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Better or worse than expected? Aging, learning, and the ERN

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Abstract

This study examined age differences in error processing and reinforcement learning. We were interested in whether the electrophysiological correlates of error processing, the error-related negativity (ERN) and the feedback-related negativity (FRN), reflect learning-related changes in younger and older adults. To do so, we applied a probabilistic learning task in which we manipulated the validity of feedback. The results of our study showed that learning-related changes were much more pronounced (a) in a response-locked positivity for correct trials compared to the ERN and (b) in a feedback-locked positivity for positive feedback compared to the FRN. These findings provide an important extension to recent theoretical accounts [Holroyd, C. B., & Coles, M. G. H. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review, 109*, 679–709; Nieuwenhuis, S., Ridderinkhof, K. R., Talsma, D., Coles, M. G. H., Holroyd, C. B., Kok, A., et al. (2002). A computational account of altered error processing in older age: Dopamine and the error-related negativity. *Cognitive, Affective and Behavioral Neuroscience, 2, 19–36*] since they suggest that positive learning signals on correct trials contribute to the reward-related variance in the response- and feedback-locked ERPs. This effect has been overlooked in previous studies that have focused on the role of errors and negative feedback for learning. Importantly, we did not find evidence for an age-related reduction of the ERN, when controlling for performance differences between age groups, which questions the view that older adults are generally impaired in error processing. Finally, we observed a substantial reduction of the FRN in the elderly, which indicates that older adults are less affected by negative feedback and rely more on positive feedback during learning. This finding points to an age-related asymmetry in the processing of feedback valence.

Keywords: Age differences; ACC; Dopamine; ERP; Error processing; Reinforcement learning

1. Introduction

The aim of this study is to examine age-related modulations in reinforcement learning and their potential impact on the ability to adaptively acquire and maintain new behavior. We focus on the role that the processing of error information plays for reinforcement learning by investigating age differences in the behavioral and electrophysiological correlates of error processing.

The basic principle of reinforcement learning has already been formulated in the early 1920s by Thorndike. It suggests that actions that are followed by feelings of satisfaction are more likely to be generated again in the future, whereas actions that are followed by negative outcomes are less likely to reoccur (Thorndike, 1911). In recent years several researchers became interested in the neurophysiological basis of reinforcement

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learning and especially in the role of dopamine for learning. For instance, electrophysiological studies in primates have shown that learning based on rewarding outcomes depends on the activity of dopaminergic neurons in the ventro-anterior midbrain (substantia nigra and ventral tegmental area) (for reviews, see Montague, Hyman, & Cohen, 2004; Schultz, 2002). Schultz, Dayan, and Montague (1997) integrated these electrophysiological findings in primates with learning models from artificial intelligence. They showed that changes in the activity of dopaminergic neurons during learning could be formalized using a temporal difference learning model (see Barto & Sutton, 1997). Dopaminergic neurons from the ventral tegmental area seem to signal the extent to which a rewarding outcome deviates from a prediction during learning. That is, they code prediction errors that reflect changes in the value of ongoing events, when events are suddenly better or worse than expected (Schultz et al., 1997). According to this model, learning is induced when a reinforcer occurs that is better than predicted (positive prediction error). In contrast, a reinforcer that is worse than predicted or

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omitted (negative prediction error) leads to extinction of learned behavior. A positive prediction error is reflected in a phasic burst of activity in mesencephalic dopamine neurons, whereas a negative prediction error is reflected in a phasic depression of activity of these neurons. On the basis of this learning mechanism the dopamine system allows us to flexibly acquire new behavior and by this plays a key role in several higher order cognitive functions such as working memory, attention, and cognitive control.

One of the main target areas of the mesencephalic dopamine system is the anterior cingulate cortex (ACC) (for a review, see Paus, 2001). The ACC has been suggested to be involved in several cognitive control functions such as conflict monitoring (see Botvinick, Braver, Barch, Carter, & Cohen, 2001; Yeung, Botvinick, & Cohen, 2004) and error processing (Gehring, Goss, Coles, Meyer, & Donchin, 1993; Scheffers & Coles, 2000). Moreover, recent neurophysiological research in monkeys revealed that the ACC also plays an important role in reward processing (Matsumoto, Suzuki, & Tanaka, 2003; Shidara & Richmond, 2002). Ito, Stuphorn, and Schall (2003) showed that the ACC contains a diversity of reward-related neurons that respond to the omission of reward as well as to earned or unexpected reward. This is in line with results from Bush et al. (2002), who used a reward-based decision making task and functional imaging (fMRI) in humans and showed increased activation in the ACC for unexpected reductions of reward. Together, these findings suggest that the ACC receives input from the mesencephalic dopamine system and uses these signals to evaluate whether the outcome of an action deviates from a prediction.

It is well known that aging is associated with pronounced changes in the dopamine system and its target areas in the prefrontal cortex (PFC) (for reviews, see Bäckman, Nyberg, Lindenberger, Li, & Farde, 2006; Braver & Barch, 2002). Several authors have suggested that the deficits of older adults in cognitive control can be attributed to disturbances in dopamine function (Braver et al., 2001; Li, Lindenberger, & Sikström, 2001). It has been shown that the availability of dopamine D2 receptors in the striatum declines with age and is correlated with performance on tasks that are assumed to involve the PFC, such as the Wisconsin Card Sorting Test and the Stroop task (Volkow et al., 1998). Interestingly, the availability of striatal dopamine D2 receptors was also correlated with glucose metabolism in the ACC, a region that is involved in error and reward processing (Volkow et al., 2000).

Thus, there is evidence that age-related deficits in the mesencephalic dopamine system and its target areas in the PFC may contribute to some of the impairments of older adults in cognitive control functions such as conflict monitoring and error processing.

1.1. ERP correlates of reinforcement learning

One ERP component that has been recently associated with reinforcement learning is the error-related negativity (ERN) (see Holroyd & Coles, 2002; Nieuwenhuis et al., 2002). The ERN (Gehring et al., 1993) or error negativity (Ne) (Falkenstein, Hohnsbein, & Hoormann, 1995) is a negative ERP deflection at fronto-central electrodes that can be observed around 80 ms after a participant's erroneous response. Imaging data (Carter et al., 1998; Holroyd et al., 2004), dipole analyses (Miltner et al., 2003; Van Veen & Carter, 2002), and neuropsychological studies (Swick & Turken, 2002) support the view that the ERN is generated in the dorsal part of the ACC. Interestingly, ERNs are not only found for error trials but also in response to external error feedback. The so-called feedback-ERN (called FRN in the following) was first observed by Miltner, Braun, & Coles (1997). It shows a similar medial frontal topography as the ERN and can be observed between 200 and 300 ms after the onset of a negative feedback stimulus. Using fMRI, Holroyd et al. (2004) showed that internal and external error feedback activated the same region in the dorsal ACC, which underlines the view that ERN and FRN both reflect the activity of an error processing system involving the dorsal ACC.

In order to investigate the role of the error processing system associated with the ACC for reinforcement learning Holroyd and Coles (2002) examined changes in the ERN/FRN during probabilistic learning. In the probabilistic learning task they used participants had to learn stimulus-response mappings by trial and error based on feedback information. The results of this study showed that the ERN increased with learning, whereas the FRN decreased with learning. On the basis of these findings, Holroyd and Coles (2002) proposed that the increase of the ERN with learning reflects the development of an internal representation of the correct response. The idea is that learning of the correct response leads to an increased mismatch signal (negative prediction error) when an incorrect response is given. In contrast, the decrease of the FRN with learning might be due to the decreasing information value of the feedback stimulus. On the basis of these findings Holroyd and Coles (2002) proposed the reinforcement learning (R-L) theory of error processing that integrates the role of dopamine for learning with the error processing function associated with the ACC. According to this theory, the ERN is generated when a negative reinforcement learning signal from the dopamine system is conveyed to the ACC. More precisely, the model states that errors induce phasic decreases in mesencephalic dopaminergic activity. The ERN is generated when such a dip in dopaminergic input disinhibits neurons in the ACC. In other words, their model suggests that the ERN reflects a negative prediction error and is generated when the outcome of an action is worse than expected.

Nieuwenhuis et al. (2002) extended the R-L theory in order to explain older adults' deficits in error processing and reinforcement learning. They proposed that the reduced ERNs, that are typically found for older adults (see Band & Kok, 2000; Falkenstein, Hoormann, & Hohnsbein, 2001; Mathewson, Dywan, & Segalowitz, 2005; West, 2004), are a consequence of a weakened signal of the mesencephalic dopamine system in the elderly. To test this hypothesis, Nieuwenhuis et al. (2002) measured performance and ERNs in younger and older adults during probabilistic learning. Their learning task included different learning conditions in which they manipulated the validity of feedback information. The results for younger adults generally replicated the findings from Holroyd and Coles (2002) and further supported the R-L theory. In contrast, for older adults they found reduced ERNs and less pronounced differences in the ERN between learning conditions compared to younger adults. The FRN was also reduced in the elderly, but it did not vary as a function of learning condition. Nieuwenhuis and colleagues concluded that the reductions of the ERN and the FRN as well as the learning deficits of older adults are consistent with the dopamine hypothesis of altered error processing with aging.

Even though the study by Nieuwenhuis et al. (2002) provides some important insights into the role of error processing during reinforcement learning, several critical issues are unsolved. First, as Nieuwenhuis et al. (2002) state, the ERN seems to be generated when the outcome of an action is worse than expected. By this the ERN depends on the formation of expectations (by learning) on the correctness of the response. If older participants are worse in learning which button they have to press, they are less able to build up expectations about the correctness of their response, and as a consequence, perceive less mismatch (and produce smaller ERNs) if they press the incorrect button. Thus, one major aspect of the present study was to design a learning task that would enable older adults to learn on a comparable performance level as younger adults do. This would allow us to compare the ERNs of the two age groups in the absence of performance differences.

The second important aspect addressed in this study is how the ERN changes over the course of learning in younger and older adults. In the study by Nieuwenhuis et al. (2002) learning was investigated by comparing different learning conditions in which the validity of feedback was manipulated and by this more or less learning was possible. Although the study by Nieuwenhuis et al. (2002) also provided some evidence for an increase of the ERN with block half, age differences in the learning-related effects were only marginally significant. Thus, one important further goal of the present study was to precisely track age differences in error processing during the time-course of learning.

The present study addresses these issues using a probabilistic learning task. In this task, the participants were asked to make a two-choice decision upon presentation of an imperative stimulus and received positive or negative feedback. Feedback validity was manipulated in three conditions (100%, 80%, or 50% validity). In the 100% validity condition, feedback was always valid. In the 80% validity, it was valid in 80% of the trials but also invalid in 20% of the trials (80% validity condition). In the 50% validity condition, which served as control condition, feedback was delivered randomly so that no learning was possible. In order to enable similar learning effects in younger and older participants, we introduced an algorithm that adaptively adjusted the response deadline (for details, see Section 2.4). This was done because it is well known that aging is accompanied by a substantial general slowing that accounts for several age-related impairments in cognitive tasks (see e.g., Salthouse, 1996). Using an equal response deadline for both age groups would lead to a disproportional time pressure for older adults, thereby impairing their ability to learn. The adaptive algorithm allows each individual to take time for responding by maintaining moderate time pressure.

Based on the neurocomputational models reviewed above, we derived the following hypotheses. First, the use of an adaptive response deadline should increase learning rates in older adults. Thus, we expected older adults to perform comparably to younger adults, at least in the 100% validity condition in which feedback information is always valid. Second, based on the dopamine hypothesis of aging (Nieuwenhuis et al., 2002) we expected older adults to show reduced ERN components during learning. However, if age differences in the ERN are confounded by performance differences between age groups an equation of performance levels can be expected to result in comparable ERNs for younger and older adults. Third, the R-L theory (Holroyd & Coles, 2002) predicts that the ERN should increase with learning in younger adults and the findings by Nieuwenhuis et al., 2002 suggest that this increase should be smaller for older adults. Given that we succeed in equating learning rates between age groups and given that the ERN is indeed performance-sensitive rather than age-sensitive, we expect that we should find comparable increases of the ERN with learning for both age groups. Finally, the R-L theory predicts that the FRN should decrease over the course of learning since participants rely less on the feedback. However, since in the Nieuwenhuis et al. (2002) study the effects of learning on the FRN were rather small and no age differences in the learning effects were obtained it is necessary to replicate these findings and to explore whether the FRN indeed changes as a function of learning.

2. Methods

2.1. Participants

Forty-two adults participated in the study. The experimental procedure lasted about 3 h and the subjects received 22.5 Euro for participation. One younger adult had to be excluded from data analysis due to technical problems during data acquisition. Three younger and two older adults had to be excluded because they did not commit enough errors to analyze the error-related ERP components over the course of learning. The effective sample consisted of 18 younger adults (mean age = 20.8 years, S.D. = 1.8, 9 females) and 18 older adults (mean age = 68.5 years, S.D. = 2.8, 9 females). According to self-report, all participants were healthy, had a right-hand preference, no color blindness, and no history of neurological or psychiatric problems.

2.2. Stimuli and task

Stimuli were presented in color against a dark grey background on a 17 in. computer screen. The stimulus set consisted of 36 colored images of objects from the Snodgrass and Vanderwart (1980) picture database. The objects belonged to one of the following six categories: clothes, vehicles, fruit, vegetables, furniture, and domestic appliances. The German words 'RICHTIG' ('correct') printed in green and 'FALSCH' ('incorrect') printed in red served as feedback stimuli. When the response deadline was missed, the German words 'ZU LANGSAM' ('too slow') were presented.

We asked our subjects to make a two-choice decision upon presentation of the imperative stimulus and to press one of two response keys (C and M on a standard computer keyboard). They were instructed to infer the stimulus–response mappings by trial and error based on the feedback. In order to increase the motivation of our participants, we told them that they could win between 50 Euro Cents and 450 Euro Cents per block, depending on their performance. At the end of each block, they received feedback about the amount of money they had won during the block. This monetary feedback depended on the mean performance in the 100% validity condition and participants were able to win between

Table 1
Mean accuracy (S.D.) in the three validity conditions (100%, 80%, and 50% validity), displayed separately for the four bins and the two age groups

Bin	Accuracy in % cor	rect, validity				
	Younger adults			Older adults		
	100%	80%	50%	100%	80%	50%
1	0.64 (0.07)	0.60 (0.07)	0.49 (0.04)	0.59 (0.10)	0.53 (0.08)	0.50 (0.03)
2	0.74 (0.11)	0.68 (0.10)	0.49 (0.05)	0.69 (0.13)	0.61 (0.10)	0.50 (0.05)
3	0.77 (0.09)	0.71 (0.11)	0.49 (0.04)	0.71 (0.15)	0.62 (0.13)	0.51 (0.04)
4	0.77 (0.10)	0.71 (0.11)	0.53 (0.05)	0.74 (0.14)	0.65 (0.15)	0.49 (0.04)

50 Euro Cents (mean performance = .50 - .60) and 450 Euro Cents (mean performance = .90 - 1.0).

2.3. Experimental design

The design involved three learning conditions in which we manipulated the validity of feedback. In the 100% validity condition, in which the feedback was always valid, one stimulus (A) was mapped to the right response key and the other stimulus to the left response key (B). If participants responded to A with a right button press, they always received positive feedback, whereas they always received negative feedback if they responded with a left button press (and vice versa for stimulus B). Two other stimuli (C and D) were associated with the 80% validity condition. If participants responded to C with a left button press, they received positive feedback in 80% and negative feedback in 20% of the button presses. If they responded with a right button press, they received negative feedback in 80% of the button presses and positive feedback in 20% of the button presses (and vice versa for Stimulus D). In the 50% validity condition, positive and negative feedback for responses to the stimuli E and F was delivered randomly. The assignment of stimuli and responses was randomized across subjects. For all validity conditions feedback was drawn with replacement, thus the percentage of feedback validity was equal for each bin.

2.4. Trial procedure

At the beginning of each trial a fixation cross was displayed for 500 ms, which was followed by the imperative stimulus for again 500 ms. The response deadline was adapted in 100 ms steps in a range of 600-1000 ms depending on the proportion of time-out trials relative to performed trials. Each participant started with a response deadline of 800 ms. After the first trial the algorithm kept track of the proportion of time-out trials (number of time-out trials relative to the trials performed). If the proportion of time-out trials was smaller than 2%, a response deadline of 600 ms was applied. With steps of 2%, the response deadline increased for 100 ms and reached a maximum deadline of 1000 ms with over 8% of time-out trials. This was done in order to make sure that all subjects produced a similar proportion of time-out trials (M = .02, S.D. = .01, for younger adults, M = .06, S.D. = .04, for older adults), and thereby had a similar opportunity to learn from feedback. For similar deadline procedures see Light, Chung, Pendergrass, and van Ocker (2006) and Rinkenauer, Osman, Ulrich, Müller-Gethmann, & Mattes (2004). Following the key press, a blank screen was displayed for 500 ms and then the feedback stimulus appeared for again 500 ms. Then participants entered the next trial.

2.5. Procedure

First, each participant filled out an informed consent and a short demographic questionnaire. Then, they performed the two psychometric tests. The experiment consisted of one practice block and five experimental blocks. Each block involved a new set of six imperative stimuli, which were drawn randomly (without replacement) from the six stimulus categories (see Section 2.2). In a practice block (150 trials) the participants were familiarized with the experimental setting. Finally, they performed the five experimental blocks. In the experimental blocks, each of the six imperative stimuli was presented 50 times in random order. Thus, each participant performed 300 trials per experimental block, yielding in a total number of 1500 trials.

2.6. Data recording

2.6.1. Behavioral data

An IBM compatible computer was used for collecting reaction times (RTs) and accuracy data. The stimuli were presented on a CTX 17-in. color monitor with a dark grey background. Responses were registered using the response keys C and M on a standard computer keyboard. The experiment was controlled by the Software E-Prime.

2.6.2. Electroencephalogram (EEG) recording

EEG and EOG activity were recorded continuously (Brain Amp DC Recorder and Brain Vision Recorder acquisition software) from 64 Ag/AgCl electrodes (10–10 system) using EasyCaps recording caps. The left mastoid was used as reference and the right mastoid was recorded as an active channel. The EEG and EOG signals were filtered online from DC-70 Hz and digitized at 500 Hz. Vertical and horizontal EOG was recorded from two electrode pairs placed 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 . To increase S-R ratio, the EEG data were offline low-pass filtered with 30 Hz prior to statistical analyses.

2.7. Data analyses

2.7.1. Behavioral data

Responses faster than 167 ms (more than 2 S.D. from the mean reaction time in both age groups) and responses that exceeded the response deadline (younger adults: M = 706 ms, S.D. = 117 ms; older adults: M = 851 ms, S.D. = 126 ms) were excluded from data analysis. The accuracy data was analyzed by averaging mean accuracy rates individually for each subject and validity condition into four bins (of 75 trials), reflecting the four quarters of the learning blocks (see Table 1).¹ The mean accuracy rates (% correct) were then subjected to an analysis of variance (ANOVA). In order to quantify the learning-related changes in the accuracy data, we fitted the learning curves separately for each subject and for the three validity conditions using a linear $(Y = b_0 + (b_1 t))$ and an inverse function $(Y = b_0 + (b_1/t))$, as implemented in SPSS. The slope $(b_1 \text{ or } \beta)$ parameters of the functions that fitted the data most adequately (inverse learning function for the 100% and the 80% validity condition and linear function for the 50% validity condition, see Table 2) were then subjected to the analyses of variance. The mean fit parameters (R^2) and the mean slope parameters (β) of the learning functions are displayed separately for the two age groups and the three validity conditions in Table 2.

2.7.2. ERP data

The EEG epochs were averaged with respect to response and feedback onset to obtain response-locked and feedback-locked ERPs. The response-locked EEG

¹ The accuracy rates in the 80% condition reflect the mean accuracy for the 80% valid trials of this condition. For the 20% invalid trials mean accuracy is lower than chance (M = .33, S.D. = .10 for younger adults; M = .39, S.D. = .14 for older adults) since participants learned to respond according to the dominant (but here incorrect) mapping. For the analysis of the response-locked ERPs valid and invalid trials were aggregated in the 80% condition since there should be no difference between these trial types at the level of the response. For the feedback-locked ERPs only valid trials were averaged in the 80% condition.

Age group	Validity (%)	Accuracy				Response	locked positi	vity		ERN				Feedback-	locked positi	ivity	
		R^2		β		R^2		β		R^2		β		R^2		β	
		lin	inv	lin	inv	lin	inv	lin	inv	lin	inv	lin	inv	lin	inv	lin	inv
Younger	100	.61 (.27)	.77 (.23)	0.04 (.02)	-0.18 (.01)	.47 (.32)	.54 (.33)	0.90 (.80)	-3.48 (3.2)	.41 (.30)	.45 (.30)	0.81 (1.4)	-3.47 (5.3)	.60 (.29)	.62 (.33)	-1.34 (0.7)	5.42 (3.2)
	80	.48 (.32)	.58 (.33)	0.03(.03)	-0.15(.14)	.50 (.33)	.57 (.31)	0.83 (.84)	-3.38 (3.7)	.28 (.35)	.31 (.32)	0.10(1.0)	-0.76(3.5)	.36 (.29)	.42 (.31)	-0.32(1.1)	2.04 (4.5)
	50	.24 (.31)	.22 (.29)	0.01 (.02)	-0.02 (.07)	.44 (.31)	.41 (.31)	0.08 (.79)	-0.37 (2.7)	.38 (.32)	.39 (.32)	0.22 (0.9)	-0.64 (3.0)	.46 (.36)	.40 (.31)	0.08 (1.0)	-0.53 (3.8)
Older	100	.69 (.31)	.78 (.27)	0.05 (.03)	-0.20 (.14)	.52 (.28)	.51 (.30)	0.78 (.80)	-3.14(3.0)	.35 (.32)	.37 (.30)	0.13(0.7)	-0.97 (2.3)	.50 (.36)	.50 (.34)	-0.70 (0.8)	2.62 (3.4)
	80	.61 (.38)	.58 (.35)	0.04 (.04)	-0.15 (.15)	.47 (.30)	.40 (.36)	0.43 (.96)	-1.75(3.0)	.39 (.33)	.39 (.32)	-0.05(1.1)	-0.04(3.8)	.47 (.31)	.43 (.30)	-0.41(0.7)	1.82 (2.7)
	50	.22 (.25)	.16 (.20)	0.00 (.02)	0.00 (.05)	.53 (.34)	.52 (.32)	0.41(.86)	-1.30(3.3)	.34 (.34)	.35 (.33)	0.23(0.8)	-0.73(2.9)	.45 (.28)	.43 (.34)	0.03(0.9)	-0.39(3.7)

Table 2

data was baseline corrected by subtracting the average activity during the 200 ms preceding the imperative stimulus. For the feedback-locked EEG data, the average activity from -100 ms to feedback onset served as baseline.

Prior to averaging, trials containing eye-movement artifacts or other artifacts were excluded from further analysis using a threshold criterion (standard deviations greater than 30 μ V within a sliding window of 200 ms). Remaining vertical and horizontal eye movements were corrected using a modified version of the linear regression approach developed by Gratton, Coles, and Donchin (1983), as it is implemented in EEProbe software (ANT Software).

In a first step, we analyzed the difference waveforms of the response- and feedback-locked ERP components. In the second step we analyzed the ERPs separately for correct and incorrect responses (positive and negative feedback). The response-locked components were measured as the mean amplitudes in a 0–100 ms time window post-response at the electrode FCz. Difference waves were created by subtracting the mean amplitudes for correct responses from the mean amplitudes for incorrect responses. The feedback-locked components were measured as the mean amplitudes for the peak of the FRN at the electrode FCz (260 ms in younger adults and 300 ms in older adults). Difference waves were created by subtracting the mean amplitudes for negative feedback. In a third step, we specifically analyzed the ERN, CRN and FRN by means of peak-to-peak measurements (see Frank, Woroch, & Curran, 2005; Yeung & Sanfey, 2004).

For the peak-to-peak analyses, response-locked as well as feedback-locked EEG data were filtered using a 15 Hz low-pass filter in order to obtain more reliable peak amplitude measures. Following Frank et al. (2005) and Yeung and Sanfey (2004), we defined the ERN and the CRN (in older adults) as the peak-to-peak voltage difference between the most negative peak between -50 and 150 ms around the response and the preceding positive peak. The FRN was defined as the difference between the most negative peak within 200–400 ms and the preceding positive peak. Scalp potential topographic maps of selected ERP results were generated using all electrode positions by means of a two-dimensional spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989) and a radial projection from CZ, which respects the length of the median arcs. Whenever necessary the Geisser–Greenhouse correction was applied (Geisser & Greenhouse, 1958). In these cases the original *F*-value, the adjusted *p*-values, and the Epsilon values are reported.

As for the behavioral data, we averaged the ERPs into four bins reflecting the four quarters of the learning blocks. To quantify the learning-related changes, we fitted each individuals learning curves separately for the three validity conditions using a linear $(Y=b_0 + (b_1t))$ and an inverse function $(Y=b_0 + (b_1/t))$, as for the analysis of the behavioral data. The slope $(b_1 \text{ or } \beta)$ parameters that were estimated using these functions were then subjected to the analyses of variance. The mean fit parameters (R^2) and the mean slope parameters (β) of the learning functions are displayed separately for the two age groups and the three validity conditions in Table 2.

3. Results

3.1. Psychometric tests

The participants performed two psychometric tests, one from the domain of fluid intelligence (the Digit-Symbol Substitution test; adapted from Wechsler, 1982) and one from the domain of crystallized intelligence (the Spot-a-Word test; adapted from Lehrl, 1977). As expected on the basis of prior findings (Verhaeghen & Salthouse, 1997) and the two component model of intelligence (Baltes, Staudinger, & Lindenberger, 1999), younger adults reached a higher score (M = 62, S.D. = 7.7) than older adults (M = 43, S.D. = 9.1) on the Digit-Symbol Substitution test, F(1, 34) = 43.66, p < .0001, which reflects the age-related decline in perceptual speed of processing. In contrast, in the Spot-a-Word test both age groups reached comparable scores, F(1, 34) = 0.42, p < .52 (M = 25, S.D. = 3.1 for



Fig. 1. Accuracy learning curves for the three validity conditions (100%, 80% and 50% validity) displayed separately for younger (left) and older (right) adults. The *y*-axis indicates the accuracy in percent correct; the *x*-axis shows the course of learning averaged into four bins of trials. The β -parameters indicate the steepness of the learning functions (for details, see Section 2.7.1).

younger adults and M = 26, S.D. = 4.1 for older adults), which speaks for age-related stability in semantic knowledge.

3.2. Behavioral data

3.2.1. Accuracy data

The accuracy data (see Fig. 1 and Table 1) was analyzed with an ANOVA design with the factors Age group (young, old), Validity (100%, 80% and 50% validity), and Bin (Bin1, Bin2, Bin3, Bin4). The ANOVA revealed a significant effect of validity, F(2, 68) = 91.24, p < .0001, $\varepsilon = .88$. Contrasts for each of the levels of the factor validity showed a higher accuracy for the 100% compared to the 80% validity condition and for the 80% compared to the 50% validity condition (p's < 0.0001). Moreover, we obtained a marginally significant effect of age group, F(1, 34) = 3.50, p < 0.07 and a marginally significant interaction between age group and validity, F(2, 68) = 2.55, p < .09, ε = .88. Separate ANOVAs for each of the validity conditions revealed significant age differences only in the 80% validity condition, F(1, 34) = 4.94, p < .03, indicating that older adults performed worse than younger adults in this condition (see Fig. 1 see footnote 1).

3.2.2. Learning effects

Of most interest in the present study were the learning effects in the different validity conditions. The analysis showed a significant effect of bin, F(3, 102) = 41.69, p < .0001, $\varepsilon = .78$ and a significant interaction between validity and bin F(6, 204) = 15.69, p < .0001, $\varepsilon = .75$. Separate ANOVAs for each of the validity conditions revealed significant effects of bin for the 100% and the 80% validity conditions (p's < .0001). As expected, no significant effect of bin was found for the 50% validity condition (p = .63), indicating that the accuracy increased over the course of learning only in the 100% and 80% condition (see Fig. 1).

In order to investigate age differences in accuracy during learning we performed three post hoc contrasts making pairwise comparisons for each of the levels of the factor validity separately for the four bins. These contrasts revealed significant differences between all of the validity conditions in all of the bins (p's < .001). However these contrasts did not reveal significant age differences for the 100% condition compared to the 80%

and 50% validity conditions in any of the four bins (p's > .09). In contrast, in line with the age differences in overall accuracy in the 80% validity condition, we found significant age differences for the 80% compared to the 50% condition for the first, second, and third bin (p's < .02). However, at the end of learning (in the fourth bin), no significant age differences were obtained (p = .60). These findings show there are no age differences in accuracy in the 100% validity condition over the course of learning. In contrast, we found age differences in the 80% condition at beginning of learning, but these age differences are absent at the end of learning.

To analyze age differences in the learning curves as a function of validity conditions, we performed an ANOVA on the slope parameters of the learning functions (for details, see Section 2.7.1). The ANOVA involved the factors Age group and Validity. Results revealed a significant effect of validity, F(2, 68) = 43.92, p < .0001, $\varepsilon = .94$. Contrasts for each of the levels of the factor Validity showed higher slope parameters for the 100% and 80% validity conditions compared to the 50% validity condition (p's < .0001). However, only a marginally significant difference was obtained between the 100% and the 80% validity condition (p = .08). Importantly, we did not find age differences in the slope parameters.

To summarize, the analysis of the accuracy data showed learning in the 100% and the 80% validity condition (see Fig. 1). Overall, accuracy increased with feedback validity and age differences were only obtained in the 80% validity condition in which older adults showed a reduced overall accuracy. An analysis of the time course of learning showed that age differences in the 80% condition were most pronounced at beginning of learning but absent at the end of learning. No age differences were obtained for the slope parameters of the learning functions, which were comparable for the two age groups (see Fig. 1). This finding confirms our expectation that the adaptive adjustment of the response deadlines leads to similar learning rates in younger and older adults.

3.2.3. ERP data

In the following response-locked and feedback-locked ERPs will be presented. In a first step, we will examine the ERP difference waves for correct and incorrect responses (positive and negative feedback) in order to parallel our results with those from previous studies (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002, see Fig. 2). In a second step we will analyze the ERP components for correct and incorrect responses (positive and negative feedback) separately. This was done because as Figs. 3 and 6 shows the ERPs varied as a function of validity for correct as well as for incorrect responses (positive and negative feedback). In the third step, we will use peak-to-peak measurements for an additional quantification of the ERN and FRN. We decided for peak-to-peak measurements because the mean amplitude measures of these components are confounded by an overlapping positivity (see Figs. 3 and 6). As for the accuracy data, learning-related effects in the ERP components will be investigated by analyzing the slope parameters of the learning functions (for details, see Section 2.7.2).



Fig. 2. Top: mean accuracy for the three validity conditions separately for younger (left) and older (right) adults. Middle: mean amplitude of the grand average difference wave for correct and incorrect responses at the electrode FCz, displayed for the three validity conditions separately for younger (left) and older (right) adults. Bottom: mean amplitude of the grand average difference wave for positive and negative feedback the electrode FCz, displayed for the three validity conditions separately for younger (left) adults. Error bars indicate standard deviations.

3.3. Response-locked ERPs

Fig. 3 shows the response-locked ERPs for correct and incorrect responses in the three validity conditions (100%, 80% and 50% validity) separately for younger and older adults at electrode FCz. In both age groups incorrect responses were followed by a phasic negativity, the error-related negativity (ERN) that seemed to be larger the more valid the feedback. However, as also apparent from Fig. 3, correct responses were followed by a positivity that also varied as function of the feedback validity, being largest for the 100%, intermediate for the 80% and smallest for the 50% validity condition. This component will be termed response-locked positivity in the following. In older adults, superimposed on this response-locked positivity, a small negativity for correct trials (CRN) can be observed that seemed to get larger the more invalid the feedback. Fig. 3 also displays the topographical distribution of the difference between correct and incorrect responses for all validity conditions and the two age groups. As can be seen in the topographical maps the difference wave is maximal at fronto-central electrodes, which is in line with ERN topographies reported in previous studies (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002).

3.3.1. Difference waves

To analyze the difference waves for the response-locked ERPs we applied an ANOVA with the factors Age group, Validity, and Bin. The analysis revealed a significant main effect of age group, F(1, 34) = 11.19, p < .002, which reflects the larger difference waves for younger compared to older adults (see Fig. 2). Moreover, we obtained a significant main effect of validity, F(2, 68) = 56.58, p < .0001, $\varepsilon = .89$, and a significant interaction between age group and validity, F(2, 68) = 8.20, p < .001, $\varepsilon = .89$. Contrasts for each of the levels of the factor validity showed that the difference wave increased with feedback validity (p's < .0001). This increase was more pronounced for younger than for older adults (p's < .05) (see Fig. 2). The analysis of difference waves also showed significant learning-related effects. We obtained a significant main effect of bin F(3, 102) = 10.09, p < .0001, $\varepsilon = .90$, and a significant interaction between validity and bin, F(6, 204) = 2.81, p < .03, $\varepsilon = .71$. Separate analyses for the factor validity showed that the amplitude of the difference wave increased with learning for the 100% and the 80% validity condition (p's < .008), but not for the 50% validity condition (p = .23). However, the learning-related effects were not significantly larger for younger compared to older adults (p = .30).

3.3.2. Analysis of correct and incorrect responses

In order to examine the extent to which each of the response types contributed to the observed effects in the difference measure, we analyzed the response-locked ERPs separately for correct and incorrect responses. The same ANOVA design as for the difference wave with an additional factor Response type (correct, incorrect) was applied. We found a significant main effect of response type, F(1, 34) = 87.03, p < .0001, and an interaction between age group and response type, F(1, 34) = 11.19, p < .002. Moreover, we also found a reliable interaction between



Younger adults

Fig. 3. Response-locked grand average ERPs for the three validity conditions (100%, 80% and 50% validity) displayed separately for correct (solid lines) and incorrect (dashed lines) trials for younger (top) and older (bottom) adults at the electrode FCz. Tick spacing on the x-axis is 200 ms, arrows indicate the onset of the response and the grey bars highlight the time windows that were used for statistical analysis.

response type and validity, F(2, 68) = 56.58, p < .0001, $\varepsilon = .89$. Separate ANOVAs for the factor response type revealed significant main effects of validity for correct as well as incorrect responses (p's < .0001). These findings show that the responselocked positivity for correct trials as well as the error-related negativity (ERN) both get larger with increasing feedback validity (see Fig. 3). Furthermore, we obtained a significant three-way interaction between age group, validity, and response type, F(2, $(68) = 8.20, p < .001, \varepsilon = .90$. A significant interaction between age group and validity was only obtained for correct responses, F(2, 68) = 7.74, p < .002, $\varepsilon = .81$, but not for incorrect responses (p = .23). To further investigate these age differences on correct responses we performed three post hoc contrasts comparing each of the levels of the factor validity, separately for the two responses types. This analysis revealed significant age differences for correct responses in the 100–50% and the 100–80% contrasts (p's < .02). As can be seen in Fig. 3, these results reflect the fact that the increase of the response-locked positivity with

feedback validity is more pronounced in younger than in older adults.

3.3.3. Learning-related effects in the response-locked positivity

Since the focus of this study was on the time course of learning, we were most interested in interactions involving the factor Bin. Indeed, we obtained significant interactions between response type and bin, F(3, 102) = 10.09, p < .0001, $\varepsilon = .90$ and between validity, response type, and bin, F(6, 204) = 2.81, p < .03, $\varepsilon = .71$. Separate analyses for the factor response type showed a significant main effect of bin, F(3, 102) = 13.89, p < .0001, $\varepsilon = .83$ and a significant interaction between validity and bin, F(6, 204) = 3.94, p < .002, $\varepsilon = 83$, only for correct trials. For incorrect trials, neither the main effect of bin nor the interaction between validity and bin (p's > .29) was significant. Post hoc tests for the factors response type and validity showed significant main effects of bin on correct trials for the 100% and



Fig. 4. Response-locked grand average ERPs over the course of learning (averaged into four bins) for the 100% validity condition displayed separately for correct (solid lines) and incorrect (dashed lines) trials for younger (top) and older (bottom) adults at the electrode FCz. Tick spacing on the *x*-axis is 200 ms, arrows indicate the onset of the response and the grey bars highlight the time windows that were used for statistical analysis.

80% validity conditions (p's < .0001), but not for the 50% validity condition (p = .20). This pattern of results reflects the fact that the response-locked positivity, and not the response-locked negativity (i.e., the ERN), increased with learning (see Fig. 4 for the 100% validity condition).

In order to further analyze the learning-related effects in the response-locked positivity, we subjected the slope parameters of the learning functions (for details, see Section 2) to an ANOVA involving the factors Age group and Validity. The analysis revealed a significant main effect of validity, F(2, 68) = 21.21, p < .0001, $\varepsilon = .93$, however, we neither obtained a significant main effect of age group (p = .21) nor a significant interaction between age group and validity (p = .43). Post hoc contrasts for each of the levels of the factor validity revealed significantly larger slope parameters for 100% and the 80% compared to the 50% validity condition (p's < .0001). The comparison between the 100% and the 80% validity condition was not significant (p = .14). The fact that this pattern of results was obtained for younger adults (p's < .002 for the 100% and 80% validity conditions) as well as for older adults (p's < .02) indicates that both age groups showed comparable learning-related effects in the response-locked positivity for the two learning conditions (see Fig. 5a).

3.3.4. Peak-to-peak analysis of the ERN

The peak-to-peak measures of the ERN were statistically analyzed using an ANOVA with the factors Age group, Validity, and Bin. The ANOVA showed a significant main effect of validity, F(2, 68) = 9.10, p < .002, $\varepsilon = .70$, a significant main effect of bin, F(3, 102) = 2.94, p < .04, $\varepsilon = .87$, and a significant interac-

tion between validity and bin, F(6, 204) = 2.45, p < .04, $\varepsilon = .84$. In separate analyses for the factor validity, we observed a significant main effect of bin only for the 100% validity condition, F(3, 102) = 4.31, p < .01, $\varepsilon = .79$. No significant main effect of bin was obtained for the 80% or 50% validity conditions (p's > .22) (see Fig. 5b). Moreover, it is important to note that the analysis did neither reveal a significant main effect of age (p = .93) nor any significant interactions involving the factor age group (p's > .26). This finding is in line with results from the analysis of the mean amplitude measures and shows that the ERN is not reduced for older compared to younger adults.

3.3.5. Peak-to-peak analysis of the CRN

Since the correct response negativity (CRN) could not be measured reliably in younger adults (see Fig. 3), we focused the analysis on the CRN in older adults. The CRN was analyzed using an ANOVA involving the factors Validity and Bin. The analysis revealed a significant main effect of validity, F(2), 34)=4.41, p < .02, $\varepsilon = .98$. Contrasts for each of the levels of the factor validity showed that the CRN was increased for the 50% compared to the 100% validity condition (p < .01), suggesting that it was larger the more invalid the feedback (see Fig. 3). Moreover, the analysis revealed a significant interaction between validity and bin, F(6, 102) = 3.14, p < .01, $\varepsilon = .78$ and separate ANOVAs for the factor validity showed a significant effect of bin only for the 50% validity condition (p < .02). Post hoc contrasts for each of the bins in the 50% validity condition showed that the CRN was reduced at the end of the learning in the fourth bin $(M = -3.99 \,\mu\text{V}, \text{ S.D.} = 1.78 \,\mu\text{V})$ compared to the third bin $(M = -2.94 \,\mu\text{V}, \text{ S.D.} = 1.84 \,\mu\text{V}) \ (p < .006).$



(a) Response-locked positivity

Fig. 5. (a) Learning curves for the response-locked positivity for the three validity conditions (100%, 80% and 50% validity) displayed separately for younger (left) and older (right) adults. The *y*-axis indicates the amplitude in μ V, the *x*-axis shows the course of learning averaged into four bins of trials. The β -parameters indicate the steepness of the learning functions (for details, see Section 2.7.2). (b) Learning curves for the ERN (measured peak-to-peak) for the three validity conditions (100%, 80% and 50% validity) displayed separately for younger (left) and older (right) adults. The *y*-axis indicates the amplitude in μ V, the *x*-axis shows the course of learning averaged into four bins of trials. The β -parameters indicate the steepness of the learning functions (for details, see Section 2.7.2).

3.3.6. Summary response-locked ERPs

To summarize, most of the results of the difference wave analysis were consistent with previous findings (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002). We found that the difference wave increased with feedback validity and that this increase was larger for younger than older adults. However, a separate analysis of correct and incorrect responses showed that both, the negativity for incorrect responses (ERN) and the positivity for correct responses (response-locked positivity) increased with feedback validity (see Fig. 3). Interestingly, the increase of the responselocked positivity with feedback validity was more pronounced for younger than older adults, suggesting that the elderly may have been less able to differentiate between the validity conditions (see Fig. 3). However, this finding was in part due to the fact that in older adults there was a CRN superimposed on the response-locked positivity (see Fig. 3). The CRN in older adults was larger the more invalid the feedback, which suggests that older adults were less certain about the appropriate response when feedback was invalid. In contrast to several recent findings (Band & Kok, 2000; Falkenstein et al., 2001; Mathewson et al., 2005; Nieuwenhuis et al., 2002; West, 2004), we did not find evidence for a reduction of the ERN in older adults, neither with peak-to-peak nor with mean amplitude measures (see Fig. 3). As expected, the analysis of the difference waves showed learning-related increases for the two learning conditions, but not for the 50% validity condition. However, separate analyses for correct and incorrect responses did not reveal significant learning-related changes in the ERN as measured using mean amplitude values. As shown in Fig. 4, changes over the course of learning were only observed for the response-locked positivity on correct trials (see Fig. 5a). In contrast to the analysis of the mean amplitude measures, the peak-to-peak analysis of the ERN showed a significant learning-related increase, however, only in the 100% validity condition (see Fig. 5b). Taken together, our data suggest that learning-related effects, though present in the ERN (when measured peak-to-peak), are much more pronounced in the response-locked positivity for correct trials.

3.4. Feedback-locked ERPs

Fig. 6 displays the ERPs for positive and negative feedback and the topographical distribution of the difference between both feedback types in the three validity conditions (100%, 80%, and 50% validity) separately for younger and older adults. For younger adults, a pronounced feedback-related negativity (FRN) for negative compared to positive feedback can be observed for all validity conditions. In contrast, for older adults the FRN is strongly reduced for all validity conditions. As illustrated in Fig. 6, for younger adults the difference wave is fronto-centrally distributed and gets larger the more invalid the feedback. In con-



Fig. 6. Feedback-locked grand average ERPs for the three validity conditions (100%, 80%, and 50% validity) displayed separately for positive (solid lines) and negative (dashed lines) feedback for younger (top) and older (bottom) adults at the electrode FCz. Tick spacing on the *x*-axis is 200 ms, arrows indicate the time of feedback onset and the grey bars highlight the time windows that were used for statistical analysis.



Fig. 7. Feedback-locked grand average ERPs over the course of learning (averaged into four bins) for the 100% validity condition displayed separately for positive (solid lines) and negative (dashed lines) feedback for younger (top) and older (bottom) adults at the electrode FCz. Tick spacing on the *x*-axis is 200 ms, arrows indicate the time of feedback onset and the grey bars highlight the time windows that were used for statistical analysis.

trast, for older adults no such effect can be observed (see Fig. 6). Similar to the response-locked ERPs, learning-related effects seem to be most evident in a positivity for positive feedback, which will be called feedback-locked positivity in the following. In contrast, the FRN seems to remain stable over the course of learning (see Fig. 7).

3.4.1. Difference waves

For the analysis of the difference waves we applied an ANOVA involving the factors Age group, Validity, and Bin. The analysis revealed a significant main effect of age group, F(1,(34) = 14.93, p < .0005, a significant main effect of validity F(2, p) $(68) = 8,10, p < .001, \varepsilon = .93$, and a marginally significant interaction between age and validity F(2, 68) = 2.73, p < .08, $\varepsilon = .93$. Contrasts for each of the levels of the factor validity revealed that the difference wave was larger for the 50% validity condition than for the 100% and 80% validity conditions. Separate analyses for the two age groups showed a significant main effect of validity for younger adults (p < .005) but not for older adults (p = .19). These findings suggest that for younger adults the difference wave increased the more invalid the feedback, which was not the case for older adults. Furthermore, the ANOVA showed a significant interaction between validity and bin F(6, 204) = 3.00, p < .01, $\varepsilon = .82$. Separate analyses for the factor validity showed a significant main effect of bin for the 100% and the 80% validity conditions (p's < .04) but not for the 50% validity condition (p = .39). This result indicates that the amplitude of the difference wave decreases with learning in the two learning conditions.

3.4.2. Analysis of positive and negative feedback

To investigate the relative contribution of positive and negative feedback to the observed effects of validity and learning on the difference waves, we examined the ERPs separately for the two feedback types. The feedback-locked components were analyzed using the same ANOVA design as for the difference waves including the additional factor Feedback type (positive, negative). We obtained a significant main effect of age, F(1, 34) = 6.68, p < .01, a significant main effect of feedback type, F(1, 34) = 32.29, p < .0001, and a significant interaction between age and feedback type, F(1, 34) = 15.98, p < .0003. Separate ANOVAs for the two age groups showed a significant main effect of feedback type for younger adults, F(1, 17) = 42.93, p < .0001, but not for older adults (p = .23). As illustrated in Fig. 6, this finding suggests a differential sensitivity to negative and positive feedback between younger and older adults. Consistent with the difference wave analysis, we obtained a significant interaction between feedback type and validity, F(2, 68) = 7.85, p < .001, $\varepsilon = .91$, which reflects the fact that the effects of feedback type were larger the more invalid the feedback (see Fig. 6).

3.4.3. Learning-related effects in the feedback-locked ERPs

Again, we were most interested in the time course of learning in the feedback-locked ERPs. We obtained a significant main effect of bin, F(3, 102) = 8.44, p < .0003, $\varepsilon = .73$, a significant interaction between validity and bin, F(6, 204) = 7.42, p < .0001, $\varepsilon = .90$, and a significant three-way interaction between feedback type, validity, and bin, F(6, 204) = 2.94, p < .02, $\varepsilon = .81$. Most interestingly, separate ANOVAs for the factor feedback type revealed a significant interaction between validity and bin only for positive feedback, $F(6, 204) = 11.62, p < .0001, \varepsilon = .78$, but not for negative feedback (p = .31). Post hoc tests for the factors feedback type and validity revealed significant effects of bin for positive feedback for the 100% and 80% validity conditions (p's < .0005), but not for the 50% validity condition (p = .49). Thus, the feedback-locked positivity decreased with learning in both learning conditions, whereas no learning effect was obtained for the FRN (see Figs. 7 and 8).

In order to quantify the learning-related effects in the feedback-locked positivity we subjected the slope parameters of the learning functions (for details, see Section 2.7.2) to an ANOVA involving the factors Age group and Validity. The analysis showed a significant main effect of validity, F(2, 68) = 20.65, p < .0001, $\varepsilon = .96$ and a significant interaction between age group and validity F(2, 68) = 3.11, p < .05, $\varepsilon = .96$. Separate ANOVAs for the two age groups showed significant effects of validity for younger adults (p < .0001), as well as older adults (p < .009). Post hoc contrasts for each of the levels of the factor validity showed larger slope parameters for the 100% compared to the



Fig. 8. Learning curves for the feedback-locked positivity for the three validity conditions (100%, 80%, 50% validity) displayed separately for younger (left) and older (right) adults. The *y*-axis indicates the amplitude in μ V, the *x*-axis shows the course of learning averaged into four bins of trials. The β -parameters indicate the steepness of the learning functions (for details, see Section 2.7.2).

80% validity condition (p < .0008), as well as for the 80% compared to the 50% validity condition (p < .009) (see Fig. 8). These findings show that the learning-related effects in the feedbacklocked positivity were the larger the more valid the feedback and were more pronounced in younger compared to older adults.

3.4.4. Peak-to-peak analysis of the FRN

The peak-to-peak measures of the FRN (for details, see Section 2) were subjected to an ANOVA involving the factors Age group, Validity, and Bin. This analysis only revealed a significant main of age, F(1, 34) = 10.33, p < .003, which reflects the reduced FRNs for older compared to younger adults. However, neither the main effects of validity or bin nor their interaction or interactions with age turned out to be significant (p's > .15).

3.4.5. Summary feedback-locked ERPs

Taken together, the analyses of the differences waves replicated most of the findings reported in previous studies (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002). Consistent with previous results, we found that for younger adults the amplitude of the difference wave increased the more invalid the feedback, which was not the case for older adults. A separate analysis for positive and negative feedback showed a significant effect of feedback type only for younger adults, but not for older adults. The peak-to-peak analysis showed that this effect was due to the FRN, which was strongly reduced for the elderly in the present study. In contrast to the study of Nieuwenhuis et al. (2002), we found learning-related effects in the difference waves, indicating that the difference between positive and negative feedback decreased with learning. Yet, most importantly, similar to the response-locked ERPs, a separate analysis for positive and negative feedback showed that learning-related effects were only obtained for positive, but not for negative feedback (see Fig. 7). Thus, our data does not speak for learning-related effects in the FRN, but for a reduction of the feedback-locked positivity with learning.

4. Discussion

In the present study we aimed at investigating age-related impairments in reinforcement learning and their potential impact on the ability to adaptively acquire and maintain new behavior. We focused on the role of error processing for learning and the question whether the ERP-correlates of error and feedback processing, the ERN and the FRN, respectively reflect learningrelated changes in younger and older adults. The study was based on a recent neurocomputational account to altered error processing in older age (Nieuwenhuis et al., 2002) that is an extension of the reinforcement learning (R-L) theory that has been proposed by Holroyd and Coles (2002). This account suggests that the impairments of older adults in error processing and learning are the result of age-related changes in the mesencephalic dopamine system.

The goal of the present study was to test the predictions that can be derived from this account and to replicate and extend recent findings on age differences in learning and error processing. We applied a probabilistic learning paradigm in which feedback validity was manipulated in three validity conditions (100%, 80% and 50% validity). By this, we varied the possibility to learn stimulus–response contingencies on the basis of feedback (100% and 80% validity condition) relative to a control condition in which no learning was possible (50% validity condition). In order to equate performance levels in the two age groups we introduced an algorithm that adaptively adjusted the response deadline depending on the number of time outs.

4.1. Behavioral data

We expected that the use of an adaptive response deadline should increase the learning rates in older adults. Indeed, we did not obtain age differences in overall accuracy in the 100% validity condition. Thus we succeeded in equating performance levels between age groups in this condition. Age differences in accuracy only showed up in the 80% validity condition in which older adults performed overall worse than younger adults (see Fig. 1). The analysis of the time course of this effect showed that age differences in the 80% condition were most pronounced at beginning of learning, but absent at the end of learning. An analysis of the learning functions revealed that learning rates were comparable for the two age groups in both learning conditions (see Fig. 1), indicating that older adults were not impaired in learning per se. In contrast, Nieuwenhuis et al. (2002) found age differences in all learning conditions and suggested that older adults might be generally impaired in reinforcement learning. However, one has to keep in mind that in this study both age groups were treated using the same response deadlines (700 ms), which produces a disproportionate time pressure on older adults and impairs their ability to learn. Moreover, the time pressure on older adults can be expected to result in an increased number of time-outs, which lowers the number of trials in which they can learn from feedback. On the other hand, one might argue that the adaptive response deadline procedure has masked age differences in learning since it allows older adults to respond slower than younger adults.² However, it should be noted that slower reaction times in older adults are not a surprising phenomenon that per se points to a more conservative response bias in the elderly. In contrast, general slowing has been shown to be one of the hallmarks of cognitive aging (see Birren & Fisher, 1995; Salthouse, 1996, 2000) and the present study aims at accounting for these general age effects by individually adjusting the response deadlines. Whether or not the adaptive deadline procedure used in the present study has masked age differences in learning cannot be answered conclusively in the present study and is a question of future research. However, our study differed from that of Nieuwenhuis et al. (2002) not only with this respect but also in the kind of feedback provided to the subjects. Nieuwenhuis et al. (2002) used rather ambiguous feedback stim-

² Note that we succeeded in equating accuracy between age groups in the 100% condition, and in the 80% condition at the end of learning. Consequently there are no age differences in accuracy in the present study. This indicates that although there are age differences in reaction times (older adults M = 520 ms, S.D. = 132 ms, younger adults M = 407 ms, S.D. = 95 ms) the present behavioral findings are not confounded by age differences in speed-accuracy trade-offs.

uli (head of a lettuce and a carrot). In contrast, in the present study unambiguous feedback stimuli (German words for 'correct', printed in green and 'incorrect' printed in red) were used, which are easy to encode and process and might have helped older adults in learning.

Taken together, we obtained age differences in overall accuracy in the 80% validity condition, which suggests that older adults are impaired in accuracy when invalid information interferes with learning. The fact that these impairments were most pronounced at the beginning of learning, but absent at the end of learning suggests that it takes older adults longer to acquire the stimulus-response mappings when invalid information occurs. Thus, our behavioral data indicates that the basic reinforcement learning mechanisms are similar in younger and older adults. However, invalid information seems to impair older adults' overall accuracy during learning, which points to the view that they are more susceptible to interference during learning than younger adults. This result is consistent with findings on age differences in reversal learning (Mell et al., 2005), and on agerelated impairments in performance monitoring (Ridderinkhof & Span, 2002).

4.2. Response-locked ERPs

The analysis of the response-locked difference waves replicated most of the findings of previous studies (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002). Consistent with the results of these studies, we found that the difference wave increased with feedback validity and that this increase was larger for younger than for older adults. Moreover, consistent with the previous data, we found learning-related changes in the difference waves for the two learning conditions compared to the 50% validity condition. Yet, in contrast to the existing data (Nieuwenhuis et al., 2002), we did not obtain age differences in the learningrelated effects, which is probably due to fact that performance levels were equated between age groups in the present study.

However, based on difference waves it is not possible to determine how much either of the response types contributed to the observed effects. As illustrated in Figs. 3 and 4, learning-related changes seem to be more pronounced in the response-locked positivity for correct trials than in the ERN. In order to address this important question, we decided to separately analyze the ERPs to correct and incorrect responses. Consistent with the R-L theory (Holroyd & Coles, 2002), we found that the ERN increases with feedback validity, suggesting that the more participants are able to build up expectations on the correctness of their response the larger the ERN (see Fig. 3). Moreover, when the ERN is captured most precisely using peak-to-peak amplitude measures there is also evidence that the ERN increases with learning in the 100% validity condition (see Fig. 5b). In order to investigate the time course of these learning-related effects in the ERN, we performed analyses on the intercepts of the ERN learning functions as well as the ERN in the first bin of the learning blocks (see footnote 4). The outcome of these analyses indicated that the differentiation between the 100% and the other validity conditions in the ERN occurs from the first to second bin of the learning blocks (see Fig. 5b). Thus, our data suggest that the

ability to internally represent an incorrect response (as reflected in the ERN) increases with learning. This increase of the ERN is most pronounced at the beginning of learning from the first to the second bin of the learning blocks, but is only observed if feedback is fully valid.

However, our data also show that not only the ERN but also the response-locked positivity for correct trials increases with feedback validity (see Fig. 3). Most importantly, learning-related changes were much more pronounced in the response-locked positivity for correct trials compared to the ERN (see Fig. 4). In contrast to the ERN that showed a learning-related increase only in the 100% condition, the response-locked positivity increased with learning in both learning conditions (100% and 80% validity). The analysis of the slope parameters showed that the learning effects in the response-locked positivity were larger for the two learning conditions compared to the 50% validity condition. Yet, they were not significantly different between the two learning conditions, which is in line with the findings in the accuracy data.

The learning-related increase in the response-locked positivity fits nicely with neurophysiological findings on reinforcement learning in monkeys (Schultz et al., 1997). These findings show that at the beginning of learning phasic increases in the activity of the dopamine neurons are found for the reward. With learning this positive prediction error propagates back in time and is then elicited by the conditioned stimulus. Thus, the monkey is now able to predict the reward. In line with these findings, it seems reasonable to assume that the increase of the response-locked positivity with learning reflects the increasing ability of participants to predict reward based on the knowledge they acquired through learning. Hence, our data suggest that learning-related changes are reflected in the response-locked ERPs for correct as well as incorrect trials. That is, our findings are consistent with the idea that learning is driven by both, negative prediction errors when the outcome of an action is worse than expected and positive prediction errors when the outcome of an action is better than expected (see O'Doherty et al., 2004; Schultz, 2002; Seymore et al., 2004).

At first glance this interpretation seems inconsistent with the original version of the R-L theory (Holroyd & Coles, 2002), which focuses on the role of negative predictions errors and the ERN for learning. In order to integrate our findings with the R-L theory, one needs to suggest that a positive prediction error as reflected in phasic increases of mesencephalic dopaminergic activity inhibits the ACC, and by this leads to the generation of the response-locked positivity (see Holroyd, 2004; Holroyd, Nieuwenhuis, Yeung, & Cohen, 2003). Yet, similar to the original version of the R-L theory such a view presupposes several assumptions. At first, it suggests that a positive prediction error leads to an inhibition of ACC activity. This is probably difficult to show in humans, however, neurophysiological data from monkeys suggest that the ACC not only plays a role in error processing but also in reward-based motor selection (Matsumoto et al., 2003; Shima & Tanji, 1998) and reward expectancy (Shidara & Richmond, 2002). Thus, there is evidence that the ACC is implicated in reward processing, however, its exact role during reinforcement learning and the nature of its modulation

by dopaminergic input remains to be established. A second assumption would be that the response-locked positivity should be generated in the ACC. Given the poor spatial resolution of the EEG data, this question cannot be answered conclusively in the present study. However, the topographical maps in Fig. 4 show that the reward-related variance in the difference wave is distributed fronto-centrally, which is generally in line with an involvement of the ACC in the generation of the ERN as well as the response-locked positivity. Taken together, there is some evidence that the learning-related changes in the response-locked positivity might reflect modulations of ACC activity.

However, there is also an alternative explanation for this positivity that needs to be explored. According to this alternative account the component reflects the response-locked part of the P300 to the stimulus. Such a view would suggest that the learning-related effects in the response-locked positivity might reflect increasing decision confidence with learning (see Cutmore & Muckert, 1998; Finnigan, Humphreys, Dennis, & Geffen, 2002). This idea receives support by the fact that the positivity increases from frontal to parietal electrodes³ as would be expected for the P300. However, this view would also suggest that the stimulus-evoked P300 should show similar learningrelated changes as the response-locked positivity. That is, the P300 should increase with decision confidence in the two learning conditions but not in the 50% validity condition. Yet, an analysis of the stimulus-locked averages (see footnote 3) showed that in contrast to this prediction the P300 increased with time on task for all validity conditions. This does not support the P300 account since there is no reason why decision confidence should increase in the 50% condition. To summarize, the present data points to the view that the response-locked positivity reflects response-related activity that is potentially driven by the ACC and reflects the increasing ability of participants to predict reward based on the information that has been acquired through learning. These findings provide an important extension to recent theoretical accounts (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002) by showing that reward-related variance in the response-locked ERPs is to a large extent driven by positive learning signals on correct trials.

On the basis of previous findings (Nieuwenhuis et al., 2002), we expected older adults to show reduced ERN components during learning. However, in contrast to this prediction and several other studies on age differences in error processing and the ERN (Band & Kok, 2000; Falkenstein et al., 2001; Mathewson et al., 2005; West, 2004), we did not find evidence for a reduction of the ERN in the elderly in the present study. Interestingly, this was the case for mean amplitudes as well as peak-to-peak measures of the ERN, which suggests that this null effect of aging on the ERN does not depend on the type of measurement. In most of the studies mentioned above (Band & Kok, 2000; Mathewson et al., 2005; Nieuwenhuis et al., 2002; West, 2004), age differences in the ERN were paralleled by age differences in accuracy. However, given that the mismatch model of the ERN (and the R-L theory) suggest that the ERN depends on an intact internal representation of the correct response it seems rather important to avoid accuracy differences when comparing the ERN between age groups. In the present study, we did not find age differences in the ERN, suggesting that it is not age per se, but differences in performance level (in the expectation on the correctness of the response) that drive the ERN (for a similar finding see Pietschmann, Endrass, & Kathmann, 2007). Moreover, in contrast to our hypothesis, there is also no evidence that the ERN develops differentially over the course of learning for older compared to younger adults (see Fig. 4). This is in line with the absence of age differences in the behavioral learning functions. Instead, we obtained age differences in the response-locked positivity. Whereas younger adults showed a pronounced increase in the response-locked positivity with feedback validity this increase was less pronounced in older adults, indicating that the elderly may have been less able to differentiate between validity conditions (see Fig. 3). This is in line with the outcome of an analysis that focused on age differences in the response-locked positivity at the beginning of learning.⁴ This analysis revealed that in the first bin of trials younger adults were already able to differentiate the 100% condition from the other validity conditions at the level of the response, which was not the case for older adults. Since older adults also performed

³ The response-locked positivity increased from anterior to posterior in the 100% validity condition for younger adults (Fz: $M = 3.44 \,\mu$ V, S.D. = 5.44; Pz: $M = 9.62 \,\mu$ V, S.D. = 5.31) and for older adults (Fz: $M = 2.52 \,\mu$ V, S.D. = 3.34; Pz: $M = 4.34 \,\mu$ V, S.D. = 3.79). This is in line with the view that the response-locked positivity reflects stimulus-evoked P300 activity. An inspection of the stimulus-locked averages at the electrode Pz showed that the stimulus-evoked P3 increased with learning for the 100% validity condition (p < .0002) (younger adults: Bin 1: $M = 7.15 \,\mu$ V, S.D. = 4.58, Bin 4: $M = 9.36 \,\mu$ V, S.D. = 5.12; older adults: Bin 1: $M = 3.09 \,\mu$ V, S.D. = 4.02, Bin 4: $M = 4.89 \,\mu$ V, S.D. = 3.9). However, the stimulus-evoked P300 increased for the 50% validity condition as well (p < .001) (younger adults: Bin 1: $M = 5.71 \,\mu$ V, S.D. = 4.49, Bin 4: $M = 7.09 \,\mu$ V, S.D. = 4.83; older adults: Bin 1: $M = 2.64 \,\mu$ V, S.D. = 3.17, Bin 4: $M = 3.48 \,\mu$ V, S.D. = 3.87). This result does not support the view that the response-locked positivity reflects stimulus-evoked P300 activity.

⁴ In order to investigate age differences in the ERPs at the beginning of learning we performed additional analyses on the intercept values of the learning functions, as well as the ERPs in the first bin of the learning blocks. For the ERN (measured peak-to-peak) we obtained significantly larger intercepts for the 100% compared to the other validity conditions (p's < .04). No significant difference was obtained for the 80% compared to the 50% condition (p = .15). Moreover, we found no significant interaction between age group and validity (p = .19). Since the analysis of the ERN in the first bin did not show a significant effect of validity (p = .10) these findings suggest that the differentiation between the 100% and the other validity conditions in the ERN occurs from the first to the second bin of trials. However, these learning-related changes do not seem to be affected by age. For the response-locked positivity we found a significant effect of validity (p < .0001) and an interaction between age group and validity (p < .003) in the intercepts of the learning functions. Post hoc contrasts for each of the levels of the factor validity showed larger intercepts for the 100% compared to the 80% and the 80% compared to the 50% condition for younger adults (p's < .002). For older adults a significant difference in the intercepts was only obtained for the 100% compared to 50% condition (p < .005). In the first bin a significantly larger response-locked positivity was obtained for the 100% compared to the other validity conditions for younger adults (p's < .01), but not for older adults (p's > .37). This pattern of results is in line with the fact that older adults performed somewhat (although not significantly) worse than younger adults at the beginning of learning (see Fig. 1) and might suggest that the elderly learned slower than younger adults. No effects of validity were obtained for the feedback-locked positivity at the beginning of learning.

somewhat (although not significantly) worse than younger adults in the first bin, this might indicate that it took them longer to build up an internal representation of the correct response.

The interpretation of age differences in the response-locked positivity is somewhat complicated by the fact that there was a correct response negativity (CRN) in the elderly that was superimposed on this positivity (see Fig. 3). There is an ongoing debate on the question of what the CRN reflects (see Coles, Scheffers, & Holroyd, 2001; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000; Vidal, Burle, Bonnet, Grapperon, & Hasbroucq, 2003). Yet, recent data suggests that the CRN is related to response conflict (Bartholow et al., 2005; Kray, Eppinger, & Mecklinger, 2005) and is enhanced in younger adults when the demands on conflict monitoring are increased (Eppinger, Kray, Mecklinger, & John, 2007). In contrast, in older adults the CRN has been shown to be enhanced independently of the degree of response conflict, which suggests that they are impaired in the flexible adaptation to changing demands on conflict processing (Eppinger et al., 2007). Interestingly, similar findings have been obtained in patients with lesions in the lateral PFC, suggesting that the CRN is related to the structural integrity of the prefrontal cortex (Gehring & Knight, 2000). In the present study, the CRN was increased in older adults the more invalid the feedback, being larger for the 50% compared to the 100% validity condition. Moreover, in the 50% condition the CRN in older adults decreased at the end of the learning block. This suggests that at the end of learning older adults were able to differentiate the learning conditions and became aware of the fact that no learning was possible in the 50% condition. Taken together, the present data is consistent with the idea that the CRN reflects enhanced response conflict in older adults in situations in which they are uncertain about the outcome of their response.

4.3. Feedback-locked ERPs

As illustrated in Fig. 6, the most obvious result from the feedback-locked analysis is the strongly reduced FRN component for older compared to younger adults. As the difference wave analysis revealed a main effect of age group, separate analyses for positive and negative feedback indicated that it was the FRN and not the feedback-locked positivity that was reduced in the elderly. This result was confirmed by the peak-to-peak analysis, indicating that the reduction of the FRN in older adults cannot be attributed to a larger interindividual variability of component latency. Thus, our data suggest that although older adults learned comparably to younger adults they showed reduced activity of the structures involved in the processing of negative feedback (presumably the ACC, but also the orbitofrontal cortex; see O'Doherty, Kringelbach, Rolls, Hornak, & Andrews, 2001; Rolls, 2000). This result is somewhat surprising given the absence of age differences in the ERN in the present study and may point to a functional dissociation of both components (see Nieuwenhuis, Slagter, von Geusau, Heslenfeld, & Holroyd, 2005). Similar findings on an asymmetry in the processing of valence information in older adults have been obtained in research on episodic memory and decision making (Charles,

Mather, & Carstensen, 2003; Mather & Johnson, 2000). These findings have been interpreted within the framework of the socioemotional selectivity theory of aging, which proposes that the ratio between positive and negative affect improves through adulthood and leads to what is called a "positivity effect" (for a review, see Mather & Carstensen, 2005). The idea is that older adults focus more on emotion regulation and implement cognitive control mechanisms that enhance positive and diminish negative information. Interestingly, recent fMRI findings from Larkin et al. (2007) using a gain and loss anticipation task support this view and suggest that older adults are less affected by potential losses than younger adults, whereas both age groups are equally excited by potential gains. To our knowledge, the present data provides the first electrophysiological evidence for an agerelated asymmetry in valence processing and by this supports the idea of a positivity effect in older adults. Given the absence of age differences in the ERN in the present study, which suggests that error processing is not impaired per se in the elderly, it seems reasonable to assume that older adults might focus less on negative feedback in order to maintain self-esteem and positive affect in higher age.

Along with the age differences in the FRN, we also found effects of validity on the feedback-locked ERPs. For younger adults the difference between positive and negative feedback increased the more invalid the feedback (see Fig. 2) and in line with previous data (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002), this effect showed a fronto-central distribution (see Fig. 6). For older adults no effect of feedback validity on the difference waves was observed. In the Nieuwenhuis et al. (2002) study, older adults, in contrast to younger adults, showed an increase of the difference wave the more valid the feedback. Nieuwenhuis et al. (2002) explained this effect by assuming that the amount of attention that older adults pay to a feedback might depend on their subjective probability of committing an error. However, our data showed a small increase of the difference wave the more invalid the feedback for older adults, which is more in line with the data obtained in younger adults (see Fig. 2). On the one hand, this result might be due to the fact that in the present study older adults performed similarly as younger adults and therefore most likely did not differ from younger adults with respect to their subjective probability of committing an error. On the other hand, this effect could also be a result of the different types of feedback stimuli that were used in the two studies. As mentioned above, Nieuwenhuis et al. (2002) used feedback stimuli that might have been difficult to disambiguate for older adults. In contrast, in the present study, unambiguous feedback stimuli were used, which were easy to encode and process.

Apart from these inconsistencies in the findings in older adults the overall pattern of results in the difference wave analysis is in line with the data from Holroyd and Coles (2002) and Nieuwenhuis et al. (2002). However, in contrast to the predictions of the R-L theory (Holroyd & Coles, 2002), the peakto-peak analysis showed that the FRN was not modulated by feedback validity. This suggests that it was not the FRN, but the feedback-locked positivity (on positive feedback trials), which was affected by feedback validity. This view receives further support from a comparison of the 20% invalid trials with the 80% valid trials of the 80% validity condition.⁵ For this comparison the R-L theory would suggest that the FRN should be much larger for the 20% invalid trials since in that condition a strong expectation for positive feedback is violated. Indeed, the analysis showed that there was a marginally significant difference between the FRN for valid compared to invalid negative feedback. However, the effect was much more pronounced in the positivity for positive feedback, which was significantly larger for the 20% invalid trials compared to the 80% valid trials. Moreover, this effect did not interact with age, which suggests that older adults did not differ from younger adults in the way they attended to valid or invalid positive feedback in the 80% condition. Our data is nicely consistent with recent findings by Potts, Martin, Burton, and Montague (2006) that showed that a similar feedback-related positivity, the P2a, is elicited by unpredicted rewards. They have proposed that this positivity is generated by dopaminergic input to the medial frontal cortex. This is supported by the medial frontal topography of the difference wave in younger adults in the present study and by the fact that this effect increases the more invalid the feedback, which indicates that the reward-related variance is fronto-centrally distributed (see Fig. 6). Taken together, these findings suggest that the feedbacklocked positivity on rewarding (positive) feedback trials is the larger the more unpredicted the reward, that is, the more invalid the feedback and might be elicited by dopaminergic input to the medial frontal cortex.

However, as for the response-locked positivity, an alternative account to these effects would suggest that the feedback positivity reflects a P300-like modulation. According to such a view one would suggest that the increase of the feedback positivity the more invalid the feedback might reflect the amount of information that is extracted from the feedback stimulus (Donchin & Coles, 1988; Johnson, 1986). The argumentation would then be that the more participants are able to internally represent the correct response, the less they have to rely on the feedback and the smaller the P300. However, in the present study validity effects are confounded with probability effects since correct feedback gets more frequent the more valid the feedback. Hence, one might suggest that learning-related effects in this study might be obscured by probability effects in the P300. In a recent study Gibson, Krigolson, and Holroyd (2006) addressed this question and showed that the reward-related variance in the ERP difference wave for positive and negative feedback is fronto-centrally distributed across probabilities. This questions the P300 account and favors the idea that the feedback-locked positivity reflects a reward-related modulation of activity in the medial frontal cortex.

Since the focus of this study was on the electrophysiological correlates of learning, we were most interested in changes of the feedback-locked ERPs with learning. According to the R-L theory (Holroyd & Coles, 2002), we expected that the FRN should decrease with learning, since the participants rely less on the external error feedback. Indeed, the difference wave analysis confirmed this prediction and showed that for the two learning conditions the amplitude of the difference wave decreased with learning. However, similar to the response-locked ERPs, in a separate analysis for the two feedback types, we found changes with learning only for positive but not for negative feedback (see Fig. 7). This finding is supported by the outcome of the peakto-peak analysis that did not reveal learning-related changes in the FRN. An analysis of the learning functions of the feedbacklocked positivity showed larger learning-related effects for the 100% compared to the 80% validity condition and for both learning conditions compared to the 50% condition (see Fig. 8). Moreover, these effects seem to be more pronounced in younger compared to older adults (see also Fig. 8). This fits nicely to the learning effects in the accuracy data and suggests that older adults were less able to disengage from processing positive feedback during learning. Thus, our data suggest that the more participants learn, the smaller the feedback-locked positivity. In line with the findings of Potts et al. (2006), one interpretation of the learning effects in the feedback-locked positivity would be to assume that the component reflects a positive prediction error that decreases the more participants are able to internally represent the correctness of the response (see Holroyd, 2004; Holroyd et al., 2003). Recent data from Cohen, McMorris, and Ranganath (2006) support this view by showing that as reward expectation increases (and the positive prediction error decreases) during learning, the feedback-locked positivity also decreases. Consistent with these ideas, our data points to the view that with learning participants rely less on the external feedback since they are increasingly able to internally predict the reward.

5. Conclusion

Taken together, the present study revealed several important new findings that extend current views on reinforcement learning, error processing, and aging (Holroyd & Coles, 2002; Nieuwenhuis et al., 2002). First, our data showed that learning-related changes were much more pronounced in the response-locked positivity for correct trials than in the ERN. This provides an important extension to recent findings since it suggests that the reward-related variance in the response-locked ERPs is to a large extent driven by positive learning signals on correct trials. Such a view is consistent with several studies that showed that learning is driven by phasic increases in dopaminergic activity when the outcome of an action is better (and not worse) than expected. Also in line with this view we did not find evidence for a learning-related decrease of the FRN.

⁵ In order to investigate the effects of expectancy violations on the feedbacklocked ERPs we compared the 20% invalid trials with the 80% valid trials of the 80% validity condition. The difference wave analysis showed a marginally significant difference between invalid and valid trials (p < .06). Separate analyses for positive and negative feedback revealed a larger feedback-locked positivity for invalid compared to valid positive feedback (p < .004). This was not the case for negative feedback (p = .90). The peak-to-peak analysis showed a marginally significant difference between invalid and valid trials (p < .07). In neither of these analyses significant interactions with age were obtained (p's > .13). Taken together, these findings are consistent with the other results of the present study in showing that differences between validity conditions are most pronounced on positive feedback trials. Since there is no interaction with age group there is no reason to assume that older adults differed from younger adults in the amount of information they paid to the feedback stimulus on valid compared to invalid trials of the 80% validity condition.

However, learning-related effects were obtained for a feedbacklocked positivity. The decrease of the feedback positivity with learning suggests that the more participants are able to internally predict the reward, the less they rely on the feedback. Second, in contrast to the findings of Nieuwenhuis et al. (2002) and several other studies (Band & Kok, 2000; Falkenstein et al., 2001; Mathewson et al., 2005; West, 2004), we did not find evidence for an age-related reduction of the ERN when controlling for performance differences between age groups. This questions the view that older adults are generally impaired in error processing and points to the importance of equating performance levels when comparing ERPs between different age groups. Third, we observed a pronounced reduction of the FRN in the elderly, which suggests that older adults are less affected by negative feedback and by this points to an age-related asymmetry in the processing of feedback valence.

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