To Choose or to Avoid: Age Differences in Learning from Positive and Negative Feedback

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Abstract

■ In this study, we investigated whether older adults learn more from bad than good choices than younger adults and whether this is reflected in the error-related negativity (ERN). We applied a feedback-based learning task with two learning conditions. In the positive learning condition, participants could learn to choose responses that lead to monetary gains, whereas in the negative learning condition, they could learn to avoid responses that lead to monetary losses. To test the stability of learning preferences, the task involved a reversal phase in which stimulus–response assignments were inverted. Negative learners were defined as individuals that performed better in the negative than in the positive learning condition (and vice versa for positive learners). The behavioral data showed strong individual differences in learning from positive and negative outcomes that persisted throughout the reversal phase and were more pronounced for older than younger adults. Older negative learners showed a stronger tendency to avoid negative outcomes than younger negative learners. However, contrary to younger adults, this negative learning bias was not associated with a larger ERN, suggesting that avoidance learning in older negative learners might be decoupled from error processing. Furthermore, older adults showed learning impairments compared to younger adults. The ERP analyses suggest that these impairments reflect deficits in the ability to build up relational representations of ambiguous outcomes. ■

INTRODUCTION

Whether, and under which conditions, we learn more from our bad than our good choices is a matter of current debate (Klein et al., 2007; Frank, Seeberger, & O'Reilly, 2004). Aside from this debate, most researchers agree with the view that the neurotransmitter dopamine plays a critical role in learning and choice behavior (Schultz, 2007). Aging has been associated with changes in various aspects of the dopamine system, ranging from age-related deficits in presynaptical markers of dopamine to reductions in the availability of D1 and D2 receptors in older age (Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006; Braver & Barch, 2002). Decline in the availability of D2 receptors in older adults is correlated with age-related impairments in cognitive control and reductions in glucose metabolism in ACC, a region involved in error and reward processing (Volkow et al., 1998, 2000). Based on these findings, it has been proposed that age-related deficits in reinforcement learning are the result of decline in dopaminergic function in older age (Nieuwenhuis et al., 2002). The present study investigates whether age differences in learning from positive and negative outcomes are reflected in the error-related negativity (ERN), an ERP component that has been suggested to reflect dopaminergic input to ACC during learning (Holroyd & Coles, 2002).

The ERN (Gehring, Goss, Coles, Meyer, & Donchin, 1993), or error negativity (Ne) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990), is a negative ERP deflection that occurs at around 80 msec after a participant's erroneous response. The ERN is maximal at fronto-central electrodes and several findings suggest that the component is generated in ACC (Holroyd, Nieuwenhuis, et al., 2004; Swick & Turken, 2002). Results from ERP studies on reinforcement learning indicate that the ERN increases with learning (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002). This has been taken as evidence for the so-called reinforcement learning (R-L) theory of the ERN, which assumes that the component reflects negative reinforcement learning signals from the midbrain dopamine system (Holroyd & Coles, 2002). More specifically, the R-L theory proposes that the ERN is generated in ACC when input from the dopamine system signals that the outcome of an action has been worse than expected.

Interestingly, findings by Frank, Woroch, and Curran (2005) suggest that the amplitude of the ERN not only reflects learning but is also associated with individual differences in learning. In that study, a probabilistic selection task was applied that allows the separation of individuals that learn more from their good choices (positive learners) from individuals that learn more from their bad choices (negative learners). The results showed a larger ERN for negative than positive learners, suggesting that negative learning in younger adults is associated with a larger sensitivity to errors. Based on previous findings in Parkinson

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patients, Frank et al. (2005) concluded that this learning bias might be due to individual differences in dopamine levels.

The recent literature shows increasing evidence for age-related deficits in feedback-based learning (Weiler, Bellebaum, & Daum, 2008; Schmitt-Eliassen, Ferstl, Wiesner, Deuschl, & Witt, 2007; Mell et al., 2005). However, an important point that remains relatively unaddressed is the question whether aging has a general detrimental effect on learning, or whether it changes the way individuals learn from positive and negative feedback. A recent study by Frank and Kong (2008) indicated that older seniors, but not younger seniors, show a bias toward learning from negative feedback. Frank and Kong suggest that, in analogy to findings in Parkinson patients' (Frank et al., 2004), loss-avoidant behavior in older adults might result from reduced dopamine levels. Although these findings suffer from the lack of a younger control group and thus cannot be generalized to the adult life span, they have some interesting theoretical implications.

One prediction that could be derived from these findings is that if older adults (or a subgroup of older adults) showed increased negative learning, this should be reflected in a larger ERN, as it is the case in younger adults (see Frank et al., 2005). In contrast to this prediction, most of the studies on error processing in older adults and Parkinson patients showed a reduced ERN (Willemsen, Mueller, Schwarz, Falkenstein, & Beste, 2009; Stemmer, Segalowitz, Dywan, Panisset, & Melmed, 2007; Nieuwenhuis et al., 2002; Falkenstein, Hoormann, & Hohnsbein, 2001; Band & Kok, 2000). However, these studies focused on age differences in the ERN, rather than on individual differences within younger and older adults.

The present study investigates whether older adults have an increased bias to avoid negative outcomes and whether this negative learning bias is reflected in the ERN. We applied a feedback-based learning task with two learning conditions. In the positive learning condition, participants could learn to choose responses that lead to monetary gains, whereas in the negative learning condition, they could learn to avoid responses that lead to monetary losses. Positive learners were defined as participants who performed better in the positive than the negative learning condition and vice versa for negative learners. To examine the stability of learning biases, each learning block involved a learning phase in which participants learned the stimulus–response assignments, and a reversal phase in which the mappings were inverted. That is, stimuli that were previously associated with the positive learning condition were then associated with the negative learning condition, and vice versa. The two block phases allowed us to test whether individuals who have a certain learning bias in the learning phase switch according to their preference and show a similar bias in the reversal phase.

Given the findings by Frank et al. (2005), we expected significant learning biases in both age groups that should persist throughout the reversal phase. Based on the findings by Frank and Kong (2008), we predicted that older adults should learn more from negative than positive outcomes. Furthermore, according to Frank et al. (2005), the ERN should be associated with negative learning in younger adults. If individual differences in learning biases are magnified in older age (Frank & Kong, 2008), this should be reflected in a larger ERN for older negative compared to older positive learners.

METHODS

Participants

Thirty-one younger adults and 30 older adults participated in the study. Two younger adults were excluded because they did not commit enough errors to analyze the ERN. One older adult had to be excluded due to technical problems. We defined positive learners as participants who showed a higher mean accuracy in the positive than in the negative learning condition of the learning phase (and vice versa for negative learners). In the group of younger adults ($n = 29$, mean age = 22.1 years, $SD = 2.2$), 13 were negative learners and 16 were positive learners. In the group of older adults ($n = 29$, mean age = 69.7 years, $SD = 2.8$), 16 were negative learners and 13 were positive learners (see Table 1).

The participants performed two psychometric tests, one from the domain of fluid intelligence (the Digit–Symbol Substitution test, DSS; Wechsler, 1982) and one from the

Table 1. Means, Standard Deviations, and Ranges for the Demographic and Psychometric Measures, Displayed Separately for Younger and Older Adults and Positive and Negative Learners

	Younger Adults		*Older Adults*	
	Positive Learners	*Negative Learners*	*Positive Learners*	*Negative Learners*
n/Sex	16/7 female	13/7 female	13/7 female	16/7 female
Age range	19–27	20–27	65–74	66–75
Age, mean (*SD*)	21.8 (1.9)	22.5 (2.5)	69.9 (2.8)	69.6 (2.8)
Digit–Symbol Substitution test, mean (*SD*)	62.9 (12.0)	63.2 (13.1)	44.9 (9.0)	45.8 (8.5)
Spot-a-Word test, mean (*SD*)	30.7 (2.2)	30.4 (3.0)	33.5 (2.2)	33.1 (1.8)

domain of crystallized intelligence (the Spot-a-Word test; Lehrl, 1977). Consistent with previous findings (Verhaeghen & Salthouse, 1997), older adults reached lower scores than younger adults on the DSS ($p < .001$, $\eta^2 = .42$), reflecting age-related decline in processing speed (see Table 1). In contrast, older adults reached higher scores in the Spot-a-Word test ($p < .001$, $\eta^2 = .27$), which speaks for age-related improvement in semantic knowledge. In both age groups, positive and negative learners did not differ significantly with respect to age or psychometric measures (*p*s > .60; see Table 1).

Stimuli and Task

The stimulus set consisted of 32 colored images of objects (Snodgrass & Vanderwart, 1980). The feedback stimuli indicated a loss of 50 euro cents (−50), a gain of 50 euro cents (+50), or a neutral outcome (*00). If the response deadline was missed, the German words "ZU LANGSAM" ("too slow") were presented. The participants were asked to make a two-choice decision upon stimulus presentation and to press one of two response keys. They were instructed to learn the stimulus–response assignments by trial and error based on the feedback and were motivated to maximize their profit. Each subject received €22.5 for participation and could win a performance-dependent bonus of €7.50, which was awarded based on average accuracy across learning blocks (younger adults: >78%; older adults >66%).

Experimental Design

Each experimental block consisted of two phases, a learning phase, in which stimulus–response assignments were learned, and a reversal phase, in which the assignments were inverted and had to be relearned. Furthermore, the design involved two learning conditions, a positive learning condition, in which participants could learn to choose responses that lead to monetary gains, and a negative learning condition, in which they could learn to avoid responses that lead to monetary losses (see Figure 1).

Two stimuli (A and B) of each block phase were associated with the positive learning condition. If participants responded with a left keypress to A, they won 50 Euro Cents; if they responded with the right key, they received a neutral outcome (and vice versa for B). The other two stimuli (C and D) were associated with the negative learning condition. If participants responded with a right keypress to C, they received a neutral outcome; if they responded with the left key, they lost 50 euro cents (and vice versa for D). To avoid ceiling effects in younger adults, feedback was valid in 90% of the trials.

Stimuli that were associated with the positive learning condition in the learning phase were associated with the negative learning condition in the reversal phase (and vice versa) (see Figure 1). To equate performance levels between participants at the time of the switch from the learning to the reversal phase, we enforced a performance criterion (mean accuracy of 0.65 across learning conditions). If participants reached this criterion within 70 trials, the mappings were reversed. If this was not the case, the subjects performed additional trials, until they reached the criterion, or performed a maximum trial number of 100 trials.[1] The same procedure was applied for the reversal phase. The assignment of stimuli and responses was randomized across subjects.

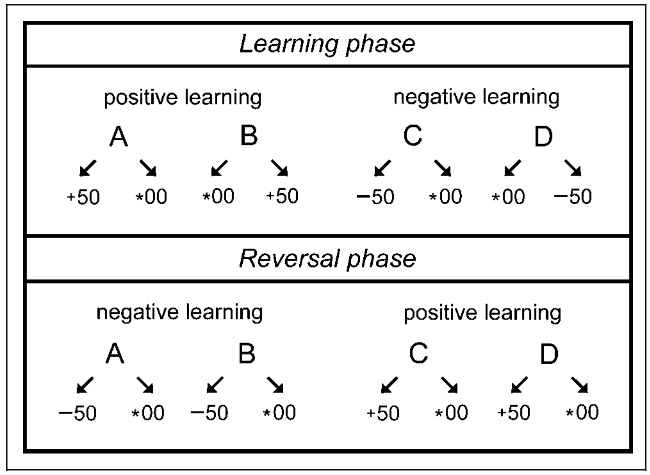


Figure 1. Schematic illustration of the learning paradigm.

Trial Procedure

Each trial started with a fixation cross (500 msec), which was followed by the imperative stimulus (500 msec). After the keypress, a blank screen was displayed (500 msec), and then the feedback appeared (500 msec). Stimuli were displayed in the middle of the screen. Similar to a previous study, we applied an adaptive deadline procedure to ensure that all subjects produced a similar proportion of timeouts (younger adults: $M = 0.01$, $SD = 0.01$; older adults: $M = 0.04$, $SD = 0.05$), and thereby had a similar opportunity to learn from feedback (see Eppinger, Kray, Mock, & Mecklinger, 2008). The response deadline was individually adjusted in 100-msec steps in a range of 700 to 1100 msec, depending on the proportion of timeouts.

Procedure

First, each participant filled out an informed consent and a demographic questionnaire. Then, they performed the two psychometric tests. The experiment consisted of one practice block (100 trials) and eight experimental blocks. Each block involved a new set of four imperative stimuli. Each of the four stimuli was presented 18–25 times in random order in each block phase, depending on whether the participants reached the performance criterion (see Experimental Design).

Data Recording

The stimuli were presented on a 17-in. color monitor with a dark gray background. Responses were registered on a response pad (Cedrus Corporation, San Pedro, CA) and the experiment was controlled by the software E-Prime (Psychology Software Tools, Pittsburgh, PA). EEG and EOG activity were recorded continuously (Brain Amp DC Recorder; Brain Vision Recorder acquisition software) from 64 Ag/AgCl electrodes (10–10 system) using EasyCap recording caps. The left mastoid was used as reference and the data were re-referenced off-line to averaged mastoids. The EEG and EOG signals were filtered on-line from DC −70 Hz and digitized at 500 Hz. Vertical and horizontal EOGs were 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 kΩ. To increase signal-to-noise ratio, the EEG data were low-pass filtered at 15 Hz (see Frank et al., 2005).

Data Analysis

Behavioral Data Analysis

Responses faster than 120 msec (younger adults: 0.9%, older adults: 3.0%) were excluded from data analysis. The accuracy data were analyzed by averaging mean accuracy for each subject, block phase, and learning condition into six bins, reflecting the six quantiles of the learning blocks (see Table 2). Each bin involved an equal number of trials (younger adults: $M = 55$; older adults: $M = 63$, averaged across blocks).[1] To analyze learning biases, we added a bin 0 to the accuracy data, assuming that each individual started at 50% accuracy in each condition and fitted the

Table 2. Means and Standard Deviations for the Accuracy Data, Displayed Separately for the Two Age Groups, the Two Learner Groups, the Two Learning Phases, the Two Learning Conditions, and the Two Block Halves

Accuracy (% Correct)			*Younger Adults*		*Older Adults*	
Block Phase	*Learning Condition*	*Bin*	*Positive Learners*	*Negative Learners*	*Positive Learners*	*Negative Learners*
Learning	Positive	1	0.56 (0.08)	0.51 (0.13)	0.53 (0.10)	0.47 (0.07)
		2	0.71 (0.11)	0.65 (0.13)	0.59 (0.11)	0.47 (0.08)
		3	0.74 (0.08)	0.66 (0.11)	0.61 (0.16)	0.53 (0.07)
		4	0.80 (0.11)	0.71 (0.16)	0.65 (0.13)	0.56 (0.14)
		5	0.84 (0.08)	0.77 (0.11)	0.68 (0.14)	0.55 (0.13)
		6	0.85 (0.09)	0.78 (0.11)	0.71 (0.07)	0.56 (0.10)
	Negative	1	0.55 (0.07)	0.54 (0.09)	0.50 (0.06)	0.55 (0.10)
		2	0.65 (0.13)	0.66 (0.11)	0.50 (0.10)	0.60 (0.11)
		3	0.67 (0.09)	0.75 (0.13)	0.50 (0.10)	0.63 (0.12)
		4	0.74 (0.08)	0.79 (0.09)	0.51 (0.09)	0.65 (0.15)
		5	0.75 (0.11)	0.82 (0.12)	0.52 (0.14)	0.66 (0.10)
		6	0.78 (0.12)	0.84 (0.06)	0.60 (0.13)	0.68 (0.11)
Reversal	Positive	1	0.48 (0.05)	0.49 (0.05)	0.50 (0.11)	0.48 (0.07)
		2	0.60 (0.09)	0.53 (0.10)	0.50 (0.06)	0.43 (0.09)
		3	0.66 (0.12)	0.59 (0.16)	0.55 (0.10)	0.43 (0.10)
		4	0.71 (0.13)	0.63 (0.14)	0.59 (0.10)	0.47 (0.10)
		5	0.77 (0.11)	0.66 (0.14)	0.60 (0.12)	0.51 (0.12)
		6	0.78 (0.13)	0.74 (0.12)	0.59 (0.11)	0.54 (0.13)
	Negative	1	0.55 (0.05)	0.50 (0.05)	0.50 (0.07)	0.57 (0.07)
		2	0.62 (0.07)	0.64 (0.10)	0.52 (0.09)	0.64 (0.09)
		3	0.65 (0.09)	0.69 (0.09)	0.50 (0.09)	0.64 (0.11)
		4	0.70 (0.10)	0.74 (0.08)	0.51 (0.08)	0.63 (0.15)
		5	0.70 (0.11)	0.76 (0.12)	0.55 (0.13)	0.66 (0.14)
		6	0.73 (0.13)	0.80 (0.12)	0.57 (0.10)	0.66 (0.10)

individual data with a linear function [$Y = b0 + (b1 \times t)$]. The mean accuracy rates (% correct) and the intercepts (b0) and slope (b1- or β-) parameters of the learning functions were then subjected to an ANOVA.

ERP Data Analysis

The EEG epochs were averaged with respect to response onset to obtain response-locked ERPs. To avoid differences in trial numbers we randomly selected 30 trials for each participant and condition. Similar to previous studies (Themanson, Hillman, & Curtin, 2006; Nieuwenhuis et al., 2002), the response-locked EEG data were baseline-corrected using a −200 and −50 msec pre-response baseline. Trials containing ocular artifacts, or other artifacts, were excluded from further analysis using a threshold criterion (standard deviations greater than 30 μV within a sliding window of 200 msec). Remaining eye movements were corrected using a linear regression approach (Gratton, Coles, & Donchin, 1983), as implemented in EEProbe software (ANT Software). As in previous studies (Eppinger et al., 2008; Frank et al., 2005), we defined the ERN as the peak-to-peak voltage difference between the most negative peak, between −50 and 150 msec around the response, and the preceding positive peak. Learning-related effects in the ERPs were examined by comparing the first to the second half of the block phases.[2]

Statistical Analyses

Accuracy and ERP data were analyzed using repeated measure ANOVAs. Bonferroni corrections were applied when necessary (p level $< .05$) and the corrected p values are reported. Whenever necessary, the Geisser–Greenhouse correction was applied (Geisser & Greenhouse, 1958) and the original F value, the adjusted p values, and the epsilon values (ε) are given. Effect sizes (eta squared, η^2) are reported (see Cohen, 1973).

RESULTS

Accuracy Data

Response accuracy was analyzed using an ANOVA design with the between-subjects factors age group (younger, older) and learner group (positive learners, negative learners), and the within-subjects factors, block phase (learning, reversal), learning condition (positive, negative), and bin (Bin1–Bin6). The analysis revealed significant main effects of age group [$F(1, 54) = 57.44$, $p < .001$, $\eta^2 = .51$] and bin [$F(5, 270) = 131.80$, $p < .001$, $\varepsilon = .63$, $\eta^2 = .61$]. The significant interaction between age group and bin shows the stronger learning effects for younger than older adults [$F(5, 270) = 29.82$, $\varepsilon = .63$, $p < .001$, $\eta^2 = .14$] (see Figure 2). Furthermore, the analysis showed significant main effects of block phase [$F(1, 54) = 44.11$, $p < .001$, $\eta^2 = .42$] and learning condition [$F(1, 54) = 10.86$, $p = .002$, $\eta^2 = .07$]. The significant interaction between block phase and learning condition [$F(1, 54) = 15.83$, $p < .001$, $\eta^2 = .21$] reflects higher accuracy in the negative than in the positive learning condition in the reversal phase ($p < .001$, $\eta^2 = .17$). These findings indicate that older adults are impaired in learning compared to younger adults. Furthermore, accuracy was increased in the negative than in the positive learning condition in the reversal phase.

Learning Biases

As expected, given our definition of the learner groups, the analysis revealed a significant interaction between learner group, learning condition, and bin [$F(5, 270) = 9.49$, $p < .001$, $\eta^2 = .14$]. Separate analyses for the two learner groups showed significant learning biases (interactions between learning condition and bin) for negative and positive learners (ps $< .03$, η^2s $> .15$) (see Figure 2). Separate analyses for the learning and the reversal phase revealed that the learning biases were stable across block phases (ps $< .03$, η^2s $> .07$).[3] No significant interaction between age group and learning condition was obtained ($p = .17$). However, the analysis revealed a significant three-way interaction between age group, learner group, and learning condition [$F(1, 46) = 7.49$, $p < .008$, $\eta^2 = .05$]. Separate analyses for the two learner groups showed significant age differences in learning biases for negative learners ($p < .03$, $\eta^2 = .07$), but not for positive learners ($p = .26$) (see Figure 2).[4] Taken together, these findings show pronounced individual differences in learning biases that persist throughout the reversal phase. Moreover, we found an increased negative learning bias for older negative learners compared to older positive learners and younger adults.

Age Differences in Learning Biases

To examine the time course of age differences in learning biases, we performed analyses on the intercept and slope parameters of the learning functions (see Methods). The analysis of the intercepts revealed a significant main effect of learning condition [$F(1, 54) = 12.09$, $p < .001$, $\eta^2 = .15$], and an interaction between age group, learner group, and learning condition [$F(1, 54) = 4.60$, $p = .04$, $\eta^2 = .06$]. Separate analyses for the two age groups and the two learner groups showed larger intercepts for the negative than the positive learning condition for older negative learners ($p < .001$, $\eta^2 = .55$). No such effect was obtained for older positive learners or younger adults (ps $> .13$). The analysis of the slope parameters showed higher learning rates for younger than older adults [$F(1, 54) = 66.77$, $p < .001$, $\eta^2 = .55$]. Moreover, we obtained a significant interaction between learner group and learning condition [$F(1, 54) = 45.97$, $p < .001$, $\eta^2 = .46$]. Separate analyses for the two learner groups revealed higher

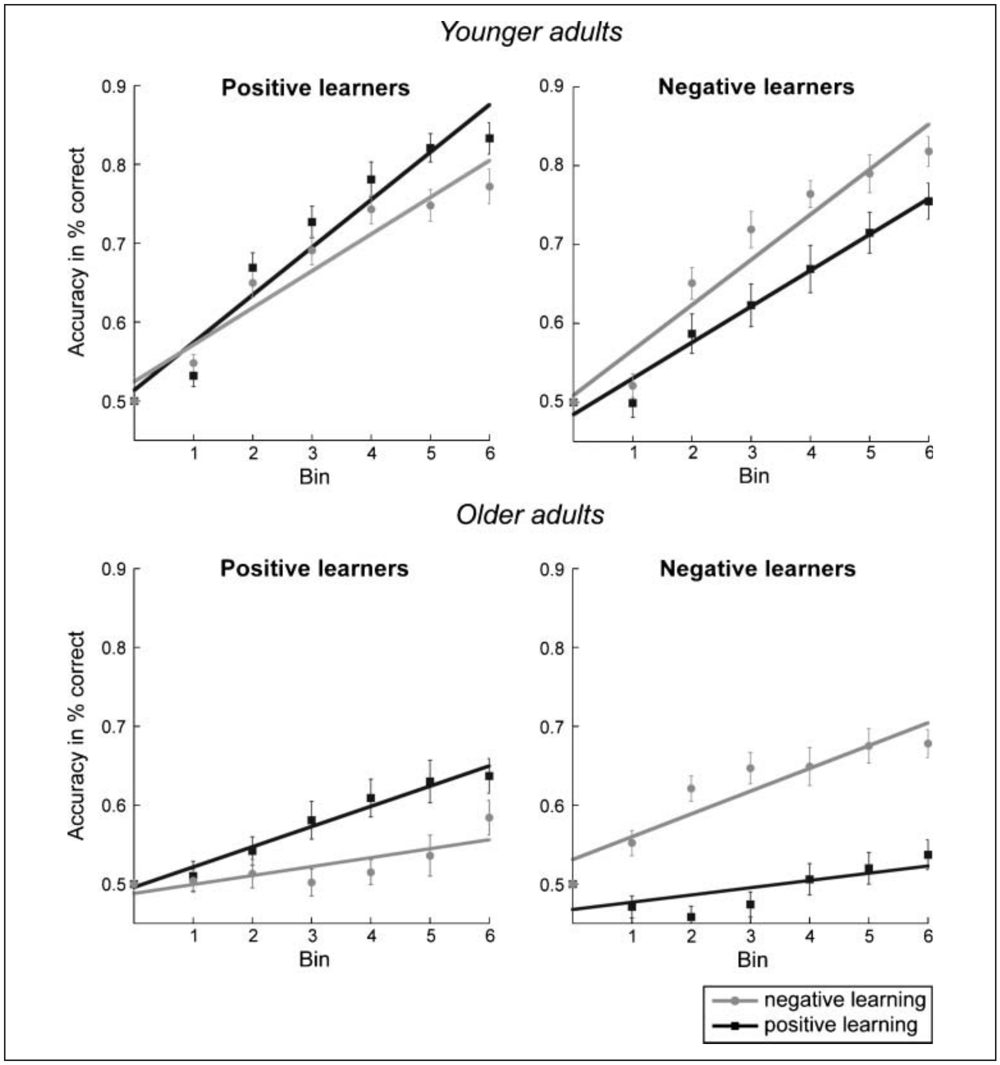


Figure 2. Mean accuracy (*SE*) learning curves for younger and older adults and positive and negative learners, displayed separately for the positive (black) and the negative (gray) learning conditions (the data were averaged across block phases).

learning rates in the positive than in the negative learning condition for positive learners, and vice versa for negative learners (ps $< .03$, η^2s $> .41$) (see Figure 2). To summarize, these findings show that the negative learning bias in older negative learners is particularly pronounced at the beginning of learning, whereas at the end of learning similar learning biases are obtained compared to older positive learners and younger adults (see Figure 2).

ERP Data

ERN

Figure 3 displays the ERPs to correct and incorrect responses, separately for younger and older adults, the learning and the reversal phase and the two bins.[2] The ERPs for younger adults show a pronounced ERN that increases with learning in the learning phase, but not in the reversal phase. For older adults, the ERN is reduced and does not change with learning or block phase.

The peak-to-peak measures of the ERN were analyzed using an ANOVA with the factors age group, learner group, block phase, learning condition, and bin. The analysis revealed a significant main effect of age group [$F(1, 54) = 14.50$, $p < .001$, $\eta^2 = .20$], indicating that the ERN was reduced for the elderly (see Figure 3). Furthermore, we found significant main effects of block phase [$F(1, 54) = 33.29$, $p < .001$, $\eta^2 = .23$] and bin [$F(1, 54) = 11.62$, $p < .001$, $\eta^2 = .15$], as well as a significant interaction between age group, block phase, and bin [$F(1, 54) = 8.43$, $p < .005$, $\eta^2 = .13$]. Separate analyses for the two age groups revealed a significant interaction between block phase and bin only for younger adults ($p < .01$, $\eta^2 > .22$). As shown in Figure 3, the ERN for younger adults increased with learning in the learning phase ($p < .001$, $\eta^2 = .33$), but not the reversal phase ($p = .08$). Thus, we observed learning-related changes in the ERN for younger, but not for older adults, which were most pronounced during the learning phase.

Learning Biases in the ERN

The analysis of the learning biases in the ERN revealed significant interactions between learner group and block phase [$F(1, 54) = 16.12$, $p < .001$, $\eta^2 = .11$], and between age group, learner group, and block phase [$F(1, 54) = 14.85$, $p < .001$, $\eta^2 = .10$]. Separate analyses for the two age groups showed a significant interaction between learner group and block phase only for younger adults ($p < .001$, $\eta^2 = .23$). As could be seen in Figure 3, younger negative learners showed a larger ERN than younger positive learners in learning phase ($p < .02$, $\eta^2 = .17$), but not in the reversal phase ($p = .94$). Taken together, these findings show a larger ERN for younger negative compared to younger positive learners in the learning, but not in the reversal phase. For older adults, no individual differences in the ERN were obtained.

Performance-matched Subgroups

To control for the effects of age differences in overall performance levels on the ERN, we performed a median split for the accuracy data and compared high-performing older adults to low-performing younger adults.[5] This analysis revealed no significant main effect of age group ($p = .10$), but a significant interaction between age group and learner group [$F(1, 21) = 4.47$, $p = .04$, $\eta^2 = .13$]. Separate analyses for the two learner groups showed a significantly larger ERN for younger than older negative learners ($p < .03$, $\eta^2 = .33$). In contrast, no significant age differences in the ERN were obtained for positive learners ($p = .74$) (see Figure 4B). These findings show that when performance is matched between groups, older negative learners still show a reduced ERN compared to younger negative learners, whereas similar ERNs are obtained for younger and older positive learners.

Response–Outcome Relations

One of the most interesting aspects of the response-locked ERP data is that older adults seem to be impaired in differentiating correct from incorrect responses, when these responses lead to ambiguous neutral outcomes. In contrast, younger adults seem to differentiate between response types, irrespectively of whether these responses are followed by ambiguous (neutral) or unambiguous (positive, negative) outcomes (see Figure 5).

To examine these effects, we analyzed the mean amplitude measures of the response-locked ERPs for the four response–outcome relations (correct-positive, incorrect-negative, correct-neutral, and incorrect-neutral). This analysis revealed a main effect of response outcome [$F(1, 54) = 67.40$, $p < .001$, $\eta^2 = .45$], and an interaction between age group and response outcome [$F(1, 54) = 27.69$, $p < .001$, $\eta^2 = .18$]. Contrasts for the four levels of the factor response outcome that were performed separately for younger and older adults revealed a significant difference in the ERPs to unambiguous response–outcome relations for both age groups (ps $< .001$, η^2s $> .44$). In contrast, for the ambiguous response–outcome relations, a significant difference was only obtained for younger adults ($p < .001$, $\eta^2 = .55$) (see Figure 5). These findings suggest that older adults were impaired in representing the correctness of a response when the response–outcome relation was ambiguous.

DISCUSSION

The aim of the present study was to investigate whether older adults have a bias to learn more from negative than

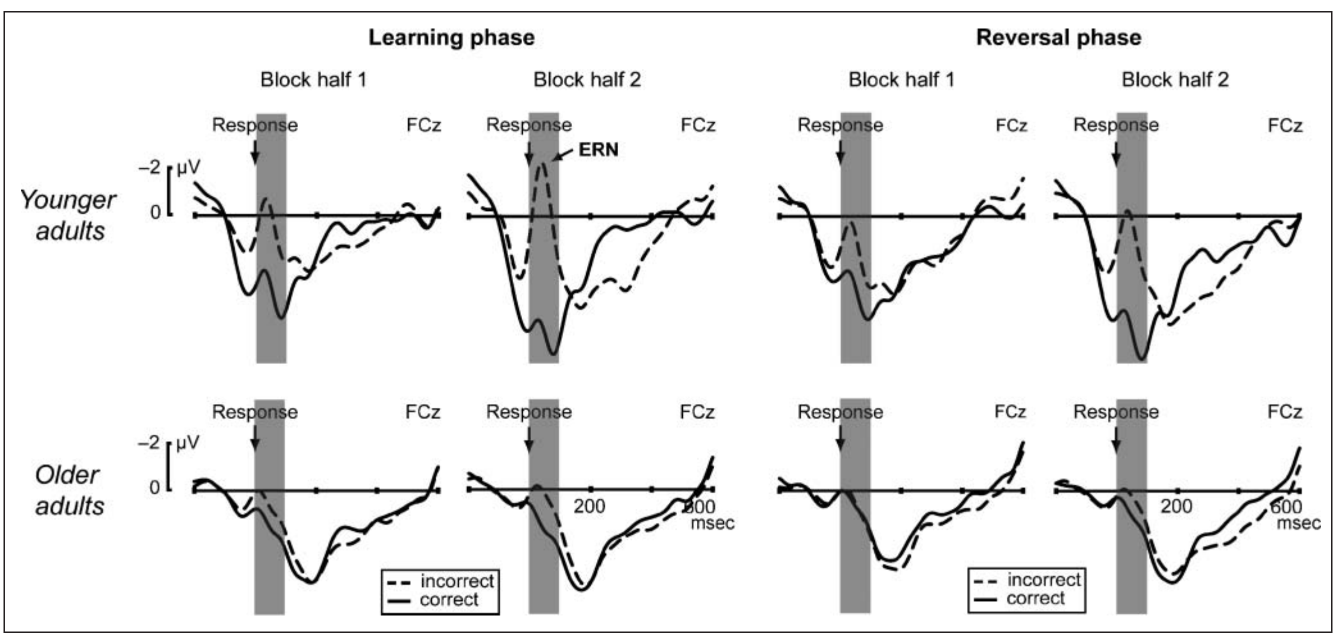


Figure 3. Response-locked grand-average ERPs to correct (solid lines) and incorrect (dashed lines) responses for younger adults (top) and older adults (bottom), displayed separately for the learning and the reversal phases and the two block halves at the electrode FCz. Tick spacing on the x-axis is 200 msec; the arrows indicate response onset. Gray bars indicate the time windows used for statistical analysis.

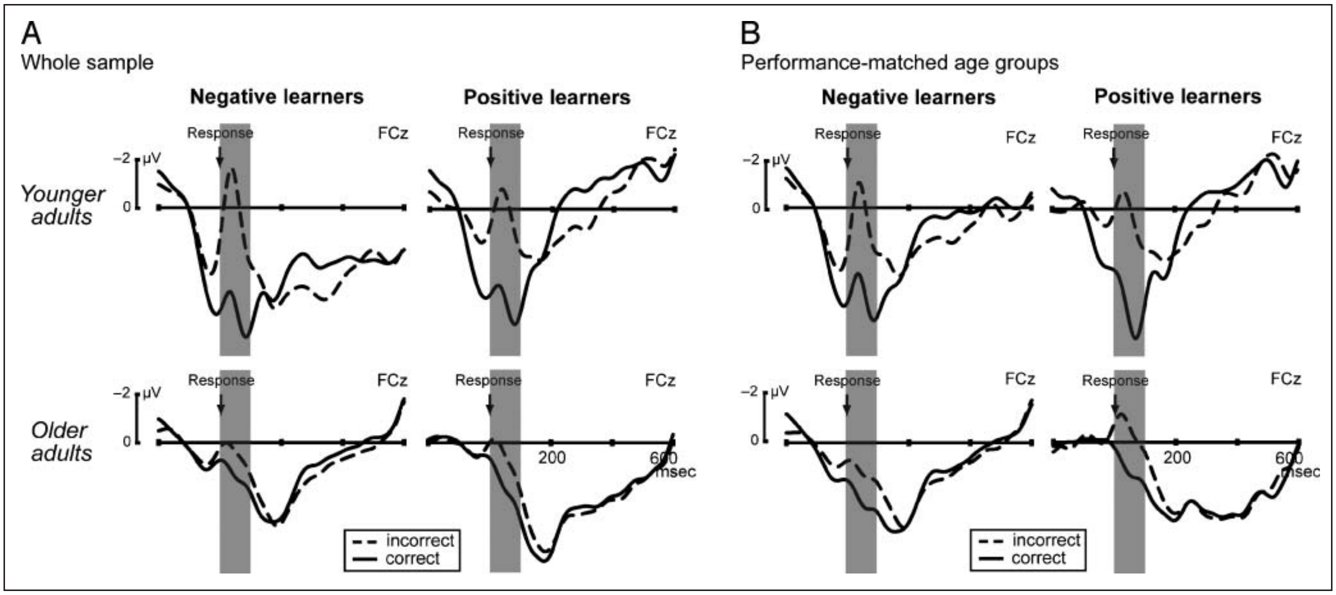


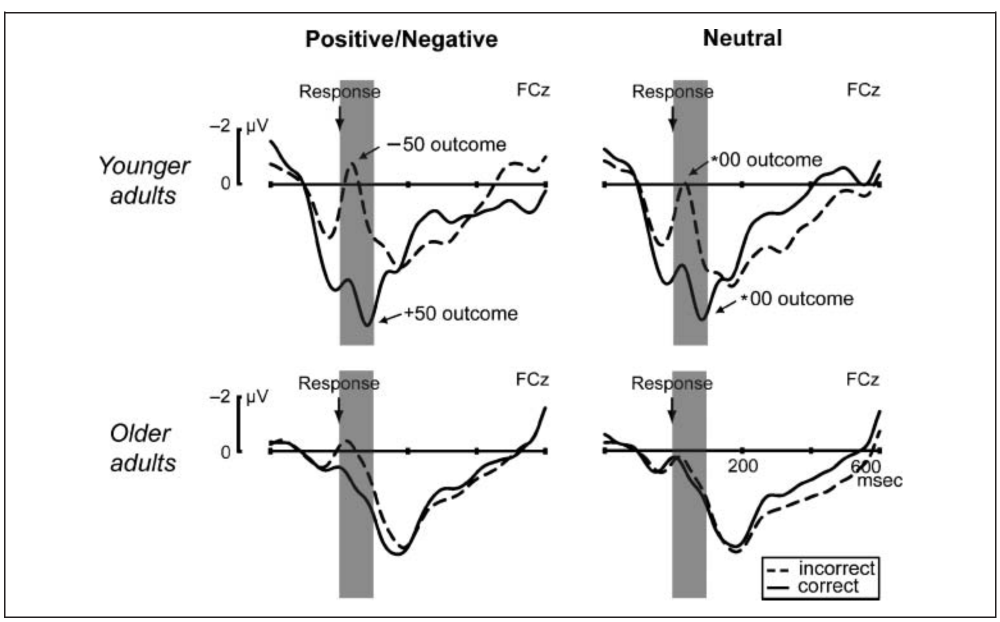
Figure 4. (A) Response-locked grand-average ERPs to correct (solid lines) and incorrect (dashed lines) responses in the learning phase, displayed separately for younger and older adults and negative and positive learners (A shows the whole sample). (B) Analogous figure for the performance matched subgroups. Tick spacing on the *x*-axis is 200 msec; the arrows indicate the response onset. Gray bars indicate the time windows used for statistical analysis.

positive feedback and whether this learning bias is reflected in the ERN. We applied a learning task in which participants could either learn to choose responses that lead to monetary gains (positive learning condition), or to avoid responses that lead to monetary losses (negative learning condition). We defined positive learners as participants who performed better in the positive than in the negative learning condition and vice versa for negative learners. To examine the stability of individual differences in learning biases, each learning block involved a reversal phase in which the stimulus–response assignments were inverted and the participants had to relearn the mappings.

Learning Biases

As expected, based on our definition of the learner groups, negative learners learned better in the negative than in the positive learning condition, and vice versa for positive

Figure 5. Response-locked grand-average ERPs to correct (solid lines) and incorrect (dashed lines) responses for unambiguous (positive/ negative) and ambiguous (neutral) response–outcomes relations, displayed separately for younger and older adults. Tick spacing on the *x*-axis is 200 msec; the arrows indicate the response onset. Gray bars indicate the time windows used for statistical analysis.



learners. Similar learning biases were obtained during reversal learning, indicating that individual differences in learning from positive and negative outcomes remained stable even if participants had to learn to switch their responses according to the inverted mappings in the reversal phase. This stability is remarkable, given the fact that the previously learned mappings produced interference, as reflected in the decreased accuracy during reversal learning. Hence, the present findings point to strong and persistent individual differences in learning preferences.

Age Differences in Learning Biases

Most interestingly, the analysis revealed an increased bias to avoid responses that lead to negative outcomes in older negative learners. To further examine the time course of age differences in learning biases, we analyzed the learning functions. The analysis of the intercepts of the learning functions revealed increased negative learning for older negative learners, whereas in the slope parameters no age differences in learning biases were observed. As shown in Figure 2, older negative learners show a strong increase in accuracy in the negative learning condition at the beginning of learning. At the same time, accuracy in the positive learning condition drops below chance level. This suggests that older negative learners had a more conservative response bias at the beginning of learning and tended to choose the neutral outcomes, even if these outcomes were worse than the alternative outcomes (as in the positive learning condition). In this respect, our findings are consistent with those of Frank and Kong (2008) and point to an increased negative learning bias in older negative learners. Furthermore, our data are in line with results from a recent study on age differences in decision-making that also showed evidence for a subgroup of older adults who have problems in shifting selections toward advantageous outcomes (Denburg, Tranel, & Bechara, 2005).

In contrast to the study by Frank and Kong (2008), we did not obtain an overall bias toward negative learning in older adults. There are several potential explanations for the absence of this effect in the present study. First, the sample that showed this bias in the Frank and Kong study was older than the present sample and it is possible that age-related changes in the dopamine system follow a nonlinear trajectory. Second, it could be argued that the acquisition of near-deterministic relationships, as in the present study, might rely more on explicit memory systems. However, as shown in Figure 2, it takes even younger adults considerable time to learn the associations and they do not seem to reach their learning asymptote, which does not suggest that they learned by retrieving explicit memory traces of the stimulus–response assignments.

In addition to the individual differences in learning biases, older adults showed lower overall accuracy and reduced learning rates than younger adults. This finding is somewhat surprising, given the results of our previous study in which we did not obtain age differences in learning effects (Eppinger et al., 2008). However, the learning tasks applied in the two studies differed in several aspects. The most obvious difference is that the number of feedback stimuli was larger in the present study, which may have made it more difficult for the elderly to differentiate the outcomes. Yet, the most likely reason for the learning impairments in older adults is that they had difficulties in disambiguating the neutral outcomes. This means that in order to learn the stimulus–response assignments in the present task, participants need to be able to differentiate situations in which the neutral outcome is better or worse in relation to the alternative outcome. This idea is supported by findings in the response-locked ERPs.

ERN

Consistent with the findings by Frank et al. (2005), we observed a larger ERN for younger negative than younger positive learners (see Figure 4A). This finding supports the idea that in younger adults, a bias toward avoidance learning is associated with a larger sensitivity to errors. Furthermore, consistent with the R-L theory (Holroyd & Coles, 2002), we found a learning-related increase in the ERN for younger adults (see Figure 3). However, the learning biases, as well as the learning effects, in the ERN were only observed for the learning phase, but not for the reversal phase. The only apparent difference between the two block phases is the fact that overall performance was reduced in the reversal phase. Hence, one explanation for the absence of these effects in the ERN could be that after the reversal participants were uncertain about the correctness of their response, and thus, perceived less mismatch and showed a smaller ERN. However, it should be noted that there is a learning-related increase in the positivity to correct responses in the reversal phase (see Figure 3). That is, by measuring the ERN as a difference in the ERPs to correct and incorrect responses, we would have obtained significant learning-related changes in the reversal phase as well (see Eppinger et al., 2008).

Learning Biases and the ERN

Based on recent theoretical ideas (Frank & Kong, 2008), we expected that the more pronounced negative learning bias in older negative learners would be associated with an increased ERN. This was not the case in the present study. In contrast, the ERN was generally reduced in the elderly, which is consistent with their performance impairments (Eppinger et al., 2008; Nieuwenhuis et al., 2002). To examine learning biases in the ERN in the absence of age differences in performance, we analyzed the ERN in performance-matched subgroups (see Figure 4B). Overall, we found no significant age differences in the ERN when performance was matched, which is nicely consistent with our previous findings (Eppinger, Mock, & Kray, 2009; Eppinger et al., 2008). However, most importantly, we found that in the absence of performance differences between age groups, older negative learners still showed a smaller ERN than younger negative learners. In contrast, older positive learners showed a similar ERN as younger positive learners. These findings further support the view that avoidance learning in older negative learners is not associated with stronger activity in the medial prefrontal error processing system, as it is in younger adults (see Frank et al., 2005). This may indicate that subcortical processes involved in learning and error processing are relatively unaffected by age, leading to the behavioral learning bias in older adults. In contrast, higher-level control processes involved in the monitoring of performance and outcomes that are reflected in the ERN are impaired, especially in those older adults who show a negative learning bias.

Of course, such an interpretation raises the question whether the observed associations between negative learning and the ERN in younger adults are causal. The present results do not support this idea and rather suggest that the ERN might be an epiphenomenon of dopaminergic changes during learning. That is, our findings point to two alternative explanations regarding learning biases and the ERN. The first interpretation would suggest that the learning bias in younger negative learners leads to an increased recruitment of control processes to optimize performance and avoid negative feedback, which is reflected in the ERN. This view is supported by a wealth of data that points to the role of the ERN in performance monitoring (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Yeung, Botvinick, & Cohen, 2004). Alternatively, it could be argued that the negative learning bias leads to an increased emotional reactivity to errors, which would be consistent with data that links the ERN to individual differences in personality traits (Pailing & Segalowitz, 2004; Luu, Collins, & Tucker, 2000). More research is needed to clarify these issues and to establish the relation between the ERN and individual differences in learning, cognitive control, and emotion regulation. Furthermore, the present findings implicate that future studies should carefully control for individual differences in learning before making conclusions about the relation between learning parameters and their neurophysiological correlates.

Another point that needs to be considered in the interpretation of the results is the fact that an overall reduction of ERP amplitudes and lower signal-to-noise ratio in the older adults' data might have contributed to the reduced ERN in older negative learners. An analysis of the stimulus-locked P1 and N1 components, which are assumed to reflect early visual and attentional processing, does not support this view. Whereas P1 seems to be unaffected by age, N1 is even increased for older than younger adults.[6] This suggests that the reduction of the ERN in older negative learners in the present study does not reflect general amplitude reductions or lower signal-to-noise ratio in the elderly.

Response–Outcome Relations

As illustrated in Figure 5, younger adults clearly differentiated correct from incorrect responses, irrespectively of whether these responses were followed by ambiguous (neutral) or unambiguous (positive, negative) outcomes. This suggests that younger adults were able to represent that in the negative learning condition the neutral outcome was better than the alternative (negative) outcome, whereas in the positive learning condition the neutral outcome was worse than the alternative (positive) outcome. Thus, they were able to build up a relational representation of the correctness of the response. These findings are consistent with results from a study by Holroyd, Larsen, and Cohen (2004), which point to similar effects of context sensitivity in the feedback negativity (FRN) in younger adults.

In older adults, the ERPs differed only for unambiguous response–outcome relations, whereas no difference for the ambiguous outcomes was obtained (see Figure 5). This finding shows that older adults were impaired in building up relational representations of ambiguous outcomes. Given that performance on the present task depends on how good participants are in differentiating the neutral outcomes, it seems reasonable to assume that the pronounced age differences in accuracy result from the fact that older adults were impaired in representing under which conditions a neutral outcome was better or worse than the alternative outcome. Consistent with this interpretation, a recent study showed age-related impairments in decision-making when information about outcomes was ambiguous and had to be learned, but not when the outcome probabilities were explicitly given (Zamarian, Sinz, Bonatti, Gamboz, & Delazer, 2008). This may suggest that the present findings reflect a more general problem of older adults in the processing ambiguous information and in building up relational representations of outcomes. This view is supported by recent findings that point to disproportional age-related changes in orbito-frontal cortex, a brain region that has been shown to play a major role in building up relative representations of reward value (Resnick, Lamar, & Driscoll, 2007; Wallis, 2007).

Conclusions

To conclude, the present results support recent findings (Frank & Kong, 2008; Frank et al., 2005) by showing that (a) the ERN in younger adults is associated with a bias toward learning more from negative outcomes, and (b) a subgroup of older adults shows an increased tendency to avoid negative outcomes. However, in contrast to theoretical considerations (Frank & Kong, 2008), the enhanced bias toward avoidance learning in older negative learners seems to be decoupled from error processing in medial prefrontal cortex, as reflected in the ERN. This may indicate that the subcortical processes that underlie negative learning are relatively unaffected by age, whereas control processes involved in monitoring and optimization of performance and outcomes are impaired. Furthermore, the present data provide two important additional findings. First, our results point to strong individual differences in learning from positive and negative outcomes that persisted throughout the reversal phase and were more pronounced for older than younger adults. Second, our data show that older adults are impaired in learning when they have to build up relational representations of ambiguous outcomes, which is consistent with recent findings that point to an increased vulnerability of orbito-frontal cortex with age (Resnick et al., 2007).

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Notes

1. Because it took older adults longer to reach the performance criterion, they performed more trials than younger adults in the learning phase (older adults: $M = 92$, $SD = 8$; younger adults: $M = 79$, $SD = 8$) and in the reversal phase (older adults: $M = 96$, $SD = 6$; younger adults: $M = 84$, $SD = 9$). In the learning phase, all younger adults reached the learning criterion at least once, 34% of the older adults never reached the criterion.
2. To obtain reliable ERPs on error trials, we had to average across the first and the second block half. Consequently, Bins 1 to 3 of the accuracy analysis correspond to Bin 1 of the ERP analysis; Bins 4 to 6 of the accuracy analysis correspond to Bin 2 of the ERP analysis.
3. Please note that positive learners were defined as participants who showed a higher mean accuracy in the positive than in the negative learning condition of the learning phase (and vice versa for negative learners). Hence, the data from the reversal phase truly reflect the stability of learning biases. See Supplementary Figure 1 for additional analyses.
4. To test whether the learning biases were significantly larger for older negative than older positive learners, we calculated the difference in mean accuracy between the two learning conditions for the two age groups and the two learner groups and performed an ANOVA on the difference values. This analysis showed a significantly larger bias for older negative learners ($M = 0.14$, $SE = 0.02$) than older positive learners ($M = 0.08$, $SE = 0.01$), ($p < .04$, $\eta^2 = .15$). In contrast, only a marginally significant difference was obtained for younger adults (negative learners: $M = 0.08$, $SE = 0.01$; positive learners: $M = 0.05$, $SE = 0.01$, $p = 0.06$). Overall, learning biases were more pronounced for older than younger adults, as reflected in a significant main effect of age group ($p < .001$, $\eta^2 = .18$). See Figure 2 and Supplementary Figure 2. These findings support the view that older negative learners have an increased learning bias compared to older positive learners and younger adults.
5. To match subgroups of younger and older adults with respect to overall accuracy, we performed a median split for the two age groups and compared high-performing older adults ($n = 16$, $M = 0.61$, $SD = 0.13$) to low-performing younger adults ($n = 14$, $M = 0.63$, $SD = 0.13$). The same ANOVA design as for the whole sample was applied. The analysis did not reveal significant age differences in overall accuracy ($p = .17$). However, similar to the whole sample, we obtained significant interactions between learner group and learning condition, and between learner group, learning condition, and bin, ($ps < .001$, $\eta^2 > .21$). Hence, the two subgroups show similar behavioral learning biases as the whole sample but do not differ with respect to overall performance.
6. To examine whether the reduction of the ERN in older negative learners might be due to a general reduction of ERP components, we performed an analysis on the stimulus-locked P1 and N1 components (defined as mean amplitudes in 60–120 msec and 115–175 msec time windows at electrode Oz). We did not obtain significant age differences or differences between learners groups in P1 ($ps > .36$), suggesting that early visual processing was unaffected by age. Furthermore, we obtained a larger N1 component for older ($M = -2.09$ μV, $SD = 0.39$ μV) than younger adults ($M = -0.11$ μV, $SD = 0.95$ μV) ($p < .02$, $\eta^2 = 09$), but again no differences between learner groups ($ps > .22$). A similar pattern of results was obtained for the performance-matched subgroups, indicating that that the reduction of the ERN in older negative learners could not be attributed to general amplitude reductions or lower signal-to-noise ratio.

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