

We remember the good things: Age differences in learning and memory

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ABSTRACT

We combined a feedback-based learning task with a recognition memory paradigm to investigate how reward-based learning affects the event-related potential (ERP) correlates of recognition memory in younger and older adults. We found that positive, but not negative learning improves memory and results in an increased early ERP old–new effect, which is typically associated with familiarity-based memory. This indicates that reward-based learning supports a fast and relatively automatic memory retrieval process. Furthermore, we found age-related impairments in reward-based learning, whereas memory for the learned information was intact in the elderly, suggesting that declarative memory might be less affected by aging.

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1. Introduction

Recent findings suggest that the way we learn from rewards and how we remember emotionally salient information changes with age. For example, older adults show reduced loss anticipation and decreased ERP responses to negative feedback during learning than younger adults (Eppinger, Kray, Mock, & Mecklinger, 2008; Samanez-Larkin et al., 2007). Furthermore, older adults tend to remember stimuli that are associated with positive emotions better than negative stimuli, suggesting that they have a memory bias towards positive, self-relevant information (Mather & Carstensen, 2005). The aim of the present study is to investigate how reward-based learning influences recognition memory and its event-related potential (ERP) correlates in younger and older adults.

Impairments in reward-based learning in older adults have been associated with age-related deficits in the function of the midbrain dopamine system (e.g., Nieuwenhuis et al., 2002). However, it seems likely that the dopamine system is not only involved in learning and reward processing, but also plays a role in episodic memory. Animal studies have shown that activation of midbrain dopamine neurons can trigger long-term potentiation in the hippocampus and by this promote memory (Li, Cullen, Anwyl, & Rowan, 2003). Findings from functional imaging (fMRI) studies support this view and suggest that stimuli that predict rewards are better remembered and elicit higher activity in the hippocampus and

midbrain than stimuli that are not rewarded (Adcock, Thangavel, Withfield-Gabrieli, Knutson, & Gabrieli, 2006; Wittmann et al., 2005).

Two-process models of recognition memory propose that two dissociable mechanisms, familiarity-based recognition and recollection, sub-serve episodic memory (Norman & O'Reilly, 2003). Familiarity-based recognition is suggested to be a fast, relatively automatic process that does not involve the recognition of the spatiotemporal context of items. ERP studies have shown that familiarity is associated with an early (300–500 ms), frontally distributed positivity for correctly classified old than new items, which is termed the early old–new effect (Mecklinger, 2000). In contrast, recollection is assumed to be a slower, more controlled process, which results in consciously accessible information about the stimulus and its context. Recollection is associated with a late (400–600 ms), left parietally distributed positivity for old than new stimuli, which is termed the late old–new effect (Rugg & Curran, 2007). Aging studies have shown that older adults are primarily impaired in recollection and not in familiarity-based recognition (Prull, Dawes, Martin, Rosenberg, & Light, 2006). This is supported by ERP findings that show a reduced late old–new effect in older adults, whereas the early old–new effect seems less affected by age (Ally, Simons, McKeever, Peers, & Budson, 2008; Morcom & Rugg, 2004; Schiltz et al., 2006).

The present study examines the effects of learning from positive and negative feedback on recognition memory and its ERP correlates in younger and older adults. We applied a learning task in which participants could either learn from monetary gains (positive learning condition) or monetary losses (negative learning condition). Then, participants performed a recognition memory

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test that involved an old–new judgment and a source memory test in which they had to indicate whether stimuli were associated with the positive or the negative learning condition in the learning task (see Fig. 1a).

Consistent with previous findings (Eppinger & Kray, *in press*), we expected that older adults should be impaired in learning from gains and losses compared to younger adults. This should be reflected in reduced learning rates for older than younger adults in the learning task. Similar impairments should be observed in memory performance. That is, we expected age-related reductions in memory accuracy, especially when participants had to indicate whether stimuli were associated with the positive or the negative learning condition in the source memory task (Prull et al., 2006). Finally, we predicted that participants should be better in remembering stimuli that were associated with positive feedback during learning (Adcock et al., 2006; Schott et al., 2007; Wittmann et al., 2005) and that this memory bias should be reflected in an increased ERP old–new effect.

2. Methods

2.1. Participants

Sixteen younger adults and 17 older adults participated in the study. Two older adults were excluded because they performed at chance level in the memory task. One younger adult was excluded because of movement artifacts. The effective sample consisted of 15 younger adults (mean age = 22.7, SD = 2.5, 7 male) and 15 older adults (mean age = 68.3, SD = 2.7, 7 male). Participants received 22.5 Euros and could win a performance-dependent bonus of 7.50 Euros.

2.2. Stimuli and tasks

2.2.1. Learning task

The stimulus set consisted of 72 colored images of objects (Snodgrass & Vanderwart, 1980). The feedback stimuli indicated a loss of 50 Euro Cents, a gain of 50 Cents, or a neutral outcome (i.e., 0 Cent). The participants were asked to make a two-choice decision upon stimulus presentation. They were instructed to learn the stimulus–response assignments based on the feedback and to maximize their wins and minimize their losses.

Each learning block involved four stimuli (two per learning condition), which were presented 15 times in random order. In the positive learning condition, one response key was associated with positive feedback (gain of 50 Cents), whereas the other key was associated with neutral feedback (0 Cents). In the negative learning condition, one response key was associated with negative feedback

Learning task

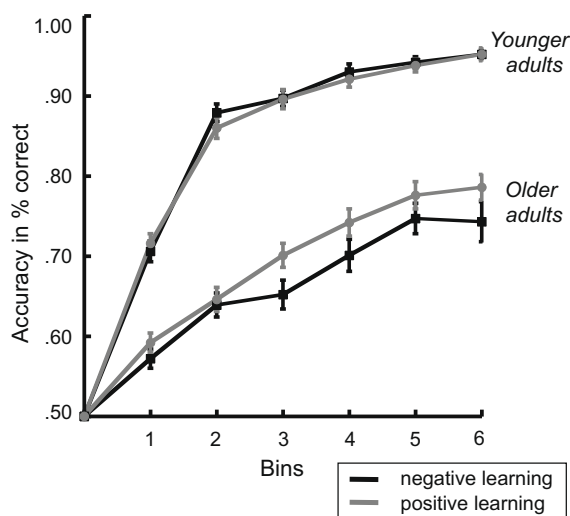


Fig. 1b. Mean accuracy (SE) learning curves for younger and older adults, displayed separately for the positive (grey) and the negative (black) learning condition.

(loss of 50 Cents) and the other key was associated with neutral feedback (see Fig. 1a). Feedback was 100% predictable.

2.2.2. Memory test

The stimulus set involved the 72 learned and 72 new stimuli. The stimuli were randomly presented and participants were asked to perform an old–new judgment. For stimuli that were classified as “Old” they had to perform a source memory test and had to indicate whether the stimuli were associated with the positive or the negative learning condition in the learning task (see Fig. 1a).

2.3. Procedure

2.3.1. Learning task

Participants performed a practice block (90 trials) and 18 experimental blocks (60 trials each). Each trial started with a fixation cross (500 ms), followed by the stimulus (500 ms). After responding, a blank screen was displayed (500 ms) then the feedback (+50 Cents, –50 Cents, 0 Cent) appeared (500 ms) and participants entered the next trial. To support learning in the two age groups, we applied a deadline procedure in which we individually adjusted

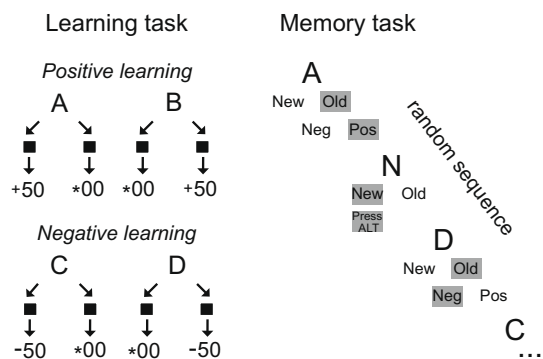


Fig. 1a. Schematic illustration of the learning and the memory task.

Memory task

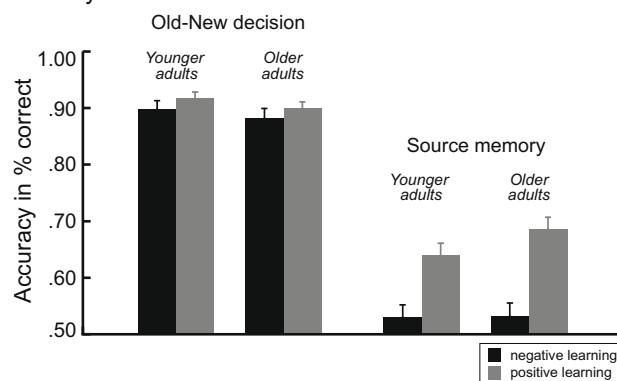


Fig. 1c. Mean accuracy (SE) for the old–new judgment and the source memory test, displayed separately for younger and older adults and the positive (grey) and the negative (black) learning condition.

the response deadlines depending on the number of time-out trials (see Eppinger et al., 2008). Mean response deadlines were 755 ms (SD = 114 ms) for younger adults and 913 ms (SD = 100) for older adults. At the end of each block participants received feedback on their mean performance.

2.3.2. Memory test

Each stimulus was presented for 1000 ms, and was followed by a blank screen (2000 ms). During this time participants were asked to make the old–new judgment. For stimuli that were classified as “Old” a source memory cue was displayed until the participant responded. For stimuli that were classified as “New” participants had to press the “Alt” key and moved onto the next trial.

2.4. Data recording

EEG and EOG activity were recorded continuously from 63 Ag/AgCl electrodes (extended 10–20 system). The data were filtered online from DC – 70 Hz and digitized at 500 Hz. Vertical and horizontal EOG was recorded from two electrode pairs on the infra- and supraorbital ridges of the right eye and on the outer canthi of the two eyes. Impedances were kept below 10 k Ω . Left mastoid was used as reference and the data were offline re-referenced to average mastoid. For the statistical analyses the EEG data were low-pass filtered at 30 Hz. For the figures a 15 Hz low-pass filter was applied.

2.5. Data analysis

The accuracy data in the learning task were analyzed by averaging mean accuracy for each participant and learning condition into six equally large bins or quantiles (five trials per bin, learning condition, and block). For the old–new judgments corrected recognition (Pr-) scores (Pr-score = hit rate – false alarm rate, see Snodgrass & Corwin, 1988) were computed. Source accuracy was computed as the number of correctly classified sources divided by the total number of items that were correctly classified as old.

The EEG epochs (–200 ms to 800 ms) were averaged to the onset of correctly classified new, old-positive and old-negative stimuli. The data were baseline-corrected by subtracting the average (–200 to 0 ms) pre-stimulus activity. Trials containing ocular, or other artifacts, were excluded from analysis using a threshold criterion. Remaining eye movements were corrected using a regression approach (Gratton, Coles, & Donchin, 1983). ERP trial numbers were similar for old-positive (younger adults: $M = 29$, range: 10; older adults: $M = 28$, range: 4) and old-negative stimuli (younger adults: $M = 29$, range: 7; older adults: $M = 30$, range: 6). No significant age differences in trial numbers were obtained (p 's > .17). For new stimuli we randomly selected 30 trials per individual. Electrode sights were averaged into six topographical regions of interest (ROI): left anterior (F3, F5, FC3), middle anterior (F1, FZ, F2), right anterior (F4, F6, FC4), left posterior (P3, P5, PO3), middle posterior (P1, PZ, P2), and right posterior (P4, P6, PO4). The time windows used for statistical analysis were based on visual inspection of the grand averages. Similar time windows have been used in previous ERP studies on recognition memory (e.g., Ecker, Arend, Bergstroem, & Zimmer, 2009; Van Strien, Langeslag, Strekalova, Gootjes, & Franken, 2009). Bonferroni-corrections were applied when necessary and corrected p -values are reported (p -level < .05). Whenever necessary the Geisser–Greenhouse correction (Geisser & Greenhouse, 1958) was applied. The original F -value, the adjusted p -values, and the Epsilon values (ϵ) are given. Effect sizes (eta squared, η^2) are reported (Cohen, 1973).

3. Results

3.1. Behavioral results

3.1.1. Learning task

Mean accuracy rates (% correct) were examined using an analysis of variance (ANOVA) with the factors age group (younger, older), learning condition (positive, negative), and bin (bin1–bin6). The analysis showed significant main effects of age group, $F(1, 28) = 53.26$, $p < .001$, $\eta^2 = .66$, and bin, $F(5, 140) = 114.77$, $p < .001$, $\epsilon = .50$, $\eta^2 = .77$. Moreover, we obtained a significant interaction between age group and bin, $F(5, 140) = 5.75$, $p = .003$, $\epsilon = .50$, $\eta^2 = .04$, indicating that learning effects were larger for younger than older adults (see Fig. 1b).

3.1.2. Old–new memory test

The Pr-scores were analyzed using an ANOVA with the factors age group and learning condition. The analysis revealed better memory performance for stimuli that were associated with the positive than the negative learning condition, $F(1, 28) = 5.99$, $p = .02$, $\eta^2 = .18$ (see Fig. 1c). No significant main effect of age group or interaction with learning condition was obtained (p 's > .71).¹

3.1.3. Source memory test

The same ANOVA as for the Pr-scores was applied to analyze source memory accuracy. The analysis showed better performance for stimuli that were associated with the positive learning condition, $F(1, 28) = 20.65$, $p < .001$, $\eta^2 = .42$ (see Fig. 1c). No significant main effect of age group or interaction with learning condition was obtained (p 's > .47).

3.2. ERP results

3.2.1. Early old–new effect

Mean amplitudes in the early time window (250–400 ms) were analyzed using an ANOVA with the factors age group, status (new, old-positive, old-negative), antpos (anterior, posterior), and hemisphere (left, middle, right). The analysis revealed a significant main effect of status, $F(2, 56) = 9.91$, $p = .001$, $\epsilon = .91$, $\eta^2 = .26$. Contrasts for the factor status revealed a significant old/new effect only for stimuli that were associated with positive learning ($p < .02$, $\eta^2 = .35$) (see Fig. 2a). Furthermore, we obtained significant interactions between the factors status and hemisphere and status and antpos (p 's < .01, η^2 's > .15). Post hoc contrasts showed that the old/new effect for positive stimuli was most pronounced at right and medial anterior ROIs (p 's < .008, η^2 's > .23) (see Fig. 2b). The analysis showed no significant main effect of age ($p = .92$) or interactions involving age group and status (p 's > .13).²

3.2.2. Late old–new effect

Mean amplitudes in the late time window (450–700 ms) were analyzed using the same ANOVA design as for the early time window. The analysis showed a significant main effect of status, $F(2, 56) = 13.49$, $p < .001$, $\epsilon = .95$, $\eta^2 = .32$. Contrasts for the factor status revealed significant old/new effects for both learning conditions

¹ Consistent with the analysis of the Pr-scores, an ANOVA on the hit rates revealed better memory performance for the positive learning condition (younger adults: $M = .95$, $SE = .02$; older adults: $M = .96$, $SE = .01$) than the negative learning condition (younger adults: $M = .93$, $SE = .01$; older adults: $M = .94$, $SE = .01$), ($p < .02$, $\eta^2 = .17$). No significant main effect of age group was obtained ($p = .75$). An analysis of the false alarm rates did not show significant age differences ($p = .17$).

² We also found significant interactions between age group and hemisphere and age group and antpos (p 's < .02, η^2 's > .10). Analyses for the two age groups showed a bilateral positivity, which increased from anterior to posterior for younger ($p < .001$, $\eta^2 > .73$), but not for older adults ($p = .37$) (see Fig. 2a). This effect may result from an overlap with the P300 component.

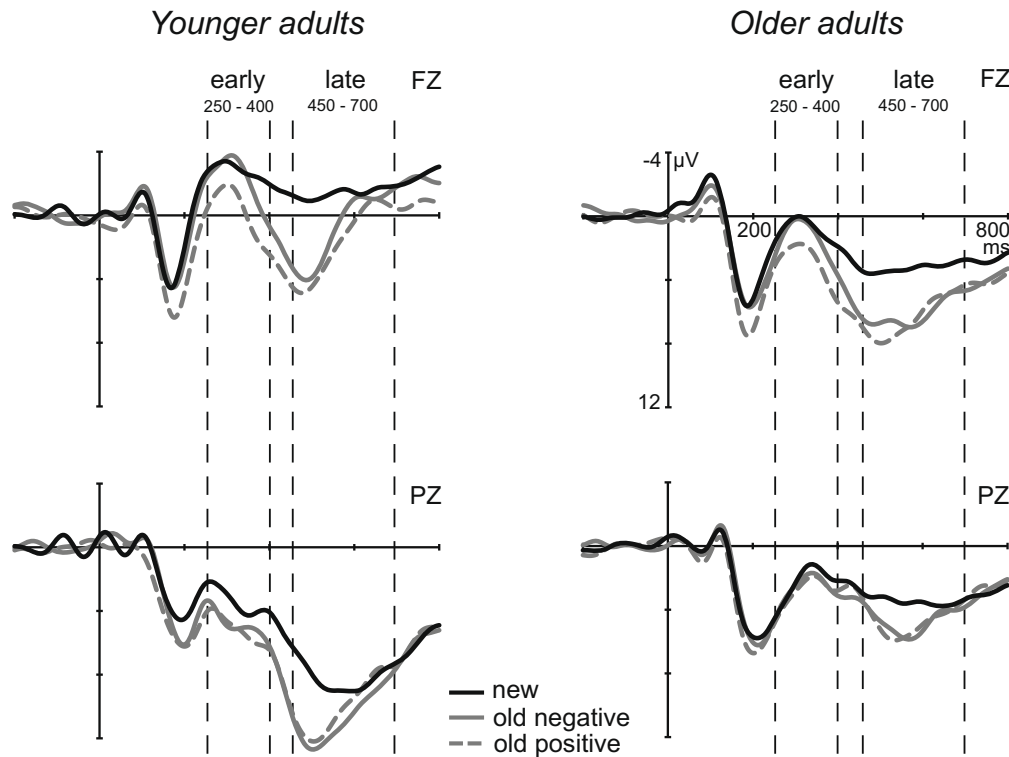


Fig. 2a. Stimulus-locked ERPs to new (black), old-negative (grey solid) and old-positive (grey dashed) stimuli displayed separately for younger and older adults at electrodes Fz and Pz. Tick spacing on the x-axis is 200 ms and dashed vertical lines indicate the time windows used for statistical analysis.

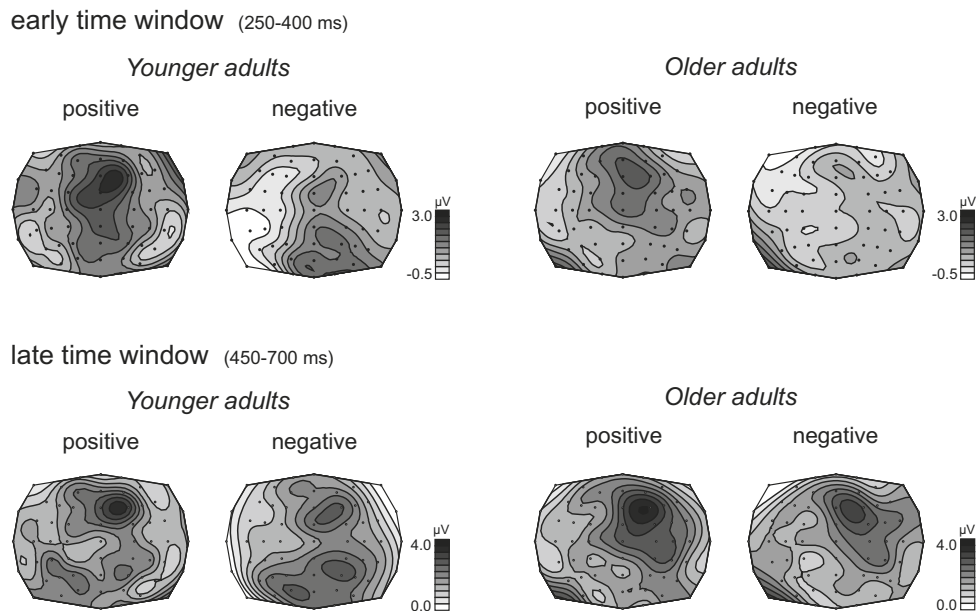


Fig. 2b. The topographic maps display the difference between the ERPs for new and old-positive and the ERPs for new and old-negative stimuli in the early (250–400 ms) and late time window (450–700 ms) and are displayed separately for younger and older adults.

(p 's < .001, η^2 's > .39) (see Fig. 2b). Furthermore, we obtained significant interactions between the factors status and hemisphere, $F(4, 112) = 3.11$, $p = .03$, $\varepsilon = .77$, $\eta^2 = .09$, and between status, antpos, and hemisphere, $F(4, 112) = 4.79$, $p = .004$, $\varepsilon = .74$, $\eta^2 = .14$. Separate analyses for the factor antpos showed an interaction between status and hemisphere for anterior ROIs ($p < .003$, $\eta^2 = .15$), which reflects a stronger old/new effect for positive stimuli at medial and right frontal electrodes (see Fig. 2b).

The analysis showed no significant main effect of age group ($p = .42$). However, we obtained a significant interaction between the factors age group and antpos, $F(1, 28) = 30.39$, $p = .001$, $\eta^2 = .41$, as well as between age group, antpos, and hemisphere, $F(2, 56) = 3.18$, $p = .05$, $\varepsilon = .91$, $\eta^2 = .09$. Separate analyses for the factors antpos and hemisphere revealed larger amplitudes for older compared to younger adults at medial frontal ROIs (p 's < .008, η^2 's > .28). In contrast, younger adults showed larger amplitudes

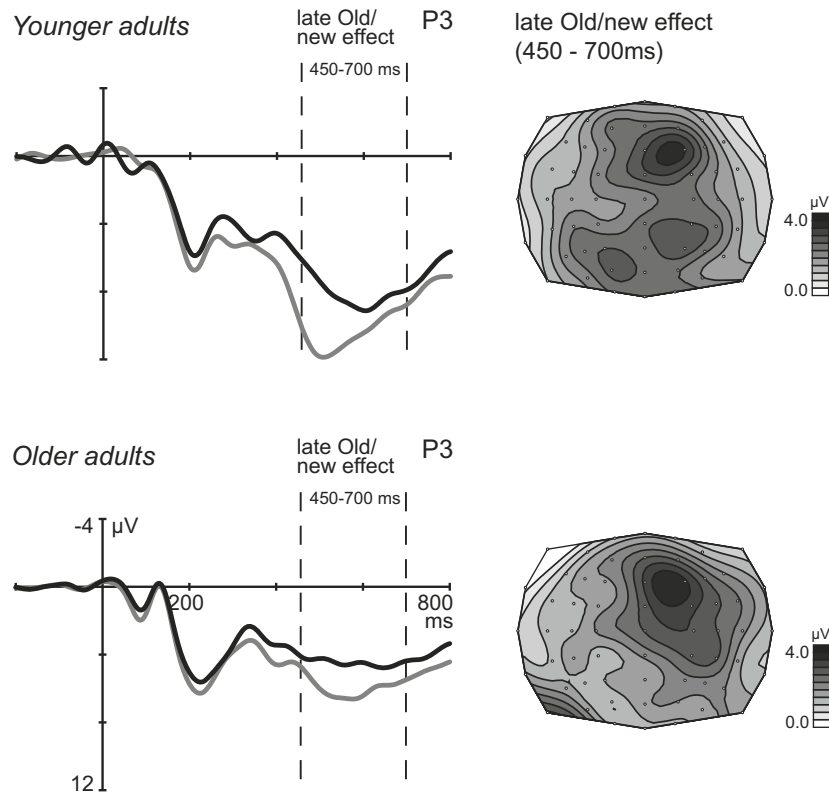


Fig. 3. Left: stimulus-locked ERPs to new (black) and old (grey) stimuli displayed separately for younger and older adults at the left parietal electrode P3. Tick spacing on the x-axis is 200 ms. The dashed vertical line indicates the time window used for statistical analysis. Right: the topographic maps display the difference between the ERPs for new and old stimuli in the late time window (450–700 ms) and are displayed separately for younger and older adults.

than older adults at left and right parietal ROIs (see Fig. 2a and b). In addition to these topographical shifts in ERP amplitudes younger adults showed a left parietal old/new effect that was not observed in older adults (see Figs. 2b and 3). To further examine this effect we performed old–new comparisons for each of the ROIs in the two age groups. These analyses revealed a significant late old–new effect at the left parietal ROI for younger adults ($p < .004$, $\eta^2 = .56$), but not for older adults ($p = .16$) (see Fig. 3).

4. Discussion

In the present study we combined a feedback-based learning task with a recognition memory paradigm to investigate how reward-based learning affects memory in younger and older adults.

Consistent with our predictions, older adults performed worse than younger adults during learning (see Fig. 1b). Results from a previous study suggest that these impairments are due to deficits in the ability to build up relational representations between the different types of feedback (positive, negative, and neutral). That is, older adults seem to have problems in differentiating under which conditions the neutral feedback is better or worse than the alternative feedback (Eppinger & Kray, *in press*).

In contrast, in the memory tests no age differences were obtained, suggesting that explicit memory for the learned stimuli was intact in the elderly. Especially the absence of age differences in source memory is surprising, given recent findings that suggest that older adults are particularly impaired when they have to retrieve context information (Prull et al., 2006). One potential explanation for the present results could be that the subjective value of positive feedback in the learning task is increased in the elderly and that the salience of this information offsets their

deficits in retrieving context in the source memory task. This interpretation is supported by the fact that although older adults perform worse than younger adults, and by this receive less positive and more negative feedback during learning, they show similar memory improvements for positive stimuli as younger adults. The idea that older adults have a memory bias towards positive information is consistent with previous data on age-related asymmetries in memory for emotional information (see Mather & Carstensen, 2005). Moreover, the present results are consistent with recent findings that suggest that reward processing is affected by emotional information. In line with the interpretation raised above it seems conceivable that older adults attribute more emotional value to positive feedback during learning and by this reduce their source memory deficits (see Wittmann, Schiltz, Boehler, & Duezel, 2008). Further research is needed to pursue this question and to establish how the present findings relate to the high *Pr* scores obtained in the memory test. For example, future studies could examine age differences in the effects of emotional valence and reward processing on memory and should manipulate reward probability and the number of stimulus repetitions during learning.

Most interestingly, both age groups showed better memory performance for stimuli that were associated with the positive learning condition. Moreover, in the source memory task participants were able to explicitly indicate that these stimuli were associated with positive feedback, whereas they performed at chance level for negative stimuli (see Fig. 1c). Hence, the present behavioral findings suggest that positive learning may be more efficient in enhancing subsequent memory performance than negative learning. However, it could also be argued that better source memory for positive than negative items may reflect a response bias in the sense that participants are generally more likely to respond

“positive” than “negative” when making these type of judgments. This interpretation alone seems not sufficient because it does neither account for the better overall memory performance for positive than negative stimuli, nor for the larger early ERP old–new effects for stimuli that were associated with positive feedback during learning.

Consistent with the memory bias for positive stimuli, we found an increased early old–new effect for stimuli that were associated with positive learning, whereas no such effect was obtained for negative stimuli (see Fig. 2a).³ This result is consistent with recent findings that showed that reward information supports episodic memory (Adcock et al., 2006; Wittmann et al., 2005). Moreover, the present results add two important new findings: first, they show that these memory improvements are specific for stimuli that are associated with positive learning, whereas negative learning does not seem to result in memory improvements. Second, our results show that positive feedback during learning predominantly affects the early old–new effect, which has been associated with familiarity-based memory. In contrast, we obtained similar late old–new effects for positive and negative stimuli, suggesting that reward information during learning does not have a specific effect on recollection (see Fig. 2). These results are consistent with recent findings that suggest that familiarity can contribute to source memory, if the source information is encoded as a feature of the stimulus (Diana, Yonelinas, & Ranganath, 2008). Such an interpretation would suggest that learning leads to a unitization of stimulus and reward, meaning that the reward gets a feature of the stimulus and by this contributes to source memory.

Age differences in memory-related ERPs were most pronounced in the late time window. As shown in Fig. 2a we found an anterior to posterior shift in the P300 for older compared to younger adults in the late time window. This shift of the P300 with age is a common finding in ERP and aging studies and has been associated with a stronger recruitment of prefrontal areas during the encoding and categorization of stimuli (see Friedman, Kazmerski, & Fabiani, 1997; Kray, Eppinger, & Mecklinger, 2005).

Furthermore, younger but not older adults showed a significant left parietal old/new effect in the late time window (see Fig. 3). This finding is consistent with previous data and suggests that older adults show reduced recollection-related activity (Ally et al., 2008; Morcom & Rugg, 2004). Findings from a combined MRI and ERP study indicate that the recollection-related late old–new effect in older adults correlates with hippocampal diffusion, a regionally selective measure of hippocampal integrity. In contrast, larger hippocampal volumes seem to be associated with changes in earlier ERP components and correlate with structural changes in the limbic system in the elderly (see Schiltz et al., 2006). Given these findings it seems tempting to suggest that better memory for rewarded items in the present study may be due to reward-related signals from the limbic system that primarily affect the early familiarity-related ERP effect (and associated PFC and MTL structures). Older adults may rely more on familiarity and by this reduce their source memory deficits, whereas younger adults rely more on recollection when retrieving source memory information. Of course, these interpretations are speculative given the limited spatial resolution of EEG. However, the present findings clearly merit further research, which might benefit from a combination of imaging techniques.

Taken together, the present findings show that positive learning improves memory and supports a fast and relatively automatic

memory retrieval process, as reflected in the early ERP old–new effect. Furthermore, our results indicate that although older adults show pronounced impairments during reward-based learning, explicit memory for the learned information seems to be intact, especially if items were associated with reward. This suggests that older adults attribute more emotional value to positive feedback during learning which may offset their source memory deficits.

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³ We also found a larger P2 component for old-positive than old-negative and new stimuli. This effect might reflect reward prediction responses that are triggered by stimuli that were associated with positive learning and are then followed by the familiarity signal, as reflected in the early old–new effect.

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