Aging*, 21, 196–200. doi:10.1037/0882-7974.21.1.196
- Duncan, K., Sadanand, A., & Davachi, L. (2012). Memory's penumbra: Episodic memory decisions induce lingering mnemonic biases. *Science*, 337, 485–487. doi:10.1126/science.1221936
- Ecker, U. H., Lewandowsky, S., Swire, B., & Chang, D. (2011). Correcting false information in memory: Manipulating the strength of misinformation encoding and its retraction. *Psychonomic Bulletin & Review*, 18, 570–578. doi:10.3758/s13423-011-0065-1
- Fandakova, Y., Shing, Y. L., & Lindenberger, U. (2013). High-confidence memory errors in old age: The roles of monitoring and binding processes. *Memory*, 21, 732–750. doi:10.1080/09658211.2012. 756038
- Forcato, C., Rodriguez, M. L., Pedreira, M. E., & Maldonado, H. (2010). Reconsolidation in humans opens up declarative memory to the entrance of new information. *Neurobiology of Learning and Mem*ory, 93(1), 77–84. doi:10.1016/j.nlm.2009.08.006
- Giovanello, K. S., Kensinger, E. A., Wong, A. T., & Schacter, D. L. (2010). Age-related neural changes during memory conjunction errors. *Journal of Cognitive Neuroscience*, 22, 1348–1361. doi:10.1006/jmla. 2002.2864
- Hardt, O., Einarsson, E. O., & Nader, K. (2010). A bridge over troubled water: Reconsolidation as a link between cognitive and neuroscientific memory

research traditions. *Annual Review of Psychology*, *61*, 141–167. doi:10.1146/annurev.psych.093008.1 00455

- Henkel, L. A. (2007). The benefits and costs of repeated memory tests for young and older adults. *Psychology & Aging*, 22, 580–595. doi:10.1037/0882-7974.22.3.580
- Hirst, W., & Echterhoff, G. (2012). Remembering in conversations: The social sharing and reshaping of memories. *Annual Review of Psychology*, 63, 55–79. doi:10.1146/annurev-psych-120710-100340
- Howe, M. L. (2011). The adaptive nature of memory and its illusions. *Current Directions in Psychological Science*, 20, 312–315. doi:10.1177/0963721411 416571
- Hupbach, A., Gomez, R., Hardt, O., & Nadel, L. (2007). Reconsolidation of episodic memories: A subtle reminder triggers integration of new information. *Learning & Memory*, 14(1–2), 47–53. doi:10.1101/ lm.365707
- Jacoby, L. L. (1999). Ironic effects of repetition: Measuring age-related differences in memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 25*(1), 3–22. doi:10.1037/0278-7393. 25.1.3
- Jacoby, L. L., Bishara, A. J., Hessels, S., & Toth, J. P. (2005). Ageing, subjective experience, and cognitive control: Dramatic false remembering by older adults. *Journal of Experimental Psychology: General*, 134, 131–148. doi:10.1037/0096-3445.134.2.131
- Jacoby, L. L., & Rhodes, M. G. (2006). False remembering in the aged. *Current Directions in Psychological Science*, 15(2), 49–53. doi:10.1111/j.0963-721 4.2006.00405.x
- Janssen, S. M., Rubin, D. C., & St. Jacques, P. L. (2011). The temporal distribution of autobiographical memory: Changes in reliving and vividness over the life span do not explain the reminiscence bump. *Memory & Cognition*, 39(1), 1–11. doi:10.3758/ s13421-010-0003-x
- Johnson, M. K., & Chalfonte, B. L. (1994). Binding complex memories: The role of reactivation and the hippocampus. In D. L. Schacter & E. Tulving (Eds.), *Memory systems 1994* (pp. 311–350). Cambridge, MA: MIT Press.
- Johnson, M. R., & Johnson, M. K. (2009). Toward characterizing the neural correlates of component processes of cognition. In F. Rosler, C. Ranganath, B. Roeder, & R. H. Kluwe (Eds.), *Neuroimaging* of human memory: Linking cognitive processes to neural systems (pp. 169–194). New York, NY: Oxford University Press.
- Karpel, M. E., Hoyer, W. J., & Toglia, M. P. (2001). Accuracy and qualities of real and suggested memories: Nonspecific age differences. *Journals of Gerontology, Series B: Psychological Sciences & Social Sciences*, 56(2), P103–P110. doi:10.1093/gero nb/56.2.P103
- Kensinger, E. A., & Schacter, D. L. (1999). When true memories suppress false memories: Effects of ageing. *Cognitive Neuropsychology*, 16, 399–415. doi:10.1080/ 026432999380852
- Koutstaal, W., & Schacter, D. L. (1997). Gist-based false recognition of pictures in older and younger

adults. Journal of Memory and Language, 37, 555–583. doi:10.1006/jmla.1997.2529

- Koutstaal, W., & Schacter, D. L. (2001). Memory distortion and aging. In M. Naveh-Benjamin, M. Moscovitch, & H. L. Roediger III (Eds.), *Perspectives on human memory and cognitive aging: Essays in honour of Fergus Craik* (pp. 362–383). Philadelphia, PA: Psychology Press.
- Koutstaal, W., Schacter, D. L., Johnson, M. K., Angell, K. E., & Gross, M. S. (1998). Post-event review in older and younger adults: Improving memory accessibility of complex everyday events. *Psychology & Aging*, 13, 277–296. doi:10.1037/0882-7974. 13.2.277
- Lacy, J. W., & Stark, C. E. (2013). The neuroscience of memory: Implications for the courtroom. *Nature Reviews Neuroscience*, 14, 649–658. doi:10.1038/ nrn3563
- Lee, J. L. (2009). Reconsolidation: Maintaining memory relevance. *Trends in Neurosciences*, 32, 413–420. doi:10.1016/j.tins.2009.05.002
- Linton, M. (1975). Memory for real-world events. In D. A. Norman & D. E. Rumelhart (Eds.), *Explorations* in cognition (pp. 376–404). San Francisco: Freeman.
- Loftus, E. F. (2005). Planting misinformation in the human mind: A 30-year investigation of the malleability of memory. *Learning & Memory*, 12, 361–366. doi:10.1101/lm.94705
- Loftus, E. F., Levidow, B., & Duensing, S. (1992). Who remembers best? Individual differences in memory for events that occurred in a science museum. *Applied Cognitive Psychology*, 6(2), 93–107. doi:10.1002/acp. 2350060202
- Madore, K. P., Gaesser, B., & Schacter, D. L. (2014). Constructive episodic simulation: Dissociable effects of a specificity induction on remembering, imagining, and describing in young and older adults. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 40*, 609–622. doi:10.1037/ a0034885
- Marsh, E. J. (2007). Retelling is not the same as recalling: Implications for memory. *Current Directions in Psychological Science*, 16(1), 16–20. doi:10.1111/j.1467-8721.2007.00467.x
- Meyer, A. N., & Logan, J. M. (2013). Taking the testing effect beyond the college freshman: Benefits for lifelong learning. *Psychology & Aging*, 28(1), 142–147. doi:10.1037/a0030890
- Mitchell, K. J., Johnson, M. K., & Mather, M. (2003). Source monitoring and suggestibility to misinformation: Adult age-related differences. *Applied Cognitive Psychology*, 17(1), 107–119. doi:10.1002/acp.857
- Nadel, L., Campbell, J., & Ryan, L. (2007). Autobiographical memory retrieval and hippocampal activation as a function of repetition and the passage of time. *Neural Plasticity*, 2007, 90472. doi:10.1155/ 2007/90472
- Nadel, L., Hupbach, A., Gomez, R., & Newman-Smith, K. (2012). Memory formation, consolidation and transformation. *Neuroscience & Biobehavioral Reviews*, 36, 1640–1645. doi:10.1016/j.neubiorev.201 2.03.001
- Naveh-Benjamin, M. (2000). Adult age differences in memory performance: Tests of an associative deficit

hypothesis. Journal of Experimental Psychology: Learning, Memory, and Cognition, 26, 1170–1187. doi:10.1037/0278-7393.26.5.1170

- Newman, E. J., & Lindsay, D. S. (2009). False memories: What the hell are they for? *Applied Cognitive Psychology*, 23, 1105–1121. doi:10.1002/acp.1613
- Rabinowitz, J. C., & Craik, F. I. (1986). Prior retrieval effects in young and old adults. *Journal of Gerontology*, 41, 368–375. doi:10.1093/geronj/41.3.368
- Roediger III, H. L., & Geraci, L. (2007). Aging and the misinformation effect: A neuropsychological analysis. Journal of Experimental Psychology: Learning, Memory, and Cognition, 33, 321–334. doi:10.1037/ 0278-7393.33.2.321
- Roediger, H. L., & Karpicke, J. D. (2006). The power of testing memory: Basic research and implications for educational practice. *Perspectives on Psychological Science*, 1, 181–210. doi:10.1111/j.1745-6916. 2006.00012.x
- Rosa, N. M., & Gutchess, A. H. (2013). False memory in aging resulting from self-referential processing. *Journals of Gerontology, Series B: Psychological Sciences* & Social Sciences, 68, 882–892. doi:10.1093/geronb/ gbt018
- Rubin, D. C., & Berntsen, D. (2009). The frequency of voluntary and involuntary autobiographical memory across the life span. *Memory & Cognition*, 27, 679–688. doi:10.3758/37.5.679
- Rubin, D. C., & Schulkind, M. D. (1997). Distribution of important and word-cued autobiographical memories in 20-, 35-, and 70-year-old adults. *Psychology* & Aging, 12, 524–535. doi:10.1037/0882-7974.1 2.3.524
- Schacter, D. L., Guerin, S. A., & St. Jacques, P. L. (2011). Memory distortion: An adaptive perspective. *Trends* in Cognitive Sciences, 15, 467–474. doi:10.1016/j. tics.2011.08.004
- Schacter, D. L., Israel, L., & Racine, C. (1999). Suppressing false recognition in younger and older adults: The distinctiveness heuristic. *Journal of Memory and Language, 40*, 1–24. doi:10.1006/jmla. 1998.2611
- Schacter, D. L., Koutstaal, W., Johnson, M. K., Gross, M. S., & Angell, K. E. (1997). False recollection induced by photographs: A comparison of older and younger adults. *Psychology & Aging*, 12, 203–215. doi:10.1037/0882-7974.12.2.203
- Schacter, D. L., Koutstaal, W., & Norman, K. A. (1997). False memories and aging. *Trends in Cognitive Sciences*, 1, 229–236. doi:10.1016/S1364-6613 (97)01068-1
- Schacter, D. L., & Loftus, E. F. (2013). Memory and law: What can cognitive neuroscience contribute? *Nature Neuroscience*, 16(2), 119–123. doi:10.1038/ nn.3294
- Schiller, D., Monfils, M. H., Raio, C. M., Johnson, D. C., Ledoux, J. E., & Phelps, E. A. (2010). Preventing the return of fear in humans using reconsolidation update mechanisms. *Nature*, 463(7277), 49–53. doi:10.1038/nature08637
- Schwabe, L., & Wolf, O. T. (2010). Stress impairs the reconsolidation of autobiographical memories. *Neurobiology of Learning and Memory*, 94, 153–157. doi:10.1016/j.nlm.2010.05.001

- Sederberg, P. B., Gershman, S. J., Polyn, S. M., & Norman, K. A. (2011). Human memory reconsolidation can be explained using the temporal context model. *Psychonomic Bulletin and Review*, 18, 455–468. doi:10.3758/s13423-011-0086-9
- Spencer, W. D., & Raz, N. (1995). Differential effects of aging on memory for content and context: A meta-analysis. *Psychology & Aging*, 10, 527–539. doi:10.1037/0882-7974.10.4.527
- St. Jacques, P. L., Olm, C., & Schacter, D. L. (2013). Neural mechanisms of reactivation-induced updating that enhance and distort memory. *Proceedings* of the National Academy of Sciences USA, 110, 19671–19678. doi:10.1073/pnas.1319630110
- St. Jacques, P. L., & Schacter, D. L. (2013). Modifying memory: Selectively enhancing and updating personal

memories for a museum tour by reactivating them. *Psychological Science*, 24, 537–543. doi:10.1177/0956797612457377

- Tun, P. A., Wingfield, A., Rosen, M. J., & Blanchard, L. (1998). Response latencies for false memories: Gist-based processes in normal aging. *Psychology & Aging*, 13, 230–241. doi:10.1037/0882-7974.13.2.230
- Widner, R. L., Jr., Otani, H., & Smith, A. D. (2000). Hypermnesia: Age-related differences between young and older adults. *Memory & Cognition*, 28, 556–564. doi:10.3758/BF03201246
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal* of Memory and Language, 46, 441–517. doi:10.1006/ jmla.2002.2864

Copyright of Memory is the property of Psychology Press (UK) and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.