

Research report

Electrophysiological reward signals predict episodic memory for immediate and delayed positive feedback events

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ABSTRACT

Previous research has shown that in reinforcement learning, the hippocampus is involved in the processing of feedback when it is delayed for several seconds. Also, better recognition memory has been reported for temporally delayed than for immediately presented feedback pictures. Event-related potential (ERP) studies have found that feedback delay affects the amplitude of the feedback-related negativity (FRN), and there is evidence suggesting that the FRN is modulated by declarative learning. In the present study, a subsequent memory paradigm was used to investigate the effects of feedback delay on the incidental encoding and subsequent retrieval of feedback events. Participants used immediate or delayed feedback to learn associations between Chinese characters and reactions. Unrelated pictures were presented simultaneously with positive or negative feedback, and recognition memory for the pictures was tested in a surprise memory test. Behaviorally, memory was better for positive than negative feedback pictures, but there was no effect of feedback delay on memory performance. Electrophysiological activity during the FRN time window was found to predict subsequent memory for positive, but not negative feedback pictures, suggesting that positive reward prediction errors as reflected in the FRN contribute to successful memory encoding. Consistent with previous studies, the FRN was reduced for delayed feedback, but only in a condition in which feedback was useful for learning. Behavioral and ERP estimates of familiarity and recollection support the view that positive feedback enhanced memory mainly by boosting familiarity-based recognition.

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1. Introduction

Reinforcement learning refers to an adaption of behavior following the experience of positive and negative outcomes of actions, a learning mechanism that depends on the nigrostriatal dopamine system. The firing rates of dopamine neurons located in the midbrain show phasic increases and decreases as a response to unexpected rewards and punishments, thereby constituting reward prediction error (RPE) signals (Schultz et al., 1997) that are used by the striatum to facilitate or inhibit actions associated with positive or negative outcomes, respectively. Apart from striatal regions, the main targets of dopaminergic projections, RPE signals are also conveyed to the hippocampus (Gasbarri et al., 1997), a brain structure crucial for declarative memory (Eichenbaum, 2004). Consequently, modulations of declarative memory by dopamine signals have become a focus of research (see Shohamy and Adcock, 2010, for a review). For example, superior memory for

information that predicts reward is associated with enhanced activation in the midbrain and the hippocampus (Adcock et al., 2006; Wittmann et al., 2005).

In studies examining event-related brain potentials (ERPs) in reinforcement learning tasks, the feedback-related negativity (FRN) has been identified as a component that is modulated by feedback valence and expectancy (Miltner, Braun and Coles, 1997; see Walsh and Anderson, 2012, for a review). The FRN is a fronto-central negativity that is maximal between 250 and 300 ms after feedback onset. The reinforcement learning theory (RL-ERN theory, Holroyd and Coles, 2002) assumes that the FRN is generated by the dorsal anterior cingulate cortex (dACC) and reflects an inhibition or disinhibition of motor neurons caused by dopaminergic RPE signals. A recent modification of the RL-ERN theory emphasises that the scalp-recorded FRN is the result of the superposition of an N200 component and a positivity following positive outcomes (feedback correct-related positivity, fCRP; Holroyd, 2004; Holroyd et al., 2008; reward positivity; see Proudfit, 2015, for a review). Whereas the N200 is generally elicited by unexpected, task-relevant events (including unexpected negative feedback; see Folstein and Van Petten, 2008, for a review),

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the fCRP/reward positivity is related to the processing of unexpected positive feedback or reward. In the following, we will continue using the term FRN as a description for an ERP correlate of feedback processing that reflects dopaminergic RPE signals, keeping in mind that probably more than one ERP component (a negativity followed by a positivity to positive feedback) contribute to the FRN.

The FRN can be conceived as an expression of the nondeclarative reinforcement learning system. In support of this view, it has been found that the FRN amplitude does predict implicit (nondeclarative), but not explicit (declarative) learning outcomes (Chase et al., 2011). On the other hand, there is evidence implicating that the FRN is related to declarative types of learning outcomes. Arbel et al. (2013) found that the FRN elicited by positive, but not negative feedback predicted successful recognition of associations between novel objects and nonwords. Their results dovetail with an fMRI study by Tricomi and Fiez (2012), who compared feedback processing in a declarative learning task while controlling for the information value of the feedback and found that activity in the caudate nucleus predicted higher confidence judgements on a test that assessed learning success, but only for word pairs that had been paired with positive feedback. Thus, successful declarative learning from positive feedback may be reflected by the FRN as well as by activity in striatal regions, which is in line with studies that have localized the generators of the fCRP/reward positivity in the basal ganglia (Foti et al., 2011).

Interestingly, it has been found that the critical role of the nigrostriatal dopamine system for reinforcement learning depends on the temporal characteristics of the outcome. Using two learning conditions with immediate and delayed feedback in an associative learning task, in amnesic patients with medial temporal lobe (MTL) lesions and Parkinson's disease (PD) patients, Foerde et al. (2013) reported a double dissociation. Amnesic patients were selectively impaired when feedback was delayed for several seconds and PD patients showed the reversed pattern. These findings support the view that the nigrostriatal dopamine pathways are critically involved in the learning from immediate feedback whereas the MTL is relevant for learning from feedback that is provided with a temporal delay. Of note, other studies have found evidence in support of the view that feedback learning is generally accomplished by a cooperation between the striatum and the hippocampus (Dickerson et al., 2011; Dickerson and Delgado, 2015). In an fMRI study with healthy young adults, Foerde and Shohamy (2011, Experiment 2) examined BOLD signals during the processing of immediate and delayed feedback. They found that RPEs derived from a standard reinforcement learning model were correlated with hippocampal and striatal BOLD signals, irrespective of feedback timing (see Dickerson et al., 2011, for a similar finding in a feedback learning task with immediate feedback). Activity in the striatum was sensitive to immediate and, to a lesser degree, delayed feedback. In contrast, the hippocampus was exclusively involved in the processing of delayed feedback. Foerde and Shohamy also predicted that hippocampal feedback processing should also be reflected in stronger episodic memory traces for the feedback event. They tested this prediction by presenting pictures of indoor and outdoor scenes to code negative and positive feedback in a delayed and immediate feedback condition of an associative learning task. After the learning task, a surprise memory test for the feedback pictures was conducted. Consistent with their prediction, delayed feedback pictures were remembered better than immediate feedback pictures.

Of note, investigating the effects of dopaminergic RPE signals on declarative memory requires controlling for motivational and attentional confounds associated with intentional learning. To

illustrate this, in the above-mentioned study by Arbel et al. (2013), participants could use positive and negative feedback to learn associations between novel objects and nonwords. On every trial, one novel object was presented together with four nonwords. Participants had to learn the association between the object and the nonword by choosing one of the nonwords and received either positive or negative feedback for their choice. Since each novel object was repeated 20 times together with the same four nonwords, participants were reinforced several times for remembering the correct association between a novel object and a nonword. Such confounds associated with intentional learning can be avoided by the use of incidental learning paradigms (e.g. Murayama and Kitagami, 2014; Wittmann et al., 2005). For instance, examining declarative memory for task-irrelevant feedback events in an incidental learning paradigm offers the opportunity to explore the impact of dopaminergic RPE signals on declarative memory at the time point of their occurrence, without the confound of learning intention and the ensuing motivational states. This procedure was employed in the present study.

The present study

Even though the brain regions involved in feedback processing and superior later episodic memory have been disclosed (Davidow et al., 2016; Foerde and Shohamy, 2011), it is less clear which aspect of feedback processing is relevant for successful memory encoding of the feedback event, what the temporal characteristics of these processes are, and how they are reflected on the electrophysiological level. In addition, it has not been systematically explored how feedback delay affects recognition memory for feedback events and its subprocesses, familiarity and recollection. Therefore, the present study aimed at investigating how feedback timing affects the incidental encoding and subsequent retrieval of feedback events. Participants performed an associative learning task, in which they used feedback to learn associations between Chinese characters and responses. Feedback arrived with a short or long temporal delay, and task-irrelevant pictures were presented together with the feedback. For half of the characters, feedback was presented randomly, so that participants equally often received positive and negative feedback (50% feedback validity). For the other characters, feedback was valid in 70% of all trials. Thus, learning the associations between characters and reactions was only possible in the 70% feedback validity condition. The 50% feedback validity condition served as a control condition, making sure that differences regarding feedback valence or delay were not affected by differences in the frequency of positive or negative feedback (see Eppinger et al., 2008; Peterburs et al., 2016, for studies that used a similar approach). After the learning task, recognition memory for the pictures was tested in a surprise memory test. To explore whether successful memory encoding modulates the electrophysiological correlate of feedback processing (i.e., the FRN) a subsequent memory paradigm was used. In this paradigm, EEG activity recorded during the learning phase was sorted according to whether a picture was subsequently remembered or forgotten; see Paller and Wagner, 2002, for a review). We hasten to clarify that we do not take the FRN as a direct reflection of memory encoding processes, but rather as an electrophysiological measure of dopaminergic RPE signals. These signals originating from the midbrain are conveyed to the striatum, where they are used to guide reinforcement learning, and also to the hippocampus, where they promote the formation of new memory traces. Thus, while many studies have shown that the FRN is related to nondeclarative (striatal) learning outcomes (e.g. Bellebaum and Daum, 2008; Chase et al., 2011; Eppinger et al., 2008; Ernst and Steinhauser, 2012; Holroyd and Coles, 2002), it is an intriguing question

whether the FRN predicts declarative memory for feedback events. This would be the case when a subsequent memory effect (SME) occurs that resembles in its spatiotemporal characteristics the FRN. In other words: Finding that the FRN amplitude differs between subsequently remembered and forgotten pictures would indicate that the processes reflected by the FRN also contribute to successful memory formation. Furthermore, several studies have reported a reduction of the FRN for temporally delayed feedback (Arbel et al., 2017; Peterburs et al., 2016; Weinberg et al., 2012; Weismüller and Bellebaum, 2016). Of note, Peterburs et al. (2016) found that FRN amplitudes measured in the original waveforms (FRN_{peak}) and FRN amplitudes measured in the negative minus positive feedback difference waves (FRN_{diff}) were differentially affected by feedback delay. Whereas the FRN_{diff} amplitude showed a linear decrease with increasing feedback, the FRN_{peak} amplitude linearly increased with increasing feedback delay. The linear decrease of the FRN_{diff} with increasing feedback delay presumably reflects a gradually decreasing involvement of the dopaminergic system in feedback processing. Consistent with the involvement of the MTL in delayed feedback processing (Foerde and Shohamy, 2011), Peterburs et al. (2016) argued that the increased FRN_{peak} amplitudes elicited by delayed feedback may be indicative of a more declarative type of feedback processing that is related to the violation of explicit outcome expectations. On the basis of these results we expected to find similar modulations of the FRN amplitude as a function of feedback delay.

Effects of feedback processing on memory retrieval were explored from a dual-process view of recognition memory, which assumes that two distinct sub-processes (familiarity and recollection) contribute to recognition memory (Yonelinas, 2002). Whereas familiarity refers to a context-free memory strength signal, recollection is a threshold process that includes retrieval of contextual details. There are several ways of estimating both retrieval sub-processes on the basis of behavioral measures (see Yonelinas and Parks, 2007, for an overview). In ERP studies, familiarity and recollection are associated with qualitatively different effects, i.e., the early mid-frontal old/new effect (also denoted as FN400) and the late left-parietal old/new effect, respectively (see Friedman and Johnson, 2000, and Rugg and Curran, 2007, for reviews; see also Paller et al., 2007, for an alternative view). In a study that explored recognition memory for objects that were associated with rewards or losses in younger and older adults, Eppinger et al. (2010) found that superior memory for rewarded objects was associated with an early mid-frontal old/new effect in both age groups. This effect was not obtained for objects learned with negative feedback. Younger adults also exhibited a late left-parietal old/new effect that did not differ as a function of feedback valence. This pattern of results suggests that positive outcomes can selectively boost familiarity-based recognition without affecting recollection. Thus, in the present study, recognition ERPs were used to obtain electrophysiological measures of familiarity and recollection. In addition confidence ratings during recognition memory studies were used to derive behavioural estimates of familiarity and recollection. Based on the results by Eppinger et al. (2010) we expected that a memory advantage for positive feedback events should be accompanied by enhanced familiarity

and therefore be associated with larger behavioral and electrophysiological estimates of familiarity. Consistent with studies showing that the processing of reward can enhance memory for unrelated information that is presented in temporal simultaneity or proximity to the reward or feedback stimulus (Davidow et al., 2016; Murayama and Kitagami, 2014), recognition memory for pictures presented together with the feedback was also expected to benefit from hippocampal processing of temporally delayed feedback (Foerde and Shohamy, 2011).

2. Results

2.1. Behavioral data

2.1.1. Learning phase

Fig. 1 shows the mean percentages of correct responses during the course of the learning phase separately for the immediate and delayed feedback conditions. The analysis of the correct responses yielded a significant main effect of Block, $F(4,88) = 3.01$, $p < .05$, $\eta_p^2 = .12$, and a significant linear trend, $F(1,22) = 11.81$, $p < .001$, $\eta_p^2 = .35$, indicating that there was a linear increase of correct responses across the five blocks of the learning phase. There was no main effect of Delay, $F(1,22) = 2.74$, $p = .11$, $\eta_p^2 = .11$, suggesting that participants learned equally well from immediate and delayed feedback.

2.1.2. Recognition memory test

The mean percentages of Pr scores and high-confidence Pr scores are given in Table 1 as a function of FB Validity, Valence, and Delay. The analysis of Pr scores yielded a significant main effect of Valence, $F(1,22) = 8.92$, $p < .01$, $\eta_p^2 = .29$, reflecting better recognition of positive than negative pictures. No other effect approached significance (all p -values $> .22$). Similarly, high-confidence Pr scores showed a significant main effect of Valence, $F(1,22) = 4.89$, $p < .05$, $\eta_p^2 = .18$, driven by higher scores for positive than for negative pictures.

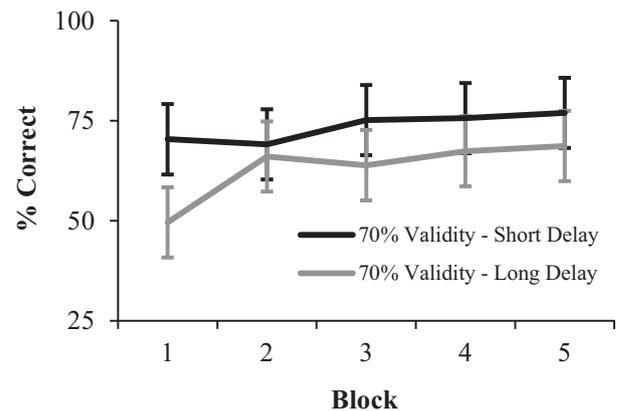


Fig. 1. Percentages of correct responses in the learning phase as a function of FB Delay and Block. Error bars indicate 95% confidence intervals according to Jarmasz and Hollands (2009) for the Delay by Block interaction.

Table 1
Mean percentages (standard errors) of Pr and high-confidence Pr scores.

	50% FB Validity				70% FB Validity			
	Short FB Delay		Long FB Delay		Short FB Delay		Long FB Delay	
	Positive FB	Negative FB	Positive FB	Negative FB	Positive FB	Negative FB	Positive FB	Negative FB
Pr	11.5 (2.4)	11.4 (3.1)	15.9 (3.1)	10.3 (2.4)	14.3 (2.8)	11.1 (2.9)	15.8 (2.8)	11.4 (3.1)
High-con. Pr	14.1 (2.3)	12.5 (2.8)	14.2 (2.5)	11.7 (1.8)	15 (2.7)	10.6 (2.6)	15.1 (2.9)	11.5 (2.9)

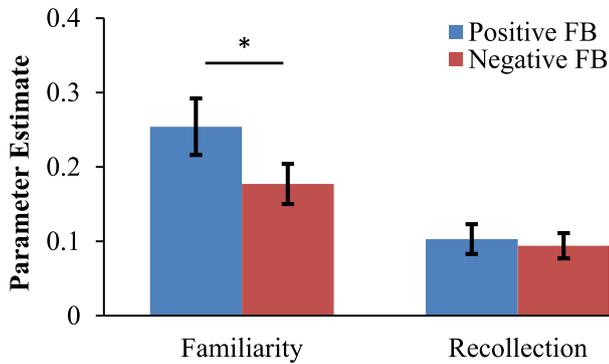


Fig. 2. Familiarity and recollection parameter estimates for positive and negative feedback pictures. Error bars represent standard errors of the mean.

The analysis of the DPSD model parameters, as illustrated by Fig. 2, showed that positive pictures were associated with larger estimates of familiarity than negative pictures, $t(22) = 2.10$, $p < .05$, $d = 0.47$, whereas no difference between positive and negative pictures was found for recollection, $t(22) = 0.80$, $p = .43$, $d = 0.10$.

2.2. Electrophysiological data

2.2.1. ERPs in the learning phase

2.2.1.1. FRN analysis. Negative minus positive feedback difference waves are shown as a function of FB Validity and Delay in Fig. 3. The corresponding mean and peak amplitude measures are displayed in Table 2. FRN_{diff} peak amplitudes were submitted to a

two (Validity: 50%, 70%) by two (Delay: Short, long) ANOVA which yielded no significant main effects, but a significant Validity by Delay interaction, $F(1,22) = 10.38$, $p < .01$, $\eta_p^2 = .32$. In the 70% validity condition, peak amplitudes were significantly more negative in the short delay than in the long delay condition, $t(22) = -2.98$, $p < .01$, $d = -0.56$. In the 50% validity condition, the short and long delay conditions were not different from each other, $t(22) = 1.40$, $p = .18$, $d = 0.42$.

Analogous to the peak amplitudes, an ANOVA for the FRN_{diff} mean amplitudes yielded no main effects, but a significant Validity by Delay interaction, $F(1,22) = 11.91$, $p < .01$, $\eta_p^2 = .35$. For the 70% validity condition, mean amplitudes in the short delay condition were more negative than in the long delay condition, $t(22) = -3.00$, $p < .01$, $d = -0.67$, whereas for the 50% validity condition, there was no significant difference between the short and long delay conditions, $t(22) = 1.80$, $p = .09$, $d = 0.57$. Taken together, the pattern of results was statistically the same for mean amplitude and peak amplitude measures. In the 70% validity condition, in which learning was possible, the FRN_{diff} was attenuated for long relative to shortly delayed feedback. In contrast, in the 50% validity condition, where learning was not possible, the FRN_{diff} did not differ significantly between long and relatively immediate feedback.

The original grand average waveforms are shown as a function of FB Validity, Delay, and Valence in Fig. 4. The corresponding FRN_{peak} amplitudes are displayed in Table 2. A two (Validity: 50%, 70%) by two (Delay: Short, long) by two (Valence: Positive, negative) ANOVA for the FRN_{peak} amplitudes yielded a significant main effect of Delay, $F(1,22) = 15.08$, $p < .001$, $\eta_p^2 = .41$, driven by higher (more negative) amplitudes for long than for shortly delayed feedback. No further effects reached significance, all p -values $> .28$.

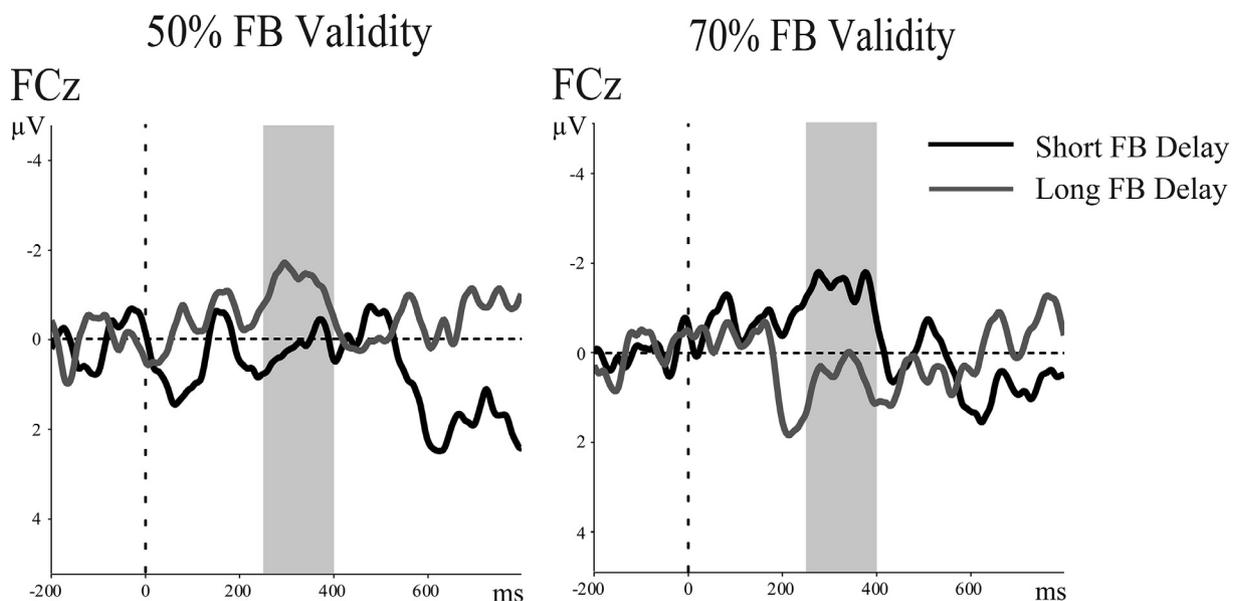


Fig. 3. Negative minus positive feedback difference waves at electrode site FCz. The time window for the FRN_{diff} analysis (250–400 ms) is marked in grey.

Table 2

Means (standard errors) of FRN_{diff} and FRN_{peak} amplitudes.

	FRN _{diff}				FRN _{peak}			
	50% FB Validity		70% FB Validity		50% FB Validity		70% FB Validity	
	Short FB Delay	Long FB Delay	Short FB Delay	Long FB Delay	Short FB Delay	Long FB Delay	Short FB Delay	Long FB Delay
Mean Amplitude	0.15 (0.57)	-1.31 (0.49)	-1.59 (0.63)	0.54 (0.69)	-5.26 (0.62)	-6.98 (0.71)	-4.55 (0.47)	-7.44 (0.71)
Peak Amplitude	-4.97 (0.81)	-6.49 (0.69)	-5.97 (0.88)	-3.71 (0.8)	-4.92 (0.69)	-6.72 (1.04)	-5.49 (0.77)	-7.15 (0.95)

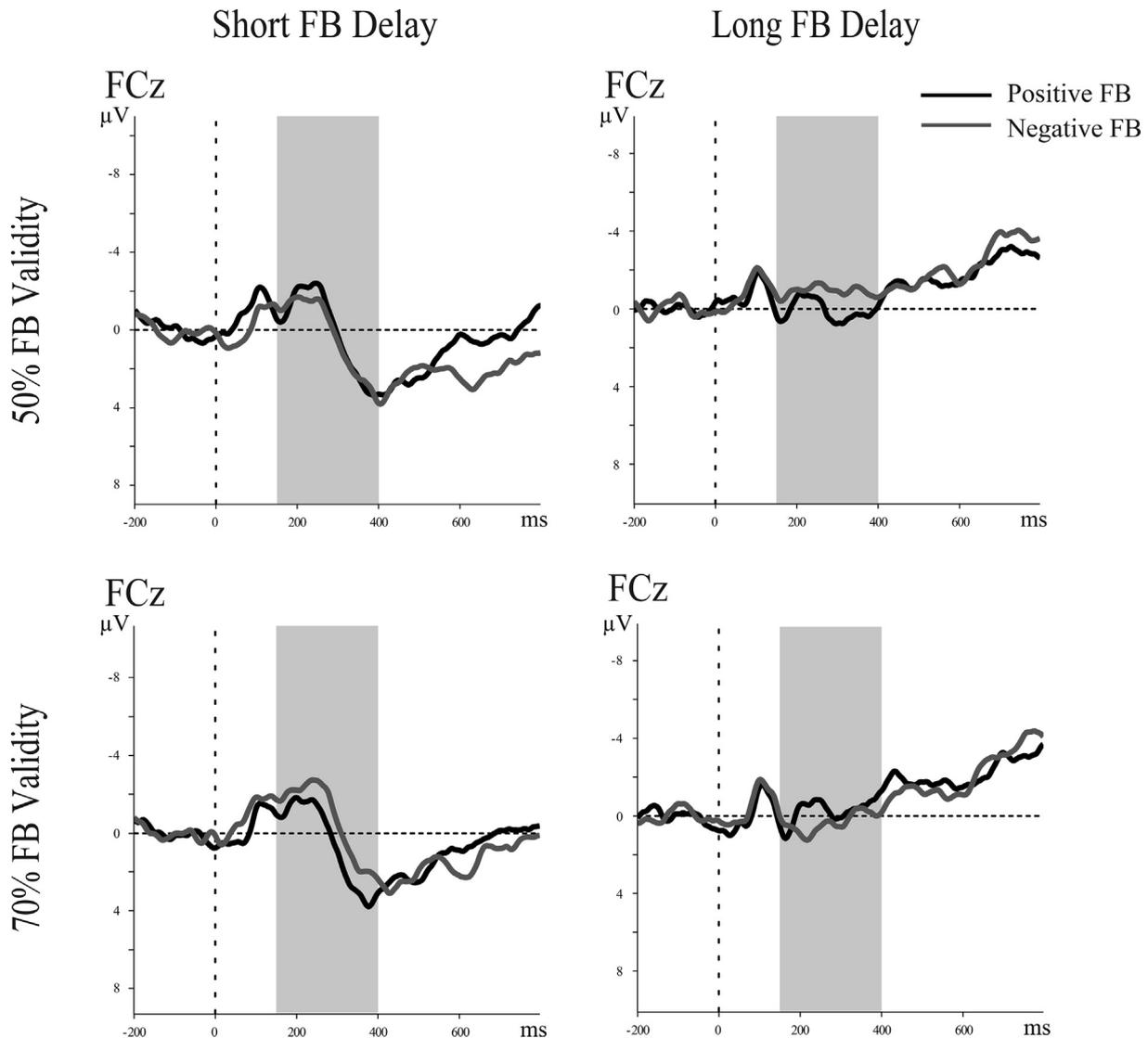


Fig. 4. Feedback-locked ERPs in the learning phase at electrode site FCz as a function of FB Validity, Delay, and Valence. The time window for peak detection (150–400 ms) is marked in grey.

As evident from Fig. 4, specifically in the 70% validity – long delay condition, negative feedback was associated with more positive amplitudes than positive feedback around 200 ms. To test the reliability of this observation, mean amplitudes between 200 and 250 ms were analyzed in a two (Validity: 50%, 70%) by two (Delay: Short, long) by two (Valence: Positive, negative) ANOVA. An interaction between all three factors was found, $F(1,22) = 7.76$, $p < .05$, $\eta_p^2 = .26$. In order to disentangle this interaction, separate ANOVAs for the Validity conditions were conducted. In the 50% Validity condition, no significant effects were found, all p -values $> .18$. In the 70% Validity condition, a significant main effect of Delay, $F(1,22) = 9.78$, $p < .01$, $\eta_p^2 = .31$, was qualified by a Delay \times Valence interaction, $F(1,22) = 14.02$, $p < .01$, $\eta_p^2 = .39$. Dependent t -tests revealed that negative feedback trials were associated with more positive mean amplitudes than positive feedback trials when feedback was delayed, $t(22) = -2.95$, $p < .01$, $d = -0.32$, but not when it was immediate, $t(22) = 1.19$, $p = .25$, $d = 0.14$.

2.2.1.2. Subsequent memory analysis. The waveforms for positive and negative feedback pictures that were subsequently remembered or forgotten are depicted in Fig. 5. The analysis of the mean

amplitudes in a 250–400 ms time window revealed no significant main effects of Valence or Memory, but a significant Valence by Memory interaction, $F(1,22) = 5.12$, $p < .05$, $\eta_p^2 = .19$. Mean amplitudes for positive FB hits were significantly more positive than for positive FB misses, $t(22) = 2.25$, $p < .05$, $d = .19$, whereas for negative FB hits and misses did not differ, $t(22) = -1.46$, $p = .16$, $d = -.10$. An analogous analysis of the FRN_{peak} amplitudes yielded no significant effects, all p -values $> .12$.

2.2.2. ERPs in the test phase

Waveforms for correct rejections, positive FB hits, and negative FB hits at a frontal and parietal recording site are shown in Fig. 6. Early and late old/new effects were analyzed in 300–500 or 500–700 ms time windows, respectively. Mean amplitudes from anterior and posterior electrodes were submitted to three (Side: Left, middle, right) by three (Item Status: Correct rejections, negative FB hits, positive FB hits) ANOVAs. In the early time window, mean amplitudes at anterior electrodes showed a marginally significant main effect of Item Status, $F(2,44) = 3.19$, $p = .05$, $\eta_p^2 = .13$. Based on our initial hypothesis, we expected to find an early frontal old/new effect only for positive FB hits, therefore we conducted

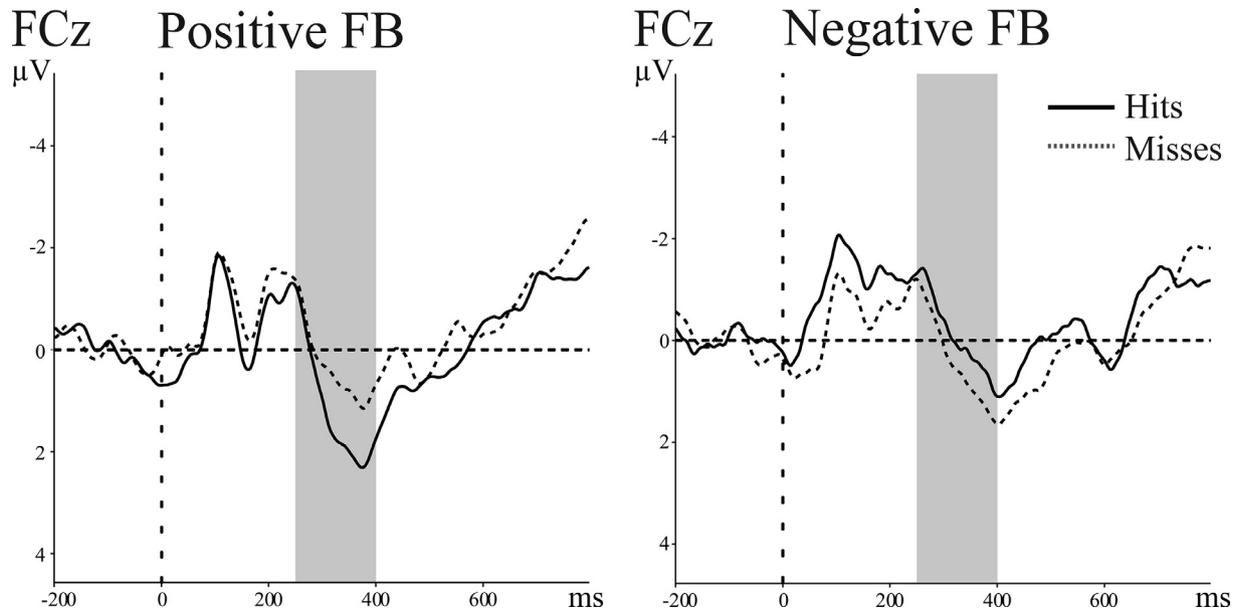


Fig. 5. Feedback-locked ERPs in the learning phase at electrode site FCz as a function of FB Valence and Memory. The time window for the subsequent memory analysis (250–400 ms) is marked in grey.

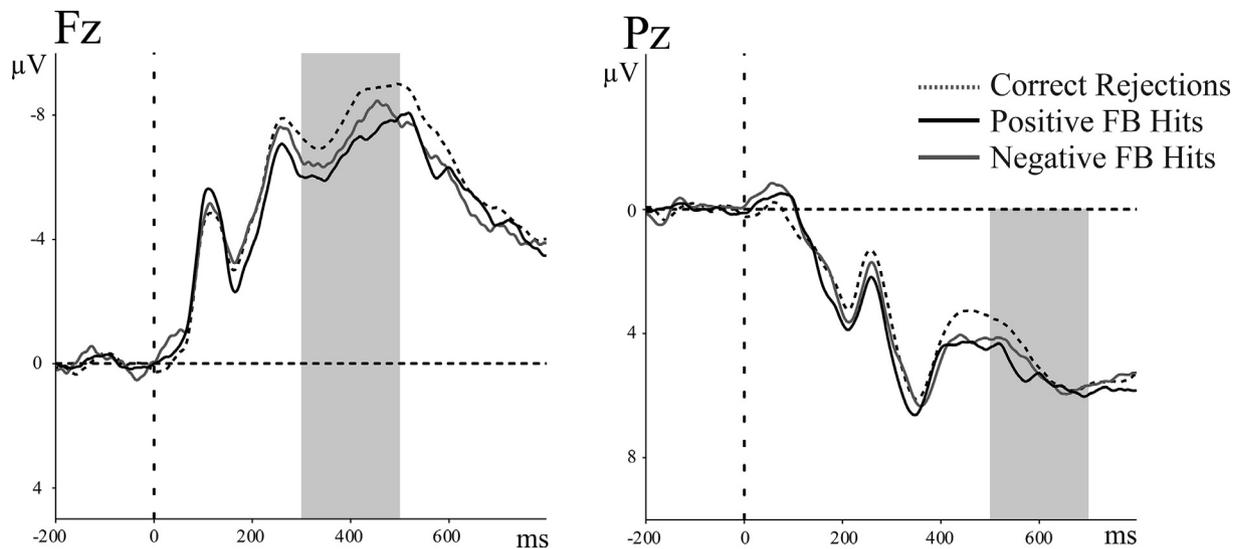


Fig. 6. ERPs in the test phase for two representative frontal and parietal electrodes. Time windows of analysis for early (300–500 ms) and late (500–700 ms) old/new effects are marked in grey.

follow-up *t*-tests that revealed more positive mean amplitudes for positive FB hits than for correct rejections, $t(22) = 2.60$, $p < .05$, $d = 0.18$. The difference between negative FB hits and correct rejections was not significant, $t(22) = 1.30$, $p = .21$, $d = 0.11$, just as the difference between positive FB hits and negative FB hits, $t(22) = 1.18$, $p = .25$, $d = 0.08$. There was no interaction between Item Status and Side, indicating that early old/new effects did not differ in amplitudes at left, middle, and right anterior electrodes. In the late time window, mean amplitudes at posterior electrodes did neither show a significant main effect of Item Status, $F(2,44) = 0.80$, $p = .46$, $\eta_p^2 = .04$, nor a Side by Item Status interaction, $F(4,88) = 1.94$, $p = .11$, $\eta_p^2 = .08$. Taken together, consistent with our initial hypothesis, an early frontal old/new effect was found for positive FB hits, but not for negative FB hits. In contrast, conclusive evidence for a late parietal old/new effect was obtained in neither condition.

3. Discussion

In the present study, we used ERPs to examine the consequences of feedback timing for the incidental episodic encoding and subsequent retrieval of positive and negative feedback events employing a paradigm in which reward was provided contingent on the performance of a separate (probabilistic learning) task. This paradigm allows an effective control of intentional learning effects on feedback processing and memory encoding. In the probabilistic learning task, participants used feedback to learn associations between four Chinese characters and two responses. In a 70% feedback validity condition, feedback was more often valid than invalid and could be used for learning. A 50% feedback validity condition served as a control condition, wherein positive and negative feedback was presented equally often and learning was impossible. Feedback was provided with a short or long temporal delay, and

task-irrelevant pictures of indoor and outdoor scenes were randomly presented together with the feedback. After the learning task, recognition memory for the pictures was tested in a surprise memory test. As the pictures were presented together with the words denoting the feedback they did not convey any learning-related information to the participants. By this, our design allowed to explore the effects of feedback processing on memory encoding and to control for effects of learning intention that otherwise could have introduced motivational and attentional confounds (Murayama and Kitagami, 2014). Of course, attentional and motivational factors cannot be completely ruled out, but detaching the pictures from the feedback learning task is one important strategy to minimize their influence on memory encoding.

As Foerde and Shohamy (2011) have demonstrated, learning from temporally delayed feedback relies both on striatal and hippocampal structures, which motivated us to hypothesize that pictures presented with long delayed feedback should be remembered better than those presented with shortly delayed feedback, whereas feedback learning should function equally well for shortly and long delayed feedback. The average performance in the 70% feedback validity condition increased throughout the course of the learning phase and did not differ between immediate and delayed feedback, suggesting that, when feedback learning was possible, participants were overall successful in learning the associations between the Chinese characters and the response buttons. To our surprise, however, we did not find better memory for pictures presented with long delayed feedback, as reported by Foerde and Shohamy (2011). Two differences in the learning task between the present study and their study could account for the divergent results. Firstly, in the present study, pictures were irrelevant for the learning task and presented in addition to the words denoting feedback. In the study by Foerde and Shohamy (2011), the picture category signalled the valence of the feedback, i.e. outdoor scenes were presented as positive feedback, and indoor scenes as negative feedback. Thus, in order to use the feedback for learning, participants had to encode the picture category (outdoor or indoor scene), and this may have resulted in stronger and/or more detailed memory traces than in the present study, in which the mapping between picture category and feedback type was arbitrary. Secondly, in the Foerde and Shohamy (2011) study, on delayed feedback trials, the cue (a Chinese character) and the choice (a colored button) remained on the screen during the delay phase, whereas in the present study, cues and choices were not presented throughout the delay phase. This may have imposed higher working memory (WM) demands in the delayed feedback trials. As evident from studies that have shown detrimental effects on memory encoding under conditions of divided attention (e.g. Craik et al., 1996), memory encoding can be impaired by high WM load. Thus, higher WM demands for delayed feedback trials may have counteracted the encoding of the pictures, thereby eliminating the enhanced encoding of pictures presented with delayed feedback.

Consistent with other ERP studies on feedback processing, we examined FRN amplitudes on the basis of negative minus positive feedback difference waves and on the basis of the original waveforms. Peak-to-peak measures of the FRN have been functionally related to the violation of action-outcome expectations, irrespective of valence (Cavanagh and Frank, 2014; Ferdinand et al., 2012). In contrast, FRN measures based on negative minus positive feedback difference waves are by definition more closely related to differences in feedback valence and more strongly reflect variance related to the processing of positive feedback (Becker et al., 2014; Holroyd et al., 2008; see Proudfit, 2015, for a review).

Several previous studies have reported a reduction of the FRN for temporally delayed feedback (Arbel et al., 2017; Peterburs et al., 2016; Weinberg et al., 2012; Weismüller and Bellebaum,

2016). As in the Peterburs et al. (2016) study, we found that feedback delay differentially affected difference wave-based and peak-to-peak measures of the FRN. While FRN_{peak} amplitudes were larger for long delayed than for shortly delayed feedback, we found a reduction of the FRN_{diff} for delayed feedback that was contingent on feedback utility. In other words, the FRN_{diff} was attenuated for delayed feedback in the 70% feedback validity condition, but not in the 50% validity condition. This contrasts with the results of Peterburs et al. (2016), who reported a gradual decrease of the FRN_{diff} with increasing feedback delay both in a 50% and a 75% feedback validity condition. However, Peterburs et al. (2016) used a more complex stimulus-response mapping in their associative learning task (six different characters were mapped on the two responses), which presumably made it more difficult for their participants to distinguish between the two validity conditions. Furthermore, while in their study correct responses were above chance level in the 75% feedback validity condition, this was already the case in the first block of their learning task, and correct responses did not increase over the course of the learning task. Therefore, participants may have ceased to use the feedback for learning after the first block. In contrast, in the present study, correct responses showed a linear increase across the blocks of the learning task (cf. Fig. 1), suggesting that participants continuously used the feedback for learning. These two differences between the study by Peterburs et al. (2016) and the present study may account for the divergent results.

Interestingly, specifically in the 70% validity – long delay condition, negative feedback was associated with more positive mean amplitudes than positive feedback between 200 and 250 ms. Even though this is a post hoc finding that requires further investigation, it dovetails with the overall pattern of results. The timing of the effect suggests that it is functionally related to the FRN_{peak} and therefore reflects stronger expectancy violations for positive feedback trials in the 70% validity – long delay condition. In the present study, participants may have prioritized the processing of positive feedback, which is also in line with the finding that pictures presented with positive feedback were remembered better than those presented with negative feedback. In further support of this interpretation, the effect occurred only in the 70% validity condition, where participants were able to form expectations about the outcomes. Taken together, besides replicating the finding that feedback delay differentially affects FRN_{diff} and FRN_{peak} amplitudes (Peterburs et al., 2016), the results of the present study show a temporal and functional dissociation of the two measures.

Comparing feedback processing for subsequently remembered or forgotten pictures we found that successful encoding was associated with more positive going waveforms for positive, but not negative feedback pictures. Of note, this effect of successful memory encoding was revealed in the same time period between 250 and 400 ms in which the FRN_{diff} was most pronounced and was also largest at the FCz recording site at which largest FRN were obtained. In contrast, FRN_{peak} amplitudes did not differ as a function of subsequent remembering. This pattern of results is consistent with the view outlined above, that whereas the FRN_{peak} is related to the processing of expectancy violations (Cavanagh and Frank, 2014; Ferdinand et al., 2012), the FRN_{diff} primarily reflects a reward positivity (Becker et al., 2014; Holroyd et al., 2008). As the observed subsequent memory effect resembles in its spatiotemporal characteristics the FRN_{diff} , we propose that it reflects positive reward prediction error signals that modulate memory encoding for events associated with positive feedback. Thus, positive feedback processing (as reflected in the FRN_{diff}) and successful memory encoding operate in parallel and covary systematically in this early time interval. Our data are not inconsistent with the view that feedback-related processing in the striatum and mnemonic processing in the hippocampus is initiated by the activity of

dopaminergic midbrain structures (Foerde and Shohamy, 2011; Shohamy and Adcock, 2010). Alternatively, it is possible that feedback learning is accomplished by a cooperation between the striatum and the hippocampus (Dickerson et al., 2011; Dickerson and Delgado, 2015). According to this view, enhanced memory for pictures associated with positive feedback may be a consequence of the hippocampal contribution to feedback learning.

In the test phase, recognition memory was better for pictures presented with positive feedback and this was paralleled by higher behavioral estimates of familiarity for these pictures. No effect of feedback valence was found for recollection estimates. Based on the results by Eppinger et al. (2010), we hypothesized that the ERP correlate of familiarity (i.e., the early mid-frontal old/new effect) should be obtained for pictures associated with positive, but not negative feedback. Our results tentatively confirmed this prediction. However, the main effect of Item Status was only marginally significant and thus needs to be interpreted with caution. This finding lends further though tentative support to the view that familiarity plays a larger role for remembering pictures that were associated with positive feedback. To our knowledge, the present study for the first time reports converging evidence for familiarity on the basis of ROCs and ERP data in the same experimental study. Consistent with Eppinger et al. (2010), reward signals elicited during positive feedback processing increased memory strength for the pictures presented together with the feedback. It is conceivable that in the task used in the present study, young adults prioritized positive feedback processing. Previous studies have shown that dopamine levels affect reinforcement learning. For example, PD patients, with depleted dopamine levels, show a strong tendency to learn by avoiding negative outcomes (Frank et al., 2004). Similarly, older adults prioritize learning from negative feedback, which may be due to decreasing dopamine levels in old age (Frank and Kong, 2008). Therefore, it is conceivable that participants in the present study prioritized learning from positive feedback due to high dopamine levels in young adulthood. Of course, since dopamine levels were not measured in the present study, this explanation has to be deemed speculative.

A significant late left-parietal old/new effect was found for neither picture type, suggesting that in general, there were only low levels of recollection for the pictures. This finding contrasts with Eppinger et al. (2010), who reported a late left-parietal old/new effect that did not differ between pictures associated with rewards or losses. However, Eppinger et al. used an intentional learning paradigm in which objects were repeated several times during learning. This led to high memory performance and presumably also to higher amounts of recollection as compared to the present study.

Conclusions

ERPs were used to investigate the effects of a temporal feedback delay on the incidental encoding and subsequent recognition of pictures presented together with the feedback. Different from other studies examining modulations of declarative memory by dopaminergic RPE signals, motivational and attentional confounds induced by intentional encoding were avoided by using an incidental learning tasks and by probing memory for pictures that were unrelated to the learning task. The pattern of results suggests that reward-related feedback processes contribute to successful memory encoding, yielding better memory and also a higher proportion of familiarity-based recognition decisions for pictures presented together with positive feedback. Thus, positive feedback in an incidental learning situation improves memory performance by increasing familiarity, a relatively fast and automatic memory retrieval process.

4. Methods and materials

4.1. Participants

Twenty-nine healthy young adults (23 female, 27 right-handed) participated in the experiment. Their age ranged between 18 and 30 years, with a median age of 22 years. All participants were German native speakers, had normal or corrected-to-normal vision and no self-reported neurological or psychiatric conditions. The experimental procedures were carried out in accordance with the Declaration of Helsinki. Participants gave their informed consent before the experiment and received money (8 € per hour) or course credit as a compensation for their participation. Due to the exclusion criteria for EEG data (see 4.4), six subjects were excluded. Thus, all analyses are based on $N = 23$ subjects.

4.2. Stimuli

A total of 400 scene pictures, consisting of 200 indoor scenes and 200 outdoor scenes were used in this experiment. Some of the indoor scenes were taken from the Change Blindness Database (Sareen et al., 2015), the other pictures were from various free internet sources. The size of the pictures was scaled to a width of maximal 600 pixels and a height of maximal 450 pixels.

4.3. Materials and procedure

The preparations for the EEG recording took about 45 min. Thereafter, participants were seated in front of a 19" computer screen with a resolution of 1280×1024 pixels in an electrically shielded and sound-attenuated booth. The experimental tasks were presented using E-Prime 2 software (Psychology Software Tools, Inc.) and participants used a keyboard for their responses.

The experiment consisted of a learning phase, a distractor task, and a recognition memory test. In the learning phase, participants learned associations between four different Chinese characters and two response keys in an associative learning task with probabilistic feedback. Task-irrelevant scene pictures were presented together with the feedback. The learning phase took about 25 min and was followed by an unrelated distractor task (an oddball task which did not cause interference with the encoded pictures). Twenty minutes after the learning phase, recognition memory of the scene pictures was tested in a surprise recognition memory test. The recognition memory test took about 35 min.

4.3.1. Learning phase

Four different Chinese characters (汉, 礼, 归, 伎) were used in the associative learning task, with one character assigned to each combination of the factors feedback validity (50%, 70%) and feedback delay (short: 500 ms, long: 6500 ms). The assignment of characters and conditions was balanced across subjects. Every character was associated with one of two responses (the "c"- and "n"-keys of the keyboard). Participants were instructed to learn the associations by trial and error and to use the feedback for this purpose. In the 50% validity condition, learning was not possible because feedback was equally often valid or invalid. Importantly, in this condition it can be ruled out that different frequencies for positive and negative feedback affect valence or delay effects because positive and negative feedback were presented equally often. Overall, there were 200 trials, which were divided into five blocks of 40 trials each. Every character was presented 10 times per block, in random order. Participants were given 10 practice trials before they started working on the task. Half of the 400 scene pictures (100 indoor and 100 outdoor scenes) were presented together with the feedback, but were not related to the task in any way.

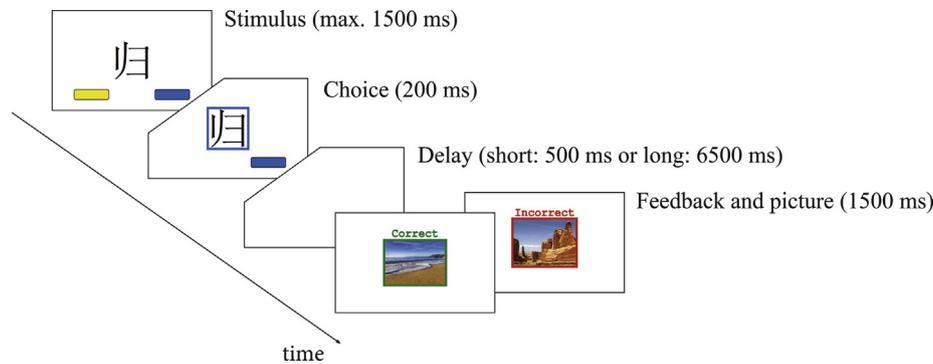


Fig. 7. The trial procedure: At the beginning of each trial, one of four Chinese characters was presented. As soon as the participant made a choice, it was displayed for a short time (200 ms). Feedback arrived with a short (500 ms) or long (6500 ms) delay. During the delay, a blank screen was presented. The feedback consisted of the word “correct” or “incorrect”, in green or red color for positive and negative feedback, respectively. Together with the feedback, a task-irrelevant picture was presented. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Picture type (indoor vs. outdoor) was randomly assigned to either the positive or the negative feedback condition.

A schematic of the trial procedure is depicted in Fig. 7. Each trial of the associative learning task started with a central fixation cross presented with a duration jittered between 500 and 1000 ms. Then, a Chinese character was presented in the centre of the screen with a maximum duration of 1500 ms. In the bottom left and right corners of the screen, a blue and a yellow button were presented. The buttons represented the left and right response keys. As soon as the participant responded with one of the keys, the chosen button remained on the screen, and the other button disappeared. At the same time, the character was surrounded by a frame of the same color as the chosen button. This screen served to make the choice salient and was shown for 200 ms. If the participants did not respond within 1500 ms after onset of the Chinese character, they were informed that their response was too slow and the trial was repeated. Then, a blank screen was presented for 500 or 6500 ms, depending on the delay condition. After this delay period, a feedback screen was presented for 1500 ms. A colored rectangle measuring 600×450 pixels was presented in the center of the feedback screen. Directly above the colored rectangle, the word “Correct” or “Incorrect”, presented in the same color as the rectangle, signaled if the feedback was positive and negative. The color of the rectangle and word was green for positive and red for negative feedback. An unrelated scene picture was presented over the colored rectangle, so that it appeared as a picture with a thick green or red frame. After the feedback, a blank screen was presented for 1000 ms before the next trial started.

4.3.2. Recognition memory test

The 200 scene pictures from the learning phase were presented together with 200 new scene pictures in random order. Participants were given a short break every 80 trials. In the beginning of each trial, a fixation cross was presented for 1000 ms, followed by a picture presented for 1500 ms. Participants were instructed to decide for every picture if it was old or new using a six-step confidence scale (“sure old”, “probably old”, “maybe old”, “maybe new”, “probably new”, “sure new”). This decision could be made as soon as the picture was presented. After the presentation of the picture, a blank screen appeared for 1000 ms. Then, the question “Old or New?” appeared, together with a depiction of the rating scale. As soon as participants made a response, a blank screen was shown for 1000 ms before the next trial started.

To assess memory performance, Pr scores (Snodgrass and Corwin, 1988) were calculated as the difference between the proportions of correct and incorrect “old”-decisions (hits and false alarms). For this purpose, the corresponding three steps of the

confidence scale were collapsed into “old”- and “new”-decisions. In addition, high-confidence Pr scores were calculated based on “sure”- and “probably”-decisions only.

The ROC toolbox (Koen et al., 2016) for Matlab (MathWorks, Inc.) was used to estimate the recollection as old (R_o) and familiarity (d'_F) parameters of the dual-process signal detection (DPSD) model of recognition memory.

4.4. EEG recording and analysis

The EEG was recorded during the learning phase and the recognition memory test from 28 Ag/AgCl scalp electrodes embedded in an elastic cap with positions according to the 10–20 electrode system (Fp1, Fp2, F7, F3, Fz, F4, F8, FC5, FC3, FCz, FC4, FC6, T7, C3, Cz, C4, T8, CP3, CPz, CP4, P7, P3, Pz, P4, P8, O1, O2, and A2). The vertical and horizontal EOG was recorded from four electrodes placed above and below the right eye and at the canthi of the left and right eyes. The electrodes were on-line referenced to a left mastoid electrode (A1), and AFz was used as a ground electrode. The EEG was amplified with a BrainAmp DC amplifier (Brain Products GmbH) from 0.016 to 250 Hz and digitized at 500 Hz. For off-line processing of the EEG data, Brain Vision Analyzer software (Brain Products GmbH) was used. Electrodes were re-referenced to the average of the left and right mastoid electrodes. The data from the learning phase and from the recognition memory test were bandpass-filtered at 0.1–40 Hz. Independent component analysis (ICA) was applied to the continuous data to correct for ocular artefacts. ICs associated with blinks and eye movements were rejected using a semi-automatic algorithm implemented in BrainVision Analyzer 2 (Ocular Correction ICA). The algorithm identified components that showed high correlations with vertical and horizontal eye channels. In a second step, IC topographies were checked manually. ICs that exhibited a typical blink or eye movement topography were rejected. Segments were extracted from the learning phase data from 200 ms before feedback onset to 800 ms thereafter, and segments of a similar duration were extracted from the test phase data relative to picture onset. The segments were baseline-corrected based on activity during the 200 ms before feedback or picture onset. Segments containing artefacts were rejected using the following criteria: A maximal allowed voltage step of $50 \mu\text{V}/\text{ms}$, a maximal difference of values of $200 \mu\text{V}$ during intervals of 200 ms, and minimal and maximal allowed total amplitudes of $\pm 100 \mu\text{V}$. On average, 1.5% and 7.9% of segments were rejected for the learning phase and for the test phase, respectively. Six subjects were excluded from all analyses upon inspection of the subject averages. Grand average waveforms were low-pass filtered at 12 Hz for illustration purposes only.

4.4.1. ERPs in the learning phase

For the FRN analysis, averages were calculated for every combination of the factors Validity (50%, 70%), Delay (Short, long), and Valence (positive, negative). We restricted the analysis to electrode FCz, because FRN effects are typically largest at this site (see Peterburs et al., 2016, for a similar approach). The difference wave-based FRN (FRN_{diff}) was quantified in the negative minus positive feedback difference waves in two different ways: 1) As the peak amplitude of the maximal negative peak in a 250–400 ms time window after feedback onset and 2) as the mean amplitude in the same time window. Furthermore, the peak-based FRN (FRN_{peak}) was quantified as the difference between the amplitudes of the maximum negative peak between 200 and 400 ms in the subject average waveforms, and the maximum positive peak in a 150–250 ms time window (i.e., the P200) at electrode FCz. For the purpose of peak detection, the subject average waveforms were low-pass filtered at 10 Hz.

For the subsequent memory analysis, averages were calculated for combinations of the factors Valence (positive, negative) and Memory (hits, misses), collapsed across the Validity and Delay factors. Subsequent hits and misses were calculated by collapsing across the three “old” and “new” steps of the confidence scale, respectively. In order to examine how feedback processing modulates successful encoding of feedback events, we analysed mean amplitudes during the FRN_{diff} time window (250–400 ms) and FRN_{peak} amplitudes in the subsequent memory analysis.

4.4.2. ERPs in the test phase

To test for old/new effects, we calculated averages for positive and negative hits and correct rejections (new pictures correctly classified as “new”), by collapsing the three corresponding steps of the confidence scale into “old”- and “new”-decisions. Mean amplitudes during an early (300–500 ms) and a late (500–700 ms) time window were analysed at left, middle, and right frontal and parietal electrode sites, respectively. The time windows used for the analysis of early and late old/new effects are typical for ERP studies of recognition memory (see Rugg and Curran, 2007, for a review) and correspond to time windows that were previously used in a study examining old/new effects for scene pictures (Gutchess et al., 2007). The electrode montage covered frontal and parietal electrode sites (left-frontal: F3, F7, FC3, FC5; mid-frontal: Fz, FCz; right-frontal: F4, F8, FC4, FC6; left-parietal: CP3, P3, P7; mid-parietal: CPz, Pz; right-parietal: CP4, P4, P8), where old/new effects are typically found in recognition memory tasks (for reviews, see Friedman and Johnson, 2000; Rugg and Curran, 2007).

4.5. Statistical analyses

All statistical analyses were conducted using IBM SPSS software. Performance during the learning phase was assessed as the proportion of correct responses in the 70% validity condition (because only in this condition learning was possible) and analysed in a two (Delay: Short, long) by five (Block: One to five) repeated measurements ANOVA. Pr scores from the recognition memory test were analysed in a two (Validity: 50%, 70%) by two (Delay: Short, long) by two (Valence: Positive, negative) repeated-measure ANOVA. The estimated DPSD model parameters d'_F (familiarity) and R_o (recollection as “old”) were compared for positive and negative pictures using dependent *t*-tests.

Peak and mean amplitudes from encoding and recognition ERPs were analyzed using dependent *t*-tests and repeated-measure ANOVAs. Only main effects and interactions involving the experimental factors are reported. Greenhouse-Geisser corrected degrees of freedom and *p*-values are reported whenever the assumption of sphericity was violated. Significant effects were decomposed using lower level ANOVAs and dependent *t*-tests. As measures of effect

sizes, partial eta squared (η_p^2) are reported for ANOVA results. For independent *t*-tests, Cohen's *d* was calculated and for dependent *t*-tests, the correlation between measurements was considered for calculations of *d*.

Declarations of interest

None.

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References

- Adcock, R.A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., Gabrieli, J.D.E., 2006. Reward-motivated learning: mesolimbic activation precedes memory formation. *Neuron* 50, 507–517. <https://doi.org/10.1016/j.neuron.2006.03.036>.
- Arbel, Y., Goforth, K., Donchin, E., 2013. The good, the bad, or the useful? The examination of the relationship between the feedback-related negativity (FRN) and long-term learning outcomes. *J. Cogn. Neurosci.* 25, 1249–1260. https://doi.org/10.1162/jocn_a_00385.
- Arbel, Y., Hong, L., Baker, T.E., Holroyd, C.B., 2017. It's all about timing: An electrophysiological examination of feedback-based learning with immediate and delayed feedback. *Neuropsychologia* 99, 179–186. <https://doi.org/10.1016/j.neuropsychologia.2017.03.003>.
- Becker, M.P.L., Nitsch, A.M., Miltner, W.H.R., Straube, T., 2014. A single-trial estimation of the feedback-related negativity and its relation to BOLD responses in a time-estimation task. *J. Neurosci.* 34, 3005–3012. <https://doi.org/10.1523/JNEUROSCI.3684-13.2014>.
- Bellebaum, C., Daum, I., 2008. Learning-related changes in reward expectancy are reflected in the feedback-related negativity. *Eur. J. Neurosci.* 27, 1823–1835. <https://doi.org/10.1111/j.1460-9568.2008.06138.x>.
- Cavanagh, J.F., Frank, M.J., 2014. Frontal theta as a mechanism for cognitive control. *Trends Cogn. Sci.* 18, 414–421. <https://doi.org/10.1016/j.tics.2014.04.012>.
- Chase, H.W., Swainson, R., Durham, L., Benham, L., Cools, R., 2011. Feedback-related negativity codes prediction error but not behavioral adjustment during probabilistic reversal learning. *J. Cogn. Neurosci.* 23, 936–946. <https://doi.org/10.1162/jocn.2010.21456>.
- Craik, F.I., Govoni, R., Naveh-Benjamin, M., Anderson, N.D., 1996. The effects of divided attention on encoding and retrieval processes in human memory. *J. Exp. Psychol. Gen.* 125, 159–180. <https://doi.org/10.1037/0096-3445.125.2.159>.
- Davidow, J.Y., Foerde, K., Galván, A., Shohamy, D., 2016. An upside to reward sensitivity: the hippocampus supports enhanced reinforcement learning in adolescence. *Neuron* 92, 93–99. <https://doi.org/10.1016/j.neuron.2016.08.031>.
- Dickerson, K.C., Delgado, M.R., 2015. Contributions of the hippocampus to feedback learning. *Cogn. Affect. Behav. Neurosci.* 15, 861–877. <https://doi.org/10.3758/s13415-015-0364-5>.
- Dickerson, K.C., Li, J., Delgado, M.R., 2011. Parallel contributions of distinct human memory systems during probabilistic learning. *Neuroimage* 55, 266–276. <https://doi.org/10.1016/j.neuroimage.2010.10.080>.
- Eichenbaum, H., 2004. Hippocampus: Cognitive processes and neural representations that underlie declarative memory. *Neuron* 44, 109–120. <https://doi.org/10.1016/j.neuron.2004.08.028>.
- Eppinger, B., Herbert, M., Kray, J., 2010. We remember the good things: age differences in learning and memory. *Neurobiol. Learn. Mem.* 93, 515–521. <https://doi.org/10.1016/j.nlm.2010.01.009>.
- Eppinger, B., Kray, J., Mock, B., Mecklinger, A., 2008. Better or worse than expected? aging, learning, and the ERN. *Neuropsychologia* 46, 521–539. <https://doi.org/10.1016/j.neuropsychologia.2007.09.001>.
- Ernst, B., Steinhauser, M., 2012. Feedback-related brain activity predicts learning from feedback in multiple-choice testing. *Cogn. Affect. Behav. Neurosci.* 12, 323–336. <https://doi.org/10.3758/s13415-012-0087-9>.
- Ferdinand, N.K., Mecklinger, A., Kray, J., Gehring, W.J., 2012. The processing of unexpected positive response outcomes in the mediofrontal cortex. *J. Neurosci.* 32, 12087–12092. <https://doi.org/10.1523/JNEUROSCI.1410-12.2012>.
- Foerde, K., Race, E., Verfaellie, M., Shohamy, D., 2013. A role for the medial temporal lobe in feedback-driven learning: evidence from amnesia. *J. Neurosci.* 33, 5698–5704. <https://doi.org/10.1523/JNEUROSCI.5217-12.2013>.
- Foerde, K., Shohamy, D., 2011. Feedback timing modulates brain systems for learning in humans. *J. Neurosci.* 31, 13157–13167. <https://doi.org/10.1523/JNEUROSCI.2701-11.2011>.

- Folstein, J.R., Van Petten, C., 2008. Influence of cognitive control and mismatch on the N2 component of the ERP: a review. *Psychophysiology* 45, 152–170. <https://doi.org/10.1111/j.1469-8986.2007.00602.x>.
- Foti, D., Weinberg, A., Dien, J., Hajcak, G., 2011. Event-related potential activity in the basal ganglia differentiates rewards from nonrewards: temporospatial principal components analysis and source localization of the feedback negativity. *Hum. Brain Mapp.* 32, 2207–2216.
- Frank, M.J., Kong, L., 2008. Learning to avoid in older age. *Psychol. Aging* 23, 392–398. <https://doi.org/10.1037/0882-7974.23.2.392>.
- Frank, M.J., Seeberger, L.C., O'Reilly, R.C., 2004. By carrot or by stick: cognitive reinforcement learning in parkinsonism. *Science* (80-) 306, 1940–1943. <https://doi.org/10.1126/science.1102941>.
- Friedman, D., Johnson, R.J., 2000. Event-related potential (ERP) studies of memory encoding and retrieval: a selective review. *Microsc. Res. Tech.* 51, 6–28.
- Gasbarri, A., Sulli, A., Packard, M.G., 1997. The dopaminergic mesencephalic projections to the hippocampal formation in the rat. *Prog. Neuro-Psychopharmacol. Biol. Psychiatry* 21, 1–22. [https://doi.org/10.1016/S0278-5846\(96\)00157-1](https://doi.org/10.1016/S0278-5846(96)00157-1).
- Gutchess, A.H., Ieui, Y., Federmeier, K.D., 2007. Event-related potentials reveal age differences in the encoding and recognition of scenes. *J. Cogn. Neurosci.* 19, 1089–1103. <https://doi.org/10.1162/jocn.2007.19.7.1089>.
- Holroyd, C.B., 2004. A Note on the Oddball N200 and the Feedback ERN. In: Ullsperger, M., Falkenstein, M. (Eds.), *Errors, Conflicts, and the Brain: Current Opinions on Performance Monitoring*. Max-Planck-Institut für Neuropsychologische Forschung, Leipzig, pp. 211–218.
- Holroyd, C.B., Coles, M.G.H., 2002. The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychol. Rev.* 109, 679–709. <https://doi.org/10.1037/0033-295X.109.4.679>.
- Holroyd, C.B., Pakzad-Vaezi, K.L., Krigolson, O.E., 2008. The feedback correct-related positivity: Sensitivity of the event-related brain potential to unexpected positive feedback. *Psychophysiology* 45, 688–697. <https://doi.org/10.1111/j.1469-8986.2008.00668.x>.
- Jarmasz, J., Hollands, J.G., 2009. Confidence intervals in repeated-measures designs: the number of observations principle. *Can. J. Exp. Psychol. Can. Psychol. Exp.* 63, 124–138. <https://doi.org/10.1037/a0014164>.
- Koen, J.D., Barrett, F.S., Harlow, I.M., Yonelinas, A.P., 2016. The ROC Toolbox: a toolbox for analyzing receiver-operating characteristics derived from confidence ratings. *Behav. Res. Methods*. <https://doi.org/10.3758/s13428-016-0796-z>.
- Miltner, W.H.R., Braun, C.H., Coles, M.G.H., 1997. Event-related brain potentials following incorrect feedback in a time-estimation task: evidence for a "generic" neural system for error detection. *J. Cogn. Neurosci.* 9, 788–798. <https://doi.org/10.1162/jocn.1997.9.6.788>.
- Murayama, K., Kitagami, S., 2014. Consolidation power of extrinsic rewards: reward cues enhance long-term memory for irrelevant past events. *J. Exp. Psychol. Gen.* 143, 15–20. <https://doi.org/10.1037/a0031992>.
- Paller, K.A., Voss, J.L., Boehm, S.G., 2007. Validating neural correlates of familiarity. *Trends Cogn. Sci.* 11, 243–250. <https://doi.org/10.1016/j.tics.2007.04.002>.
- Paller, K.A., Wagner, A.D., 2002. Observing the transformation of experience into memory. *Trends Cogn. Sci.* 6, 93–102. [https://doi.org/10.1016/S1364-6613\(00\)01845-3](https://doi.org/10.1016/S1364-6613(00)01845-3).
- Peterburs, J., Kobza, S., Bellebaum, C., 2016. Feedback delay gradually affects amplitude and valence specificity of the feedback-related negativity (FRN). *Psychophysiology* 53, 209–215. <https://doi.org/10.1111/psyp.12560>.
- Proudfit, G.H., 2015. The reward positivity: From basic research on reward to a biomarker for depression. *Psychophysiology* 52, 449–459. <https://doi.org/10.1111/psyp.12370>.
- Rugg, M.D., Curran, T., 2007. Event-related potentials and recognition memory. *Trends Cogn. Sci.* 11, 251–257. <https://doi.org/10.1016/j.tics.2007.04.004>.
- Sareen, P., Ehinger, K.A., Wolfe, J.M., 2015. CB Database: A change blindness database for objects in natural indoor scenes. *Behav. Res. Methods* 48. <https://doi.org/10.3758/s13428-015-0640-x>.
- Schultz, W., Dayan, P., Montague, P.R., 1997. A neural substrate of prediction and reward. *Science* (80-). 275, 1593–1599. <https://doi.org/10.1126/science.275.5306.1593>.
- Shohamy, D., Adcock, R.A., 2010. Dopamine and adaptive memory. *Trends Cogn. Sci.* 14, 464–472. <https://doi.org/10.1016/j.tics.2010.08.002>.
- Snodgrass, J.G., Corwin, J., 1988. Pragmatics of measuring recognition memory: applications to dementia and amnesia. *J. Exp. Psychol. Gen.* 117, 34–50. <https://doi.org/10.1037/0096-3445.117.1.34>.
- Tricomi, E., Fiez, J.A., 2012. Information content and reward processing in the human striatum during performance of a declarative memory task. *Cogn. Affect. Behav. Neurosci.* 12, 361–372. <https://doi.org/10.3758/s13415-011-0077-3>.
- Walsh, M.M., Anderson, J.R., 2012. Learning from experience: Event-related potential correlates of reward processing, neural adaptation, and behavioral choice. *Neurosci. Biobehav. Rev.* 36, 1870–1884. <https://doi.org/10.1016/j.neubiorev.2012.05.008>.
- Weinberg, A., Luhmann, C.C., Bress, J.N., Hajcak, G., 2012. Better late than never? The effect of feedback delay on ERP indices of reward processing. *Cogn. Affect. Behav. Neurosci.* 12, 671–677. <https://doi.org/10.3758/s13415-012-0104-z>.
- Weismüller, B., Bellebaum, C., 2016. Expectancy affects the feedback-related negativity (FRN) for delayed feedback in probabilistic learning. *Psychophysiology* 53, 1739–1750. <https://doi.org/10.1111/psyp.12738>.
- Wittmann, B.C., Schott, B.H., Guderian, S., Frey, J.U., Heinze, H.J., Düzel, E., 2005. Reward-related fMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. *Neuron* 45, 459–467. <https://doi.org/10.1016/j.neuron.2005.01.010>.
- Yonelinas, A.P., 2002. The nature of recollection and familiarity: a review of 30 years of research. *J. Mem. Lang.* 46, 441–517. <https://doi.org/10.1006/jmla.2002.2864>.
- Yonelinas, A.P., Parks, C.M., 2007. Receiver operating characteristics (ROCs) in recognition memory: a review. *Psychol. Bull.* 133, 800–832. <https://doi.org/10.1037/0033-2909.133.5.800>.