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Interactions Between Immediate and Delayed Feedback Processing and Memory Encoding: An Investigation Using Event-Related Potentials

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Abstract

Feedback-based learning relies on a procedural learning system mediated by dopaminergic reward prediction error (RPE) signals. Recent neuroimaging research indicates that the processing of temporally delayed feedback is supported by the hippocampus, a brain structure associated with declarative memory processes, but it is still unknown how delayed feedback processing and memory encoding interact. In this dissertation project, in a series of three experiments, a subsequent memory paradigm was employed to investigate how the incidental encoding of feedback pictures in a probabilistic learning task affects the event-related potential (ERP) correlate of RPEs in feedback processing, i.e., the feedback-related negativity (FRN), and how this interaction is modulated by feedback timing, valence, and explicit outcome expectations.

In Experiment 1, task-unrelated scene pictures were presented together with performance feedback in the learning task. In an ensuing test phase, a surprise recognition memory test for the pictures was conducted. FRN amplitudes measured in the feedback-locked ERPs recorded during the learning phase (FRN_{peak}) and in the negative minus positive feedback difference wave (FRN_{diff}) were compared for subsequently remembered and forgotten feedback pictures. Pictures were remembered better when presented together with positive than with negative feedback, and ERP amplitudes in the FRN_{diff} time window predicted subsequent memory only for positive feedback pictures. Consistent with previous studies, shortly delayed (SD, 500 ms) feedback elicited larger FRN_{diff} amplitudes than long delayed feedback (LD, 6500 ms), whereas the reverse pattern was found in FRN_{peak} amplitudes. As evidenced by behavioral estimates and ERP old/new effects, positive feedback enhanced memory by boosting familiarity-based recognition. However, feedback timing did not affect memory, presumably because participants did not need to process the scene pictures in order to learn from feedback.

In Experiment 2, the picture category signaled the valence of the feedback. LD feedback pictures were associated with better memory and more recollective processing than shortly delayed ones. Feedback processing as reflected in the $\mathrm{FRN}_{\mathrm{peak}}$ was attenuated for remembered as compared to forgotten LD feedback pictures. This suggests that when feedback was delayed, feedback processing and memory encoding competed for similar neural processing resources. As evidence by large $\mathrm{FRN}_{\mathrm{diff}}$ amplitudes in the SD condition, the evaluation of shortly delayed feedback strongly relied on the procedural learning system. A complementary model-based single trial analysis was conducted to validate models of the functional significance of the FRN. Consistent with previous studies, feedback-locked N170 and P300 amplitudes were sensitive to feedback delay.

Experiment 3 tested the hypothesis that the putative involvement of declarative learning processes in delayed feedback processing is mediated by the spontaneous generation of explicit outcome expectations during the feedback delay. A delayed feedback condition was compared with a Prediction condition in which participants were asked on each trial to predict the category of the upcoming feedback picture. Memory for the feedback pictures did not differ between the Prediction and Delay conditions. The $\mathrm{FRN}_{\mathrm{peak}}$ subsequent memory effect obtained in Experiment 2 was replicated in both conditions, but more pronounced in the Prediction condition. As evidenced by ERP old/new effects, negative feedback pictures that disconfirmed explicit outcome expectations were associated with stronger recollective processing than those presented in the Delay condition. Positive feedback pictures elicited a recognition bias and increased familiarity signals in the memory test, which could reflect a generalization of reward value to pictures of the same category (indoor or outdoor scene).

Taken together, the findings obtained in this dissertation show multiple ways by which feedback processing and memory encoding can interact, and how this interaction is shaped by feedback timing, valence, and explicit outcome expectations.

Zusammenfassung

Feedbackbasiertes Lernen beruht auf einem prozeduralen Lernsystem, das auf der neurobiologischen Ebene durch dopaminerge Belohnungsvorhersagefehlersignale vermittelt wird. Studien mit bildgebenden Verfahren weisen darauf hin, dass die Verarbeitung von zeitlich verzögertem Feedback durch den Hippocampus unterstützt wird, eine Hirnstruktur, die mit deklarativen Gedächtnisprozessen assoziiert ist. Es ist jedoch noch nicht bekannt, wie die Verarbeitung von verzögertem Feedback mit der Gedächtnisenkodierung interagiert. In diesem Dissertationsprojekt wurde in einer Serie von drei Experimenten die Methode der nachfolgenden Erinnerung verwendet, um zu untersuchen, wie die inzidentelle Enkodierung von Feedbackbildern in einer probabilistischen Lernaufgabe sich auf das im ereigniskorrelierten Potenzial (EKP) messbare Korrelat von Belohnungsvorhersagefehlern in der Feedbackverarbeitung, die Feedback-Negativierung (FRN), auswirkt und wie diese Interaktion durch zeitliche Charakteristika und Valenz des Feedbacks sowie durch explizite Ergebniserwartungen moduliert wird.

Im ersten Experiment wurden Bilder von Innenräumen und Landschaften zusammen mit dem Feedback in der Lernaufgabe präsentiert, wobei die Bilder nicht relevant für die Aufgabe waren. In der darauf folgenden Testphase wurde ein unerwarteter Rekognitionstest für die Bilder durchgeführt. FRN-Amplituden wurden in den während der Feedbackpräsentation aufgezeichneten EKP gemessen ($\mathrm{FRN}_{\mathrm{peak}}$), sowie in der Differenzwelle, die durch die Subtraktion der durch positives Feedback erzeugten EKP von den durch negatives Feedback erzeugten EKP gebildet wurde ($\mathrm{FRN}_{\mathrm{diff}}$). Beide FRN-Maße wurden für später erinnerte und später vergessene Bilder verglichen. Bilder, die zusammen mit positivem Feedback gezeigt wurden, wurden besser erinnert als solche, die mit negativem Feedback gepaart wurden, und EKP-Amplituden im Zeitfenster der $\mathrm{FRN}_{\mathrm{diff}}$ prädizierten spätere Erinnerung ausschließlich für Bilder, die zusammen mit positivem Feedback präsentiert

wurden. Übereinstimmend mit früheren Studien erzeugte kurz verzögertes Feedback (500 ms) größere FRN_{diff}-Amplituden als lang verzögertes Feedback (6500 ms), wohingegen das umgekehrte Muster für FRN_{peak}-Amplituden gefunden wurde. Wie durch behaviorale Maße und EKP-Alt/Neu-Effekte belegt, stärkte die Verarbeitung von positivem Feedback vor allem das vertrautheitsbasierte Erinnern der zeitgleich präsentierten Bilder, jedoch wirkten sich die zeitlichen Parameter der Feedbackpräsentation nicht auf das Gedächtnis aus, vermutlich weil eine Verarbeitung der Bilder nicht notwendig war, um das Feedback zum Lernen zu nutzen.

Im zweiten Experiment wurde daher die Bildkategorie (Innenraum oder Landschaft), mit der Valenz des Feedbacks verknüpft. Lang verzögerte Feedbackbilder waren mit besserer Erinnerung und stärkerer rekollektiver Verarbeitung assoziiert als solche, die mit kurzer Verzögerung präsentiert worden waren. Die Feedbackverarbeitung, gemessen als FRN_{peak}-Amplitude, war geringer für lang verzögerte Feedbackbilder, die anschließend erinnert wurden als für solche, die nicht erinnert wurden. Dies legt nahe, dass die Verarbeitung von zeitlich verzögertem Feedback und die Gedächtnisenkodierung auf ähnliche neuronale Verarbeitungskapazitäten zugreifen. Wie anhand von FRN_{diff}-Amplituden ersichtlich, beruhte die Evaluation von zeitlich kurz verzögertem Feedback in starkem Ausmaß auf dem prozeduralen Lernsystem. Eine ergänzende, modellbasierte Analyse auf der Ebene einzelner Lerndurchgänge wurde durchgeführt, um Modelle der funktionalen Bedeutsamkeit der FRN zu validieren. Übereinstimmend mit vorherigen Studien wurden durch die Feedbackverarbeitung hervorgerufene N170- und P300-Amplituden durch die zeitliche Verzögerung des Feedbacks moduliert.

Das dritte Experiment überprüfte die Hypothese, dass die mutmaßliche Beteiligung von deklarativen Lernprozessen bei der Verarbeitung von verzögertem Feedback durch die spontane Entwicklung expliziter Ergebniserwartungen während der Feedbackverzögerung vermittelt wird. Eine Bedingung mit verzögertem Feedback wurde mit einer Vorhersage-

Bedingung kontrastiert, in der die Probanden in jedem Lerndurchgang die Kategorie des Feedbackbildes prädizierten. Die Erinnerung an die Feedbackbilder unterschied sich nicht zwischen den beiden Bedingungen. Der Effekt der nachfolgenden Erinnerung in den FRN_{peak}-Amplituden, der in Experiment 2 gefunden wurde, wurde in beiden Bedingungen repliziert, war jedoch in der Vorhersage-Bedingung stärker ausgeprägt. Wie durch EKP-Alt/Neu-Effekte belegt, waren negative Feedbackbilder, die die explizite Erwartung eines positiven Ergebnisses verletzten, mit einer stärkeren rekollektiven Verarbeitung verknüpft. Positive Bilder waren im Gedächtnistest mit besonders vielen falsch positiven Gedächtnisurteilen assoziiert, was mit einer Generalisierung des Belohnungswertes zu Bildern der gleichen Kategorie zusammenhängen könnte.

Zusammengefasst zeigen die Ergebnisse dieser Dissertation, dass die Feedbackverarbeitung und die Gedächtnisenkodierung auf mehreren Wegen interagieren können. Die zeitlichen Charakteristika der Feedbackpräsentation, die Valenz des Feedbacks und explizite Ergebniserwartungen stellen wichtige Faktoren dar, die diese Interaktion beeinflussen.

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List of Publications

This dissertation is based on three studies, described in chapters 2 – 4, two of which were published as original articles in international peer-reviewed journals. I am the first author of both articles and other authors listed below contributed to the work. However, to facilitate reading I will consistently use “we” instead of “I” throughout this thesis. Both articles are presented here in the form in which they were accepted for publication, apart from minor changes in formatting and minor revisions made to figures and text. Please note that chapter 1 contains passages from both article manuscripts.

Chapter 2 – Experiment 1:

Höltje, G., & Mecklinger, A. (2018). Electrophysiological Reward Signals Predict Episodic Memory for Immediate and Delayed Positive Feedback Events. *Brain Research*, *1701*, 64–74.

Chapter 3 – Experiment 2:

Höltje, G., & Mecklinger, A. (2020). Feedback timing modulates interactions between feedback processing and memory encoding: Evidence from event-related potentials. *Cognitive, Affective and Behavioral Neuroscience*, *20*(2), 250–264.

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Abbreviations

α	learning rate parameter alpha
β	inverse temperature parameter beta
δ	reward prediction error delta
η_p^2	effect size partial eta squared
θ	scale parameter theta
μV	microvolt
ACC	anterior cingulate cortex
Ag/AgCl	silver / silver chloride
ANOVA	analysis of variance
BOLD	blood oxygen level dependent
Br	bias index
c	choice
cf.	*confer* - compare
CR	conditioned reaction
CS	conditioned stimulus
d	effect size Cohen’s d
d'_F	familiarity parameter
DA	dopamine

DPSD	dual-process signal detection
EEG	electroencephalography
e.g.	*exempli gratia* – for example
EOG	electrooculography
ERN	error-related negativity
ERP	event-related potential
F	test statistic from F-distribution
FB	feedback
fCRP	feedback correct-related positivity
fMRI	functional magnetic resonance imaging
FRN	feedback-related negativity
Hz	hertz
ICA	independent component analysis
i.e.	*id est* – that is
L	left
LD	long feedback delay
LTP	long-term potentiation
M	mean
ms	milliseconds

MTL	medial temporal lobe
n	number of cases
p	probability value
PD	Parkinson’s disease
PFC	prefrontal cortex
Pr	discrimination index
PRO	prediction of response outcome
r	reward
R	right
R_o	recollection as old parameter
RL	reinforcement learning
ROC	receiver-operator characteristic
RPE	reward prediction error
SD	standard deviation
SD	short feedback delay
SEM	standard error of the mean
SME	subsequent memory effect
SN	substantia nigra
SPE	salience prediction error

S-R	stimulus-response
t	test statistic from student’s t-distribution
t	trial index
US	unconditioned stimulus
VTA	ventral tegmental area
WM	working memory
Q	expected value

1 Introduction

External feedback is often essential for human learning and decision making. For instance, learning a motor skill, such as playing golf, strongly relies on the evaluation of outcomes associated with actions and is driven by reward prediction errors (RPEs) indicating the deviation between the expected and received outcome of an action. A novice golf player has no strong expectation about the outcome of his action; he does not know *how* to strike the ball in order to hit the hole. However, by evaluating the outcomes of his strikes, the golf player can adjust his behavior in order to maximize positive outcomes. This procedural or habitual type of learning is typically slow and hard to verbalize (non-declarative): A novice on the golf course has to strike many balls and evaluate the outcome until he knows *how* to strike the ball in order to hole it. The deviation between the expected and received outcome of an action (i.e., the RPE) gradually decreases over the course of this learning process.

In contrast to the procedural learning system upon which feedback learning relies, episodic memory (i.e., memory for autobiographical episodes) is a declarative type of memory that is consciously accessible and can be verbalized (Squire & Dede, 2015; Tulving, 1972). The golf player mentioned earlier uses feedback to learn *how* to strike the ball, but he also forms an episodic memory trace of the moment when he holes the golf ball for the first time. The episodic memory trace contains the central objects of an episode (the golf ball or the flag that marks the hole), but also the context in which these objects occurred (the golf court), and associations between these elements (Eichenbaum, Yonelinas, & Ranganath, 2007). Different from feedback learning, which is a slow, rigid, and non-declarative type of learning, episodic memory traces thus consist of flexible associations that are formed rapidly during a single encoding trial (Henke, 2010).

Feedback learning and episodic memory encoding engage distinct learning systems and brain structures: Feedback learning is guided by a procedural learning system governed by dopaminergic RPE signals (Daw & Tobler, 2014), whereas episodic memory encoding and retrieval rely on the declarative learning system and activity in the medial temporal lobes (i.e., the hippocampus and the surrounding cortical regions; Eichenbaum, 2004; Eichenbaum et al., 2007). Only recently has neuroimaging research started to focus on conditions under which the brain systems underlying these two learning systems interact (Miendlarzewska, Bavelier, & Schwartz, 2016; Shohamy & Adcock, 2010; Shohamy & Daw, 2014). For instance, reward-predicting pictures are associated with superior memory and brain activity in dopaminergic midbrain regions (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Wittmann et al., 2005). With recourse to our illustrative example of the golf player, a rewarding event, such as an unexpectedly successful strike under challenging conditions, should be remembered better due to the dopaminergic activity it elicits. In a study by Foerde and Shohamy (2011), feedback pictures presented with a delay of several seconds were associated with hippocampal activity and better memory than immediately presented feedback pictures. These results suggest that brain regions associated with declarative memory processes can support the processing of temporally delayed feedback.

The present work aims at investigating interactions between feedback processing and episodic memory encoding, and how they are reflected in event-related potentials (ERPs). In the first section, we cover the principles of feedback-based learning and introduce the feedback-related negativity, the ERP correlate of dopaminergic RPE signals in feedback processing. The next section deals with episodic memory and ERP correlates of memory retrieval. We then review research pertaining to our central research question how feedback learning and declarative memory interact.

1.1 Feedback-Based Learning

Feedback-based learning comprises the ability to learn associations between events or actions and their outcomes. *Classical conditioning* is one fundamental mechanism by which organisms can learn associations between stimuli through their repeated co-ocurrence (Pavlov, 2010). In his classic experiments, Ivan Pavlov discovered that dogs reacted with salivation (conditioned response, CR) to the ringing of a bell after this intrinsically neutral conditioned stimulus (CS) had been repeatedly paired with the deliverance of food (unconditioned stimulus, US). Furthermore, Pawlow found that a tone of a frequency similar to the ringing bell elicited the same conditioned response. Subsequent research revealed that conditioned responses can generalize to stimuli that resemble the CS along basic perceptual or more abstract categorical dimensions (Bhatt, Wasserman, Reynolds, & Knauss, 1988; Honig & Urcuioli, 1981). In a similar fashion, the learned motivational value of a stimulus can transfer to perceptually similar stimuli and bias perception and behavior (Miendlarzewska et al., 2016).

Another important learning paradigm was pioneered by Edward Thorndike (1898; 1911) who constructed a “puzzle box” that could be opened from the inside by a simple mechanism. Thorndike examined learning curves that depicted the time an animal needed to open the box as a function of learning trials. Initially, the experimental animals need a lot of time until they managed to open the box. In subsequent trials, their dwell time decreased gradually which indicates that the animals learned by trial and error and not by insight. This type of learning was labeled *instrumental conditioning*, because the animal’s action was instrumental in opening the puzzle box. In his learning theory, Thorndike (1898) formulated the *law of effect* which states that in a certain situation (in the presence of a discriminative stimulus), a reaction that leads to a reward will strengthen the association between the stimulus and the reaction and, as a consequence, the probability of showing the rewarded reaction in the same situation will be increased. Thorndike's method was later refined by B. F. Skinner who invented the *operant conditioning chamber*, also known as "Skinner box", in which animals, usually rodents or pigeons, were rewarded with food for showing a response (e.g., pressing a lever). In contrast to Thorndike's approach of measuring the time an animal needed to escape the puzzle box in discrete trials, Skinner measured the frequency of responses an animal showed as a function of a well-defined rule according to which reward was delivered (i.e., the *reinforcement schedule*). He found that the frequency of rewarded actions increased, whereas unrewarded actions were shown less frequently (e.g., Skinner, 1938).

The main difference between classical and instrumental conditioning is that the former is concerned with contingencies between stimuli and rewards, whereas the latter focuses on actions that are reinforced by rewards. Both types of learning enable organisms to show adaptive behavior in a relatively constant environment. Thus, even though Pavlov, Thorndike, and Skinner based their learning theories on animal research, they discovered fundamental principles of learning which are also applicable to learning in humans, upon which we will focus in the following.

In a typical feedback learning task, participants are instructed to learn stimulus-response (S-R) associations by trial and error. Performance feedback indicates the outcome of a response (positive or negative) and enables participants to learn the correct S-R association. Probabilistic feedback that is valid only in a proportion of trials (e.g., 70%) is used often because otherwise participants would be able to infer the correct S-R associations within a few trials. Across participants, learning curves (i.e., the proportion of correct responses over the course of the learning trials) can be used to characterize the learning process. Participants initially perform at chance level, but if they succeed in using the feedback for learning, the proportion of correct responses increases.

Reinforcement learning (RL) theory assumes that feedback learning is driven by reward prediction errors, i.e., the deviation between the expected and the received outcome (Rescorla & Wagner, 1972; Sutton & Barto, 2020). Computational reinforcement learning models can be used to estimate RPE estimates and parameters that provide additional information on the learning process in individual participants. On each trial t of a typical feedback learning task, participants respond to a stimulus by choosing either the left or the right response button (choice c_t = L or R). According to a Q-learning model (Watkins, 1989), subjects assign an expected value Q to each of the choice options. Initially, this expected value is at chance (e.g., 0.5) because participants have not developed an expectation at this point. The Q-value is subsequently updated on each trial according to the formula $Q_{t+1}(c_t) = Q_t(c_t) + \alpha \cdot \delta_t$, where α is a free learning rate parameter that indicates how readily choice behavior is changed as a reaction to reinforcement, with higher values signifying faster updating, and the prediction error $\delta_t = r_t - Q_t(c_t)$ is defined as the difference between the actually received (r_t) and the expected value of the outcome. The observation model that links the theoretically expected choice values with the probabilities of the observed choices can be assumed to follow a softmax distribution:

$$p\big(c_t = L \mid Q_t(L), Q_t(R)\big) = \frac{\exp(\beta \cdot Q_t(L))}{\exp\big(\beta \cdot Q_t(R)\big) + \exp(\beta \cdot Q_t(L))}$$

The free inverse temperature parameter β indicates the extent to which the observed choices follow the learned values of the choice options. Once the parameters specified in the model are estimated, trial-by-trial RPE estimates can be derived for each participant.

In functional neuroimaging studies, computational models are widely used to identify brain regions in which BOLD signals correlate with model-derived learning signals (for reviews, see Daw and Doya, 2006; O’Doherty et al., 2007). This line of research was inititated by the discovery that the firing pattern of dopamine neurons resembled the RPE in reinforcement learning models (Montague, Dayan, & Sejnowski, 1996; Schultz, Dayan, & Montague, 1997). In the present work, similar to the aforementioned method used in neuroimaging studies, correlations between model-derived prediction errors and single trial EEG data were used to validate models of the functional significance of the feedback-related negativity, the putative ERP correlate of reward prediction error processing in feedback learning.

1.1.1 Neurobiological Mechanisms Underlying Feedback-Based Learning

The neurotransmitter dopamine (DA) has long since been associated with motivational and reward-related processes. In 1954, James Olds and Peter Milner discovered that electrical stimulation to particular brain regions had a rewarding quality for rats (Olds & Milner, 1954). Later studies could show that this effect was especially pronounced in the ventral tegmental area (VTA), a midbrain structure containing one of the largest assemblies of dopaminergic neurons in the brain of mammals, including humans (Björklund & Dunnett, 2007). In a study by Wise, Spindler, Dewit, and Gerber (1978), rats were conditioned to press a lever for food, whereupon one group of rats was given the DA receptor blocker pimozide. Subsequently, the pimozide group and one control group of rats were continuously rewarded for lever presses, whereas another control group did not receive reinforcement any longer. Strikingly, the frequency of lever presses remained on a high level in the control group with reinforcement, but significantly decreased in the pimozide group and in the control group without reinforcement. Wise and colleagues reasoned that the detracting effect of pimozide on the normal functioning of dopaminergic transmission diminished the rewarding quality of an otherwise potent reinforcer (i.e., the *anhedonia hypothesis*). However, Berridge and Robinson (1998) argued that even rats with pharmaceutically degraded DA neurons showed hedonic behavior and proposed that DA rather signals the motivation to obtain a reward (i.e., the *incentive salience hypothesis*). A third hypothesis regarding the function of DA derived from a series of studies with monkeys in which it was found that the firing pattern of DA neurons located in the substantia nigra (SN) and in the VTA closely resembles reward prediction error signals (for a review see Schultz, 1998). The monkeys were trained to depress one out of two levers in order to obtain a drop of apple juice as a reward. On each trial, a light cue indicated which of the two levers would lead to a reward. Initially, an unexpected reward elicited a phasic increase in the firing rate of dopamine neurons. On later trials, the timing of the dopamine response shifted from responding to the reward to responding to the earlier reward-predicting cue[1]. Furthermore, the omission of an expected reward was associated with a phasic decrease of the firing rate below the baseline. These findings are hard to reconcile with previous hypotheses relating DA to the hedonic value of a reward (Olds & Milner, 1954; Wise et al., 1978) and rather indicate that DA signals unexpected rewards, which has also been confirmed in humans by intracranial EEG recordings (Zaghloul et al., 2009). However, the role of dopamine in learning and motivation goes beyond signaling reward prediction errors. Recent evidence indicates that some types of DA neurons also respond to novel and surprising events (Bromberg-Martin, Matsumoto, & Hikosaka, 2010). It is conceivable that reward prediction errors and incentive salience are coded by distinct aspects of the DA response. For instance, it has been suggested that incentive salience could be related to sustained changes in the background firing rate of DA neurons (Niv, Daw, Joel, & Dayan, 2007).

Projections from the SN to the nucleus caudatus and the putamen in the dorsal striatum (i.e., the nigrostriatal DA pathway), where DA signals modulate action selection by facilitating or inhibiting actions associated with positive or negative outcomes, respectively,

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[1] The shift of the dopamine response from unexpected rewards to reward-predicting cues indicates that dopamine signals code temporal difference RPEs, a special type of RPE that can be elicited by any event that changes the predicted reward of an action (Sutton & Barto, 2020). Please note that we will continue to use the simplified label RPE in the following.

play a crucial role in feedback learning. This is also evidenced by studies showing that Parkinson’s disease (PD) patients who suffer from a degeneration of DA neurons in the SN are significantly impaired in their ability to use feedback or reward for learning (Foerde & Shohamy, 2011; Frank, Seeberger, & O’Reilly, 2004; Knowlton, Mangels, & Squire, 1996). In contrast, projections from the VTA to the nucleus accumbens in the ventral striatum (i.e., the mesolimbic DA pathway) are primarily associated with the processing of reward.

1.1.2 ERP Correlates of Feedback Processing

1.1.2.1 Feedback-Related Negativity

In studies examining ERPs, the commitment of errors in choice reaction tasks is associated with a negativity (*error-related negativity*, ERN) that peaks between 50 and 100 after an erroneous response at fronto-central electrodes (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993). The processing of performance feedback indicating an incorrect response in a time-estimation task elicits a similar fronto-central negativity (*feedback-related negativity*, FRN) that is maximal between 250 and 300 ms after feedback onset (Miltner, Braun, & Coles, 1997). The neural generators of these two ERP components were localized in the anterior cingulate cortex (Dehaene, Posner, & Tucker, 1994; Miltner et al., 1997). Holroyd and Coles (2002) proposed that the response-locked ERN and the feedback-locked FRN reflect the transmission of a dopaminergic RPE signal to the anterior cingulate cortex (ACC). According to their *reinforcement learning theory*, a dopamine signal indicating that the outcome of an action was worse than expected (i.e., a negative RPE) disinhibits ACC neurons and elicits an error signal that is used to optimize performance on the task at hand. In support of this view, it was found that early during learning, feedback stimuli elicit a large FRN, whereas erroneous responses are not associated with a significant ERN. In contrast, when learning is completed and stable S-R associations have been built up, erroneous responses elicit a strong ERN, but the feedback-locked FRN is diminished (Eppinger, Kray, Mock, & Mecklinger, 2008; Holroyd & Coles, 2002; Nieuwenhuis et al., 2002). Thus, we can conceive of the FRN as an ERP correlate of dopaminergic RPEs elicited by performance feedback during learning (for review and meta-analysis see Walsh & Anderson, 2012; Sambrook & Goslin, 2015).

A recent modification of the *reinforcement learning theory* emphasizes that the scalp-recorded FRN signal results from an overlap between the N200 and a later positivity elicited by 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 & Van Petten, 2008, for a review), 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.

An alternative account of ACC functioning that has recently received massive empirical support (Ferdinand, Mecklinger, Kray, & Gehring, 2012; Hauser et al., 2014; Oliveira, McDonald, & Goodman, 2007; Talmi, Atkinson, & El-Deredy, 2013; Wessel, Danielmeier, Bruce Morton, & Ullsperger, 2012) is provided by the *prediction of response-outcome* (PRO) model which assumes that the ACC is rather sensitive to unexpected events regardless of their valence (Alexander & Brown, 2010, 2011). In the present work, we employed two FRN measures to examine distinct aspects of feedback processing: The $\mathrm{FRN}_{\mathrm{peak}}$, measured as the difference between the N200 and the preceding positive peak (i.e., the P200), reflects the salience (unexpectedness) of feedback, irrespective of valence (Ferdinand et al., 2012). In contrast, the $\mathrm{FRN}_{\mathrm{diff}}$ is measured as the peak amplitude in the negative minus positive feedback difference wave (i.e., the amplitude at the time point of the maximal difference between the waveforms elicited by positive and negative feedback) and primarily reflects variance related to the reward positivity.

1.1.2.2 N170

The N170 is a negative potential elicited by the processing of complex visual stimuli, especially faces, between 130 and 200 ms at occipito-temporal electrodes (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion, Joyce, Cottrell, & Tarr, 2003). In an ERP study investigating feedback-based learning in a virtual T-maze, Baker and Holroyd (2009) found a feedback-locked potential that closely resembled the N170 elicited by the processing of faces. In subsequent studies, the neural generator of this feedback N170 was localized in the right parahippocampal cortex (Baker & Holroyd, 2013; Baker, Umemoto, Krawitz, & Holroyd, 2015), a brain region adjacent to the fusiform gyrus in which the face N170 is generated (Bötzel, Schulze, & Stodieck, 1995; Deffke et al., 2007). Arbel, Hong, Baker, & Holroyd (2017) found that delayed feedback elicited larger (more negative) N170 amplitudes than immediate feedback and proposed that the N170 constitutes a marker of the involvement of the MTL in delayed feedback processing. In the present work, we therefore examined feedback N170 amplitudes and also explored whether this component predicts subsequent memory for feedback pictures.

1.1.2.3 P300

The P300, a positive potential that is typically most pronounced over parietal electrode sites, is thought to reflect the updating of the stimulus context in memory (Donchin, 1981; Polich, 2007). P300 amplitudes are modulated by the subjective probability, task relevance, and information value of a stimulus (i.e., unexpected, relevant, and informative stimuli elicit larger P300 amplitudes than expected, irrelevant, and uninformative ones; Johnson, 1986; Nieuwenhuis, Aston-Jones, & Cohen, 2005). In feedback learning tasks, the P300 is associated with higher order feedback evaluation processes such as the updating of the value associated with an action (Ullsperger, Fischer, Nigbur, & Endrass, 2014). In a study by Chase, Swainson, Durham, Benham, & Cools (2011), participants learned associations between abstract visual patterns and responses in a probabilistic reversal learning task. The correct S-R mapping was changed on a regular, but unpredictable basis. Chase and colleagues found that FRN amplitudes correlated with RPEs estimated from a reinforcement model, but only P300 amplitudes predicted behavioral adaptations after rule reversals. These results suggest that the FRN is an expression of the striatum-based procedural learning system which enables the gradual learning of S-R contingencies on the basis of RPEs, whereas the P300 rather reflects a fast and rule-based learning mechanism. Furthermore, ERP studies investigating memory encoding found that P300 amplitudes are predictive of subsequent declarative memory (Fabiani, Karis, & Donchin, 1986, 1990). In our present work investigating interactions between feedback processing and memory encoding, we therefore also considered the role of feedback-locked P300 amplitudes.

1.2 Declarative Memory

Declarative memory is a dynamic process initiated by the encoding of an event (for a review, see Moscovitch, Cabeza, Winocur, & Nadel, 2016). At this stage, the memory trace comprises a multitude of episodic details whose retrieval relies on the hippocampus (Squire & Zola-Morgan, 1991). In the subsequent phase of consolidation, neural replay transfers the memory trace into a more stable neocortical representation, whereby episodic details are discarded and the memory trace becomes *semanticized* (Winocur, Moscovitch, & Bontempi, 2010). The result of this long-term process is a semantic memory trace containing the gist of the initial learning episode. In the following, we describe how episodic memory can be measured and give special attention to the processes contributing to episodic memory retrieval and their ERP correlates.

1.2.1 Measuring Episodic Memory

Episodic memory can be probed in a recognition memory test in which participants decide for single items whether they have seen these items in a previous study phase. The encoding situation in the study phase can be either incidental, if participants perform an unrelated task on the items without the intention to encode them, or intentional, if participants learn the items for a later memory test. In the recognition memory test, the “old” items from the study phase are presented together with a number of not previously seen “new” items. According to signal detection theory (Green & Swets, 1966), memory decisions made by the participants can be divided into four categories: Hits (“old” items judged as “old”), misses (“old” items judged as “new”), correct rejections (“new” items judged as “new”), and false alarms (“new” items judged as “old”). A measure of memory accuracy corrected for the tendency to judge an item as “old” can be obtained by calculating *Pr* scores (Snodgrass & Corwin, 1988) as the difference between hit rates (numbers of hits relative to the number of “old” items) and false alarm rates (number of false alarms relative to the number of “new” items). Furthermore, a measure indicating the response bias of a participant in favor of judging an item as “old” can be obtained by calculating a *Br* score as the false alarm rate relative to the inverse of the *Pr* score (Snodgrass & Corwin, 1988).

1.2.2 Familiarity- and Recollection-Based Recognition Memory

Dual process models of recognition memory assume that two distinct processes, familiarity and recollection, contribute to the retrieval of episodic memories in recognition memory tests (Yonelinas, 2002). Whereas familiarity refers to a fast and context-free memory strength signal, recollection is a slower threshold process that includes the retrieval of contextual details. In particular this latter type of effortful memory retrieval process is mediated by hippocampal activity, whereas familiarity-based recognition is supported by the perirhinal cortex (Eichenbaum et al., 2007; Ranganath, 2010).

The recognition of single items does not require the retrieval of associations or contextual information and thus can be supported both by familiarity and by recollection. However, there are several ways of estimating both retrieval sub-processes on the basis of behavioral measures. For instance, different levels of confidence in memory decisions as measured by a confidence scale in the recognition memory test can be used to model receiver operating characteristic (ROC) curves from which familiarity and recollection parameter estimates can be derived (see Yonelinas and Parks, 2007, for an overview). This procedure is based on the assumption that the retrieval of contextual details associated with recollection increases the subjective confidence in the memory decision. Thus, memory decisions supported by recollection should be associated with higher confidence than those based on familiarity. Based on a similar line of reasoning, hit rates that are calculated based on high-confidence memory decisions only are another possibility to obtain a measure that relies more strongly on recollection than hit rates including all levels of confidence.

1.2.3 ERP Correlates of Memory Retrieval

In ERP studies investigating recognition memory, hits typically elicit more positive amplitudes than correct rejections, an effect which is labeled the ERP old/new effect. Familiarity and recollection are associated with qualitatively different patterns of ERP old/new effects (for reviews, see Friedman & Johnson, 2000, and Rugg & Curran, 2007; see also Paller, Voss, & Boehm, 2007, for an alternative view). Familiarity elicits an early, mid-frontal old/new effect between 300 and 500 ms after stimulus onset (also denoted as FN400), whereas recollection manifests in a late parietal old/new effect between 500 and 800 ms which often exhibits a left-lateralized topographical distribution. Consistent with what would be expected from an ERP correlate of recollection, the amplitude of the late parietal old/new effect increases with the amount of study details retrieved (Vilberg, Moosavi, & Rugg, 2006) and with confidence in recognizing studied items (Curran, 2004). In contrast, the amplitude of the early mid-frontal old/new effect is rather insensitive to the retrieval of episodic details (Vilberg et al., 2006), but generally increases with familiarity strength (Woodruff, Hayama, & Rugg, 2006).

1.3 Multiple Interacting Systems for Learning and Memory

Recent neuroimaging research has shown that, depending on the learning situation, feedback-based learning can be supported by medial temporal lobe (MTL) structures associated with declarative memory processes (Delgado & Dickerson, 2012; Shohamy & Daw, 2014). The results of some studies even suggest that feedback learning is generally accomplished by an interaction between the striatum and the hippocampus (Dickerson & Delgado, 2015; Dickerson, Li, & Delgado, 2011). Conversely, it is now known that activity in the dopaminergic midbrain and in the striatum supports declarative memory encoding (Sadeh, Shohamy, Levy, Reggev, & Maril, 2011; Schott et al., 2006) and retrieval (Scimeca & Badre, 2012). Of note, there is some evidence suggesting that memory encoding and retrieval can interfere with feedback processing and reward learning due to a competition for similar neural processing resources (Dickerson & Delgado, 2015; Wimmer, Braun, Daw, & Shohamy, 2014). In the study by Wimmer et al. (2014), participants engaged in a reward learning task in which they chose between two options that were each associated with a fluctuating reward probability. Task-unrelated pictures were presented together with the choice options. Successful memory encoding was associated with diminished reward learning, higher hippocampal-striatal connectivity, and decreased striatal RPE signals, suggesting that incidental memory encoding interfered with reward learning due to a competition for striatal processing resources.

Two types of interactions between feedback learning and declarative memory are particularly relevant for the present work and therefore covered in further detail below. Firstly, we review studies investigating modulations of declarative memory by the anticipation or reception of reward (for reviews, see Miendlarzewska et al., 2016; Shohamy & Adcock, 2010). Secondly, we focus on research showing that the processing of temporally delayed feedback engages the hippocampus and boosts memory for feedback events (Foerde & Shohamy, 2011).

1.3.1 Adaptive Memory

Apart from striatal regions, the main targets of dopaminergic projections, RPE signals are also conveyed to the hippocampus (Gasbarri, Sulli, & Packard, 1997), a brain structure crucial for declarative memory (Eichenbaum, 2004). Because dopamine signals motivationally important events and thereby promote adaptive behavior (Bromberg-Martin et al., 2010), Shohamy and Adcock (2010) coined the term *adaptive memory* to characterize dopaminergic modulations of declarative memory that have become a focus of research during the last two decades. A theoretical foundation for this line of research was laid out by Lisman and Grace (2005) who proposed that the hippocampus and the ventral tegmental area (VTA), a dopaminergic midbrain structure adjacent to the substantia nigra, form a functional loop. According to the Lisman and Grace (2005) framework, hippocampal activity associated with the processing of novel stimuli is projected to the VTA where it contributes to the novelty-dependent firing of dopaminergic cells. In the upward arm of the loop, dopamine signals are projected from the VTA to the hippocampus, where they promote long-term potentiation (LTP) and learning.

In a similar vein, Wittmann et al. (2005) argued that activity in dopaminergic midbrain regions associated with reward anticipation should facilitate the late stage of LTP in the hippocampus and thereby enhance long-term learning outcomes. In the study by Wittmann et al. (2005), participants situated in an fMRI scanner performed a number categorization task in which they had to decide as fast as possible whether a number was larger or smaller than five. Each number was preceded by the picture of a living thing or a man-made object, and only pictures from one of these categories indicated that a fast and correct response in the number categorization task would be rewarded with money. Subsequently, participants were given a surprise memory test in which they had to discriminate the cue pictures presented during the learning phase from new pictures. Three weeks later, participants returned to the lab for a second memory test that also included “remember/know” and source memory questions. Old/new discrimination did not differ between rewarded and nonrewarded pictures, neither in the immediate nor in the delayed memory test. In the delayed memory test, however, recollection as measured by “remember” responses and source memory were better for rewarded pictures than for nonrewarded ones. A subsequent memory analysis revealed that hippocampal BOLD signals were larger for recognized than for forgotten pictures. Importantly, reward-related activity measured during the learning phase in the substantia nigra predicted subsequent memory only in the delayed memory test, and only for rewarded pictures, but not for nonrewarded ones. These results indicate that dopamine signals boost memory by supporting the consolidation of hippocampal memory traces.

There is, however, evidence suggesting that reward learning can boost declarative memory well before memory consolidation takes place. In a study that explored recognition memory for objects that were associated with rewards or losses in younger and older adults, Eppinger, Herbert, and Kray (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 rapidly boost familiarity-based recognition without affecting recollection.

The beneficial effects of dopamine signals for learning are not confined to those stimuli eliciting dopaminergic activity, but also include unrelated stimuli presented in temporal proximity (Lisman, Grace, & Düzel, 2011). Consistent with this “penumbra” hypothesis, Murayama and Kitagami (2014) found that reward cues in a reaction time task enhanced long-term memory for task-irrelevant pictures of objects presented before the rewarded trials. In a study by Murty and Adcock (2014), participants performed a reaction time task while fMRI scans were taken. Each trial was preceded by a cue that signaled the chance to win a high or low reward on the upcoming trial. Participants were then repeatedly presented a color object that turned grayscale after 10 to 11 repetitions, whereupon participants were instructed to respond as fast as possible in order to win a reward. In half of the trials, the sequence of presentations of the color object was interrupted by a highly similar, but novel image ("expectancy violation"). Following the reaction time task, memory for the expectancy violations objects was probed in a recognition memory test that yielded higher hit rates for expectancy violations preceded by a high reward cue than for those preceded by a low reward cue. Murty and Adcock (2014) found that cues signaling a high reward were associated with activity in the VTA that predicted subsequent hippocampal activity during the processing of expectancy violations via a distributed network of brain regions including (medial and ventrolateral) prefrontal and visual cortices. These results could reflect a mechanism by which reward anticipation guides attentional and mnemonic processes towards encoding salient and potentially goal-relevant information.

To date, only few studies have adressed the question how the beneficial effect of dopamine signals on declarative memory encoding is reflected in ERPs elicited by rewards or performance feedback. In a study by Arbel, Goforth, & Donchin (2013), participants used feedback to learn arbitrary associations between novel objects and nonwords. On the next day, a memory test was conducted in which participants were given lists of the novel objects and nonwords presented in the learning phase and had to assign to each novel object the nonword with which it was associated in the learning phase. FRN amplitudes elicited by feedback in the learning phase were not related to subsequent declarative learning outcomes, however, a later ERP component that resembled in its spatiotemporal characteristics the reward positivity differentiated between subsequently recognized and forgotten associations. These 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 in ERPs as well as in striatal BOLD signals elicited by the processing of positive feedback, which is in line with studies that have localized the neural generators of the reward positivity in the basal ganglia (Foti, Weinberg, Dien, & Hajcak, 2011).

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 were tasked to learn the associations that were subsequently probed in the memory test. Furthermore, 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 not for the to-be-learned stimuli but for the feedback 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 experiments described in the present work.

1.3.2 Delayed Feedback Processing

Temporally delayed feedback processing is associated with a strong involvement of the hippocampus and a high proportion of correct high-confidence memory decisions for feedback pictures (Foerde & Shohamy, 2011; Lighthall, Pearson, Huettel, & Cabeza, 2018). In the study by Foerde and Shohamy, participants underwent fMRI scans while they learned associations between Asian characters and two responses by trial and error. Performance feedback was provided in the form of indoor and outdoor scene pictures and arrived either immediately after the response or with a temporal delay of three or six seconds. Shortly after completing the feedback learning task, participants were given a surprise memory test for the feedback pictures presented during the learning phase. Hippocampal and striatal BOLD signals recorded during the processing of immediate and delayed feedback correlated with RPEs derived from a computational reinforcement learning model. 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 declarative memory for delayed feedback events should benefit from the hippocampal involvement during the initial processing of these events and, consistent with their prediction, found that delayed feedback pictures were remembered better than immediate feedback pictures. These results suggest that in delayed feedback processing, the procedural and declarative learning systems interact cooperatively and without interference on either side. Rather, declarative memory for delayed feedback events benefits from the hippocampal involvement in delayed feedback processing.

Consistent with the finding obtained in fMRI studies that delayed feedback processing is associated with a decreased involvement of the striatum-based procedural learning system (Foerde & Shohamy, 2011; Lighthall et al., 2018), ERP studies found that delayed feedback processing is associated with dimished amplitudes of the $\mathrm{FRN}_{\mathrm{diff}}$ reflecting the processing of unexpected positive outcomes (Peterburs, Kobza, & Bellebaum, 2016; Weismüller & Bellebaum, 2016). Furthermore, in the study by Peterburs et al. (2016), long delayed feedback elicited larger $\mathrm{FRN}_{\mathrm{peak}}$ amplitudes than shortly delayed feedback. It is thus conceivable that the $\mathrm{FRN}_{\mathrm{peak}}$ is more sensitive to the processing of expectancy violations in the declarative learning system and is less specific for the processing of positive or negative action outcomes.

1.4 Research Questions

Even though the brain systems associated with feedback-based learning and declarative memory have been disclosed (Eichenbaum & Cohen, 2001; Shohamy & Daw, 2014), it is less clear under which circumstances these learning systems interact, and how this is reflected in electrophysiological measures of feedback processing. This dissertation aims to shed further light on these questions by investigating how feedback processing as reflected in the FRN interacts with concurrent incidental memory encoding under two different conditions, namely when feedback processing strongly relies on the procedural learning system (shortly delayed feedback) or engages the declarative learning system (long delayed feedback). 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 work aimed at investigating how feedback timing affects the incidental encoding and subsequent retrieval of feedback events.

To explore whether successful memory encoding modulates the FRN, a subsequent memory paradigm was used: EEG activity recorded during feedback picture presentation in the learning task was sorted according to whether a picture was subsequently remembered or forgotten (Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980; for reviews, see Cohen et al., 2015, or Paller & Wagner, 2002). Finding that the amplitude of the $\mathrm{FRN}_{\mathrm{peak}}$ or $\mathrm{FRN}_{\mathrm{diff}}$ differs between subsequently remembered and forgotten pictures would suggest that feedback processing and memory encoding interact electrophysiologically.

2 Experiment 1: Electrophysiological Reward Signals Predict Episodic Memory for Immediate and Delayed Positive Feedback Events

Experiment 1 investigated how the processing of shortly and long delayed feedback (500 ms vs. 6500 ms feedback delay) in a probabilistic feedback learning task interacts with the incidental encoding of task-irrelevant pictures presented together with the feedback, and how this interaction is reflected in the ERP correlate of dopaminergic reward prediction errors in feedback processing (i.e., the FRN). ERP old-new effects and behavioral estimates of familiarity and recollection were used to examine effects of feedback valence and feedback delay on recognition memory for the pictures. This study was published in *Brain Research*, *1701*, 64-74 (Höltje & Mecklinger, 2018).

2.1 Introduction

Participants performed a probabilistic feedback learning task in which they learned 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, Kray, Mock, & Mecklinger, 2008; Peterburs, Kobza, & Bellebaum, 2016, for studies that used a similar approach). After the learning task, recognition memory for the pictures was tested in a surprise memory test.

Behaviorally, we aimed to replicate the results from previous studies showing that pictures presented together with positive feedback are remembered better than those presented together with negative feedback (Davidow, Foerde, Galván, & Shohamy, 2016), and long delayed feedback pictures better than shortly delayed ones (Foerde & Shohamy, 2011). We expected to find modulations of FRN amplitudes by feedback timing similar to those obtained in previous studies: Long delayed feedback should elicit larger FRN_{peak} and smaller FRN_{diff} amplitudes than shortly delayed feedback (Peterburs et al., 2016; Weismüller & Bellebaum, 2016). Finding a subsequent memory effect (SME) that resembles in its spatiotemporal characteristics the FRN would indicate that feedback processing and incidental memory encoding interact electrophysiologically. 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.

2.2 Method

2.2.1 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 psychiatrical 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.

2.2.2 Materials and Procedure

The preparations for the EEG recording took about 45 minutes. Thereafter, participants were seated in front of a 19‘‘ computer screen with a resolution of 1280 x 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 minutes 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 minutes.

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, Ehinger, & Wolfe, 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.

2.2.2.1 Learning Phase

Four different Chinese characters (汉,礼,归,仗) 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. 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 Figure 2.1A. 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 x 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.

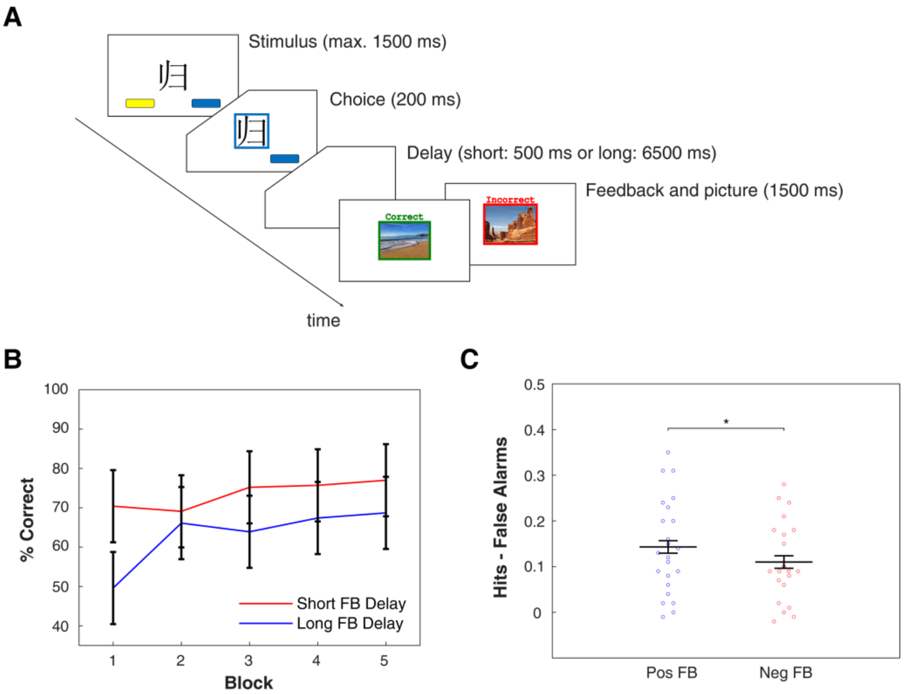

Figure 2.1: The trial procedure (A). At the beginning of each trial, one of four Chinese characters was presented. As soon as the participant made a choice, it was displayed for a short time (200 ms). Feedback arrived with a short (500 ms) or long (6500 ms) delay. During the delay, a blank screen was 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. Percentages of correct responses in the learning phase (B) and Pr scores in the test phase (C). Error bars indicate 95% confidence intervals according to Jarmasz and Hollands (2009).

2.2.2.2 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 & 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, Barrett, Harlow, & Yonelinas, 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.

2.2.3 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 µV/ms, a maximal difference of values of 200 µV during intervals of 200 ms, and minimal and maximal allowed total amplitudes of ± 100 µV. 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.

2.2.3.1 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.

2.2.3.2 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 & 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, Ieuji, & Federmeier, 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 & Johnson, 2000; Rugg & Curran, 2007).

2.2.4 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*.

2.3 Results

2.3.1 Behavioral Data

2.3.1.1 Learning Phase

Figure 2.1B 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.

2.3.1.2 Recognition Memory Test

Mean percentages of Pr scores and high-confidence Pr scores are given in Table 2.1. 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.

The analysis of the DPSD model parameters 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, $t(22) = 0.80$, $p = .43$, $d = 0.10$.

Table 2.1: 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)	15.0 (2.7)	10.6 (2.6)	15.1 (2.9)	11.5 (2.9)

2.3.2 Electrophysiological Data

2.3.2.1 ERPs in the Learning Phase

FRN analysis. Negative minus positive feedback difference waves are shown as a function of FB Validity and Delay in Figure 2.2B. The corresponding mean and peak amplitude measures are displayed in Table 2.2. FRN$_{\text{diff}}$ 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$_{\text{diff}}$ 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.

Table 2.2: Means (standard errors) of FRN_{diff} and FRN_{peak} peak and mean amplitudes.

	FRNdiff				**FRNpeak**			
	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 Amp.	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 Amp.	-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)

The original grand average waveforms are shown as a function of FB Validity, Delay, and Valence in Figure 2.2A. The corresponding FRN_{peak} amplitudes are displayed in Table 2.2. 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.

As evident from Figure 2.2A, 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 – 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 × 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, $t(22) = 1.19$, $p = .25$, $d = 0.14$.

Subsequent memory analysis. The waveforms for positive and negative feedback pictures that were subsequently remembered or forgotten are depicted in Figure 2.2C. 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 $\mathrm{FRN}_{\mathrm{peak}}$ amplitudes yielded no significant effects, all p-values > .12.

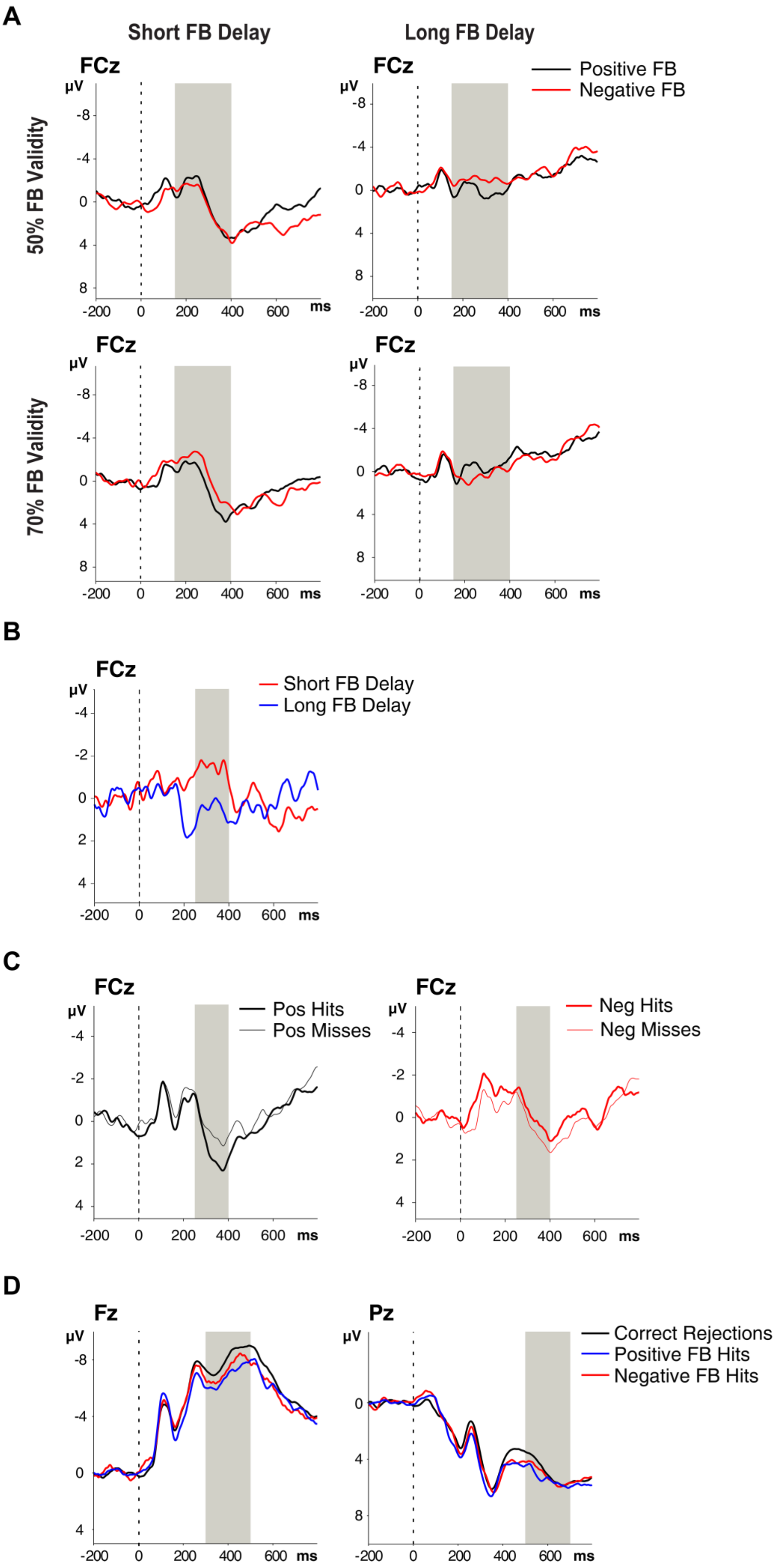
A
Short FB Delay
Long FB Delay
FCz
μV
50% FB Validity
70% FB Validity
-8
-4
0
4
8
-200
0
200
400
600
ms
Positive FB
Negative FB
B
FCz
Short FB Delay
Long FB Delay
-4
-2
0
2
4
C
FCz
Pos Hits
Pos Misses
Neg Hits
Neg Misses
D
Fz
Pz
Correct Rejections
Positive FB Hits
Negative FB Hits

Figure 2.2: Feedback-locked ERP waveforms recorded in the learning phase (A), negative minus positive feedback difference waves (B), and waveforms associated with subsequently remembered and forgotten feedback pictures (C) at electrode FCz. Shaded areas indicate the time windows used for the detection of P200/N200 peak amplitudes (150 – 400 ms) and FRN_{diff} peak and mean amplitudes (250 – 400 ms). Waveforms associated with correct memory decisions in the test phase are shown for two representative frontal and parietal electrodes (D). Shaded areas indicate the time windows in which early (300 – 500 ms) and late (500 – 700 ms) old/new effects were analyzed.

2.3.2.2 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 Figure 2.2D. 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 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.

2.4 Discussion

In Experiment 1, 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 learning paradigm that allows for 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 & 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 signalised 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, Govoni, Naveh-Benjamin, & Anderson, 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 (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, Luhmann, Bress, & Hajcak, 2012; Weismüller & 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 $\mathrm{FRN}_{\mathrm{peak}}$ amplitudes were larger for long delayed than for shortly delayed feedback, we found a reduction of the $\mathrm{FRN}_{\mathrm{diff}}$ for delayed feedback that was contingent on feedback utility. In other words, the $\mathrm{FRN}_{\mathrm{diff}}$ 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 $\mathrm{FRN}_{\mathrm{diff}}$ 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. Figure 2.1B), 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 $\mathrm{FRN}_{\mathrm{peak}}$ 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 $\mathrm{FRN}_{\mathrm{diff}}$ and $\mathrm{FRN}_{\mathrm{peak}}$ 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 $\mathrm{FRN}_{\mathrm{diff}}$ was most pronounced and was also largest at the FCz recording site at which largest FRN were obtained. In contrast, $\mathrm{FRN}_{\mathrm{peak}}$ amplitudes did not differ as a function of subsequent remembering. This pattern of results is consistent with the view outlined above, that whereas the $\mathrm{FRN}_{\mathrm{peak}}$ is related to the processing of expectancy violations (Ferdinand et al., 2012), the $\mathrm{FRN}_{\mathrm{diff}}$ 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

$\mathrm{FRN}_{\mathrm{diff}}$, we propose that it reflects positive reward prediction error signals that modulate memory encoding for events associated with positive feedback in this early time interval. Thus, positive feedback processing (as reflected in the $\mathrm{FRN}_{\mathrm{diff}}$) 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 & Shohamy, 2011; Shohamy & Adcock, 2010).

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 & 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 serval times during learning. This led to high memory performance and presumably also to higher amounts of recollection as compared to the present study.

3 Experiment 2: Feedback Timing Modulates Interactions Between Feedback Processing and Memory Encoding

In Experiment 2, a subsequent memory paradigm was employed to investigate how the incidental encoding of feedback pictures presented with a short or long temporal delay (500 ms vs. 6500 ms) in a probabilistic learning task affects the ERP correlate of RPEs in feedback processing (i.e., the FRN). In an ensuing test phase, a surprise recognition memory test for the feedback pictures was conducted. FRN amplitudes measured in the feedback-locked ERPs recorded during the learning phase ($\mathrm{FRN}_{\mathrm{peak}}$) and in the negative minus positive feedback difference wave ($\mathrm{FRN}_{\mathrm{diff}}$) were compared for subsequently remembered and forgotten feedback pictures. A complementary model-based single trial analysis was conducted to validate models of the functional significance of the FRN. We also examined how interactions between shortly and long delayed feedback processing and incidental memory encoding affect feedback-locked N170 and P300 amplitudes in the learning phase. ERP old/new effects were used to examine effects of feedback delay on recognition memory for the feedback pictures. This study was published in *Cognitive, Affective, & Behavioral Neuroscience*, *20*(2), 250-264 (Höltje & Mecklinger, 2020).

3.1 Introduction

In Experiment 1, we did not find the expected effect of feedback delay on memory for the scene pictures presented together with the feedback (i.e., better memory for pictures presented with long delayed feedback than for those presented with shortly delayed feedback). Because the pictures were not relevant for the probabilistic feedback learning task, it is conceivable that the extent of processing allotted to the pictures was not sufficient to enable them to benefit from the hippocampal activity associated with delayed feedback processing. In Experiment 2, the picture category signalled the valence of the feedback (outdoor = positive, indoor = negative) to ensure that participants needed to process the picture category in order to use the feedback for learning.

The main goal of Experiment 2 was to investigate interactions between feedback-based learning and memory encoding by focusing on the FRN as the electrophysiological correlate of reward prediction error signals in feedback processing. With regard to the FRN, we expected to replicate previous findings, namely that shortly delayed feedback is associated with larger $\mathrm{FRN}_{\mathrm{diff}}$ amplitudes than long delayed feedback, and the reverse pattern (larger amplitudes for long delayed than short delayed feedback) applies to the $\mathrm{FRN}_{\mathrm{peak}}$.

In recent years, there has been considerable debate about the question whether the FRN reflects the processing of reward prediction errors, a parameter that codes the reward value (positive or negative) and expectedness of an outcome. An alternative account states that the FRN is more sensitive to general expectancy violations irrespective of valence (e.g., Ferdinand et al., 2012; Oliveira, McDonald, & Goodman, 2007). Computational modeling is a promising method to decide between these accounts because it enables to compute trial-by-trial estimates of prediction errors. In Experiment 2, a computational reinforcement learning model was used to estimate trial-by-trial reward prediction errors (RPEs). Best fits between RPEs and EEG activity in the time periods in which FRN effects are present would confirm that the FRN reflects the processing of RPEs. We also computed unsigned RPEs that code the expectedness of an outcome without taking into account its valence (better or worse than expected). These unsigned RPEs thereby constitute salience prediction errors (SPEs) that are largest when outcomes are highly unexpected irrespective of their valence. As we assumed that the $\mathrm{FRN}_{\mathrm{peak}}$ is more sensitive to more general expectancy violations, we expected best fits between SPEs and EEG activity in the $\mathrm{FRN}_{\mathrm{peak}}$ time interval.

In addition, we also explored other ERP components elicited by feedback stimuli that have been shown to be sensitive to feedback delay manipulations, i.e., the N170 and the P300.

We expected long delayed feedback to elicit larger N170 amplitudes than shortly delayed feedback (Arbel et al., 2017). Furthermore, based on the results obtained in two recent studies (Wang, Chen, Lei, & Li, 2014; Weismüller & Bellebaum, 2016), we expected immediate feedback to elicit stronger P300 amplitudes than delayed feedback.

Another aim of the present study was to explore the effects of feedback delay on the retrieval of feedback events. Even though previous studies have shown that reward or positive feedback selectively boosts fast and context-free familiarity-based remembering and selectively modulates the mid-frontal old/new effect (Eppinger et al., 2010; Höltje & Mecklinger, 2018), it is less clear how feedback timing affects memory retrieval. Previous studies have found that delayed feedback processing is associated with an involvement of the hippocampus (Foerde & Shohamy, 2011; Lighthall et al., 2018). Because recollection relies on the hippocampus (Eichenbaum et al., 2007) we expected long delayed feedback pictures to be associated with a stronger late parietal old/new effect than shortly delayed feedback pictures.

3.2 Method

3.2.1 Participants

Fifty-eight healthy young adults participated in the experiment. All participants were German native speakers, had normal or corrected-to-normal vision and no self-reported neurological or psychiatrical conditions. The experimental procedures were carried out in accordance with the Declaration of Helsinki and approved by the ethics board of the Faculty of Human and Business Sciences at Saarland University. Participants gave their informed consent before the experiment and received money (8 € per hour) or course credit as a compensation for their participation. Fourteen participants had to be excluded from all analyses because they did not learn the associations in the learning phase (5), as determined by their performance in the final block of the probabilistic learning task (see 2.3), or performed at chance level in the test phase (9). The incidental nature of memory encoding in the probabilistic learning task may have increased task difficulty and thereby contributed to the relatively high number of participants excluded due to poor recognition performance. One further participant had to be excluded because of a technical error. Thus, the behavioral analyses are based on data from 43 participants (36 female, 36 right-handed). Their age ranged between 19 and 30 years, with a median age of 23 years. Due to the exclusion criteria for ERP data, these analyses are based on a lesser number of data sets (see 2.5).

3.2.2 Stimuli

A total of 560 scene pictures, consisting of 280 indoor and 280 outdoor scenes, were used in this experiment. Four-hundred of these pictures were the same as in the Höltje and Mecklinger (2018) study. One hundred and sixty additional scene pictures were collected 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.

3.2.3 Procedure

The preparations for the EEG recording took about 45 minutes. Thereafter, participants were seated in front of a 19‘‘ computer screen with a resolution of 1280 x 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 (25 min), a test phase (35 min), and two quiet rest phases of 15 minutes each that took place before and after the learning phase. In the learning phase, participants learned associations between four different Chinese characters and two response keys in a probabilistic learning task with probabilistic feedback. Scene pictures were presented as feedback, and the picture category designated the valence of the feedback with a fixed mapping for all participants (outdoor = correct, indoor = incorrect; cf. Foerde & Shohamy, 2011). The learning phase was followed by one block in which participants continued performing the task without feedback. The performance in this block served as a criterion for learning success, and participants who performed at chance level in this block were excluded from all analyses (see 3.2.1). In the test phase that followed approximately twenty minutes after the learning phase, recognition memory for the scene pictures was tested in a surprise memory test.

3.2.3.1 Learning Phase

Four different Chinese characters (汉,礼,归,仗) were used in the probabilistic learning task, with two characters assigned to each of the two feedback delay conditions (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. Feedback was always presented with 70% validity, meaning that when participants responded with the correct (incorrect) button, they received positive (negative) feedback in seven out of ten times. Participants were informed that the feedback would not always be valid, but the instructions emphasized that the feedback would be valid most of the time, and that it was possible to use the feedback for learning. Overall, there were 200 trials, which were divided into five blocks of 40 trials each. Each character was presented ten times per block, in pseudorandomized order, so that no character was repeated on the next trial, and not more than three characters from the same delay condition were presented in direct succession. Participants were given eight practice trials before they started working on the task. The scene pictures were divided into two lists of 280 pictures each (140 outdoor and 140 indoor scenes). The pictures from one of these lists were used as feedback pictures in the learning phase, and the pictures from the other list served as lures in the ensuing memory test. The assignment of the two lists to the feedback or lure function was balanced across subjects. Each picture was presented only once during learning, but not every picture from the list was necessarily used as a feedback picture. The reason for this is that the number of pictures presented from one category (indoor or outdoor scene) ultimately depended on the number of correct responses given by the participant. Importantly, even if a participant's responses were 100% correct (incorrect), no more than 140 outdoor (indoor) scene pictures were presented. The reason for this is that feedback was presented with 70% validity, as stated above.

A schematic of the trial procedure is depicted in Figure 3.1A. Each trial of the probabilistic learning task started with a central fixation cross (500 ms), followed by a Chinese character that was presented in the centre of the screen. 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 a duration defined by the delay condition (short: 500 ms, long: 6500 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. The delay period was followed by a central fixation cross (500 ms) and a feedback picture (1500 ms). After the feedback, a blank screen was presented for 1000 ms before the next trial started.

Performance in the learning phase was assessed as the proportion of correct responses in the probabilistic learning task and in the final block of the task without feedback. A variance-stabilizing transformation (arcsine transformation; Winer, Brown, & Michels, 1991) was applied to the proportions of correct responses before submitting them to statistical analyses.

3.2.3.2 Test Phase

The 200 feedback pictures from the learning phase were presented together with 200 new scene pictures in pseudorandomized order, so that not more than three adjacent target or lure items were presented in direct succession. Moreover, the same number of target pictures from each category (outdoor and indoor) was presented as lure pictures. Participants were admitted a short break after every 80 trials. In the beginning of each trial, a fixation cross was presented with a duration jittered between 1000 and 1500 ms, followed by a picture presented for 1500 ms. Participants were instructed to decide for every picture whether it was old or new using a six-step confidence scale („sure old“, „probably old“, „maybe old“, „maybe new“, „probably new“, „sure new“). 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. The old/new decision could be given as soon as the picture was presented. 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 & 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.

3.2.4 Computational Modeling

A standard reinforcement learning model (Q-learning; Watkins, 1989) with two free parameters (learning rate α and inverse temperature β) was fitted to each participant’s observed choices in the learning phase (Daw, 2011). The Q-value was initialized at a value of

0.5 on the first trial. The relationship between Q-values and observed choices was assumed to follow a softmax distribution. The learning rate α and inverse temperature β were estimated using a maximum likelihood estimation procedure. The MATLAB function fmincon was used to identify parameter values that minimized the inverse data likelihood (which is equal to maximizing the data likelihood). The estimation of the free parameters was iterated twenty times with random starting points and, as recommended by Daw (2011), constrained by prior distributions that penalized the data likelihood for extreme parameter values. The prior distribution used for the learning rate α was a Beta distribution with the shape parameters α = 1.1 and β = 1.1. This distribution puts a strong penalty on learning rate values smaller than 0 and larger than 1. The inverse temperature β was constrained by a Gamma distribution with the shape parameter α = 1.2 and the scale parameter θ = 5. This distribution puts a strong penalty on temperature values that are either smaller than or much larger than zero. For every participant, the parameter pair that yielded the highest likelihood was selected. These optimal parameters were averaged across subjects and used as model parameters. Initially, two separate models were fit to the short and long delay conditions, the parameters of which are given in Table 3.1. Because the estimated parameters and likelihoods did not differ between the delay conditions (learning rate α: $t(42) = 0.24$, $p = .81$, $d = 0.05$; inverse temperature β: $t(42) = 0.46$, $p = .65$, $d = 0.09$; likelihood: $t(42) = 0.26$, $p = .79$, $d = 0.04$), a combined model, collapsed across delay conditions, was fit to the data (cf. Foerde and Shohamy, 2011). Likelihood ratio tests (Daw, 2011) showed that all models provided a better fit to the data than a chance model. Individual datapoints for estimated parameters and model fits are provided in the supplementary online material. The combined model parameters were then used to calculate trial-by-trial estimates of reward prediction errors (RPEs) for every subject. Salience prediction errors (SPEs) were computed by calculating the absolute values of each RPE estimate.

Table 3.1: Reinforcement learning model parameters.

	Short Delay		**Long Delay**		**Combined**	
	Mean	*SEM*	Mean	*SEM*	Mean	*SEM*
Learning rate α	0.22	0.04	0.21	0.03	0.16	0.03
Inverse temperature β	10.37	1.25	9.72	1.10	11.13	1.18
Pseudo-R^2	0.32	0.05	0.30	0.05	0.29	0.05
Model fit (log likelihood)	-47.30	3.75	-48.35	3.72	-98.79	7.58
Chance model fit	-69.31		-69.31		-138.63	
Likelihood ratio test	p < .001		p < .001		p < .001	

3.2.5 EEG Recording and Processing

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, the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes for Matlab (MathWorks, Inc.) were 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 – 30 Hz using a second order Butterworth filter. Segments were extracted from the learning phase data from 200 ms before feedback onset to 800 ms thereafter, and segments from 200 ms before picture onset to 1500 ms thereafter were extracted from the test phase data. The segments were baseline-corrected based on activity during the 200 ms before feedback or picture onset. Independent component analysis (ICA) was applied to the segmented data to correct for ocular artifacts. Components associated with ocular artifacts were identified and rejected manually based on their activations and topographies. Segments containing artifacts were rejected using the following criteria: A minimal and maximal allowed total amplitude of ± 100 µV, a maximal difference of values of 150 µV during intervals of 200 ms (window steps of 100 ms), a maximal allowed voltage step of 30 µV/ms, and maximal 100 ms activity with a deviation of less than 0.4 µV from the maximum or minimum voltage in the segment. On average, 1.25 % and 1.6 % of all segments were rejected in the learning phase and the test phase, respectively. One data set was excluded from the learning phase ERP analysis because of more than 25 % rejected segments. For the same reason, two data sets were excluded from the test phase ERP analysis. Grand average waveforms were low-pass filtered at 10 Hz for illustration purposes.

3.2.5.1 ERPs in the Learning Phase

ERPs were averaged for every combination of the factors Delay (short, long), Valence (positive, negative), and Memory (hits, misses). Feedback pictures judged as being “old” or “new” in the test phase were counted as hits and misses, respectively. For this purpose, the three corresponding steps of the confidence scale were collapsed into “old”- and “new”-decisions. Six data sets had to be excluded from this analysis because there were not enough artifact-free trials (< 7) to calculate reliable ERPs in one of the conditions. For the purpose of peak detection, the subject average waveforms were low-pass filtered at 10 Hz.

Because FRN effects are typically largest at frontocentral sites (Holroyd & Coles, 2002; Miltner et al., 1997), FRN measures were analyzed at electrode FCz. The FRN was quantified in two ways: The $\mathrm{FRN}_{\mathrm{peak}}$ was measured according to an algorithm described in Holroyd et al. (2003; see Ferdinand et al., 2012; Holroyd et al., 2006; Peterburs et al., 2016, for studies that used a similar approach) as the difference between the N200 peak (180 – 300 ms) and the preceding P200 peak (140 – 200 ms). The FRN_{diff} was measured as the peak amplitude between 300 and 450 ms in the negative minus positive feedback difference wave (cf. Becker et al., 2014; Peterburs et al., 2016; Weismüller and Bellebaum, 2016).

For the N170 quantification, electrodes were re-referenced to the average of all electrodes (cf. Arbel, Hong, Baker, & Holroyd, 2017). This was done because the mastoid electrodes are located in close proximity to the occipito-temporal electrode sites at which the N170 is usually largest, which complicates the measurement of the N170 (Luck, 2014). N170 amplitudes were quantified as the difference between the N170 peak (140 – 200 ms) and the preceding P100 peak (90 – 150 ms) at electrodes P7 and P8.

As determined by an inspection of the waveforms, the feedback-locked P300 peaked around 500 ms at electrode Pz. P300 mean amplitudes between 450 and 600 ms were analyzed at electrodes Fz and Pz.

3.2.5.2 Single Trial EEG Analysis

From all artifact-free EEG segments recorded in the learning phase, single trial mean amplitudes at electrode FCz were extracted in 32 time bins of 25 ms duration each, ranging from 0 to 800 ms after stimulus onset. To ensure that the results of the single trial EEG analysis were based on the same data as the ERP results in the learning phase, we restricted this analysis to the same 36 subjects that were included in the ERP analysis. For every subject, standardized trial-by-trial RPE and SPE estimates derived from the reinforcement learning model (see 2.4) were used to predict standardized single-trial mean amplitudes across the experimental conditions in separate linear regression models for every time bin. The correlations (beta weights) between model-derived RPEs/SPEs and single trial EEG amplitudes were then submitted to a statistical analysis.

3.2.5.3 ERPs in the Test Phase

ERPs were averaged for every combination of the factors Valence (positive, negative) and Item Status (short delay hits, long delay hits, correct rejections). One data set had to be excluded from this analysis because there were not enough artifact-free trials (< 7) to calculate reliable ERPs in one of the conditions. Mean amplitudes were analyzed in two adjacent time windows, ranging from 300 – 500 ms and 500 – 1100 ms. The early time window is typically used for the analysis of FN400 effects in ERP studies of recognition memory (see Rugg & Curran, 2007, for a review). The later 500 – 1100 ms time window was chosen because, as evident from Figure 3.3C, an inspection of the waveforms suggested that the late old/new effect continued until approximately 1100 ms at anterior electrodes. In order to cover frontal electrode sites, where FN400 effects are largest as well as parietal electrode sites at which late old/new effects are typically most pronounced, mean amplitudes were analyzed at 15 electrodes broadly distributed across the scalp (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4).

3.2.6 Statistical Analyses

All statistical analyses were conducted using IBM SPSS software. Behavioral and electrophysiological measures were analyzed using repeated measures ANOVAs and dependent *t*-tests. 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. For dependent *t*-tests, *d* was calculated according to Dunlap, Cortina, Vaslow, & Burke (1996), taking into account the correlations between measurements. Error margins in graphs represent 95% confidence intervals based on the mean square error of the depicted effect (Jarmasz & Hollands, 2009).

3.3 Results

3.3.1 Performance in the Learning Phase

Correct responses in the probabilistic learning task are depicted as a function of Delay and Block in Figure 3.1B and were analyzed in a two (Delay: Short, long) by five (Block) ANOVA. A main effect of Block was found, $F(3.04,127.56) = 70.08$, $p_{\text{corr}} < .001$, $\eta_p^2 = .63$, indicating that the frequency of correct responses changed during the course of the learning task. Subsidiary *t*-tests revealed that correct responses increased from the first to the second block, $t(42) = 7.37$, $p < .001$, $d = 0.91$, from the second to the third block, $t(42) = 4.22$, $p < .001$, $d = 0.52$, from the third block to the fourth, $t(42) = 2.61$, $p < .05$, $d = 0.33$, and from the fourth block to the fifth, $t(42) = 2.03$, $p < .05$, $d = 0.24$. No main effect of Delay, $F(1,42) < 1$, $p = .63$, $\eta_p^2 = .01$, and no Delay by Block interaction, $F(4,168) < 1$, $p = .96$, $\eta_p^2 = .00$, were found. Correct responses in the final block of the probabilistic learning task (without feedback) are shown in Figure 3.1B and did not differ between the two Delay conditions, $t(42) = 0.98$, $p = .33$, $d = 0.20$.

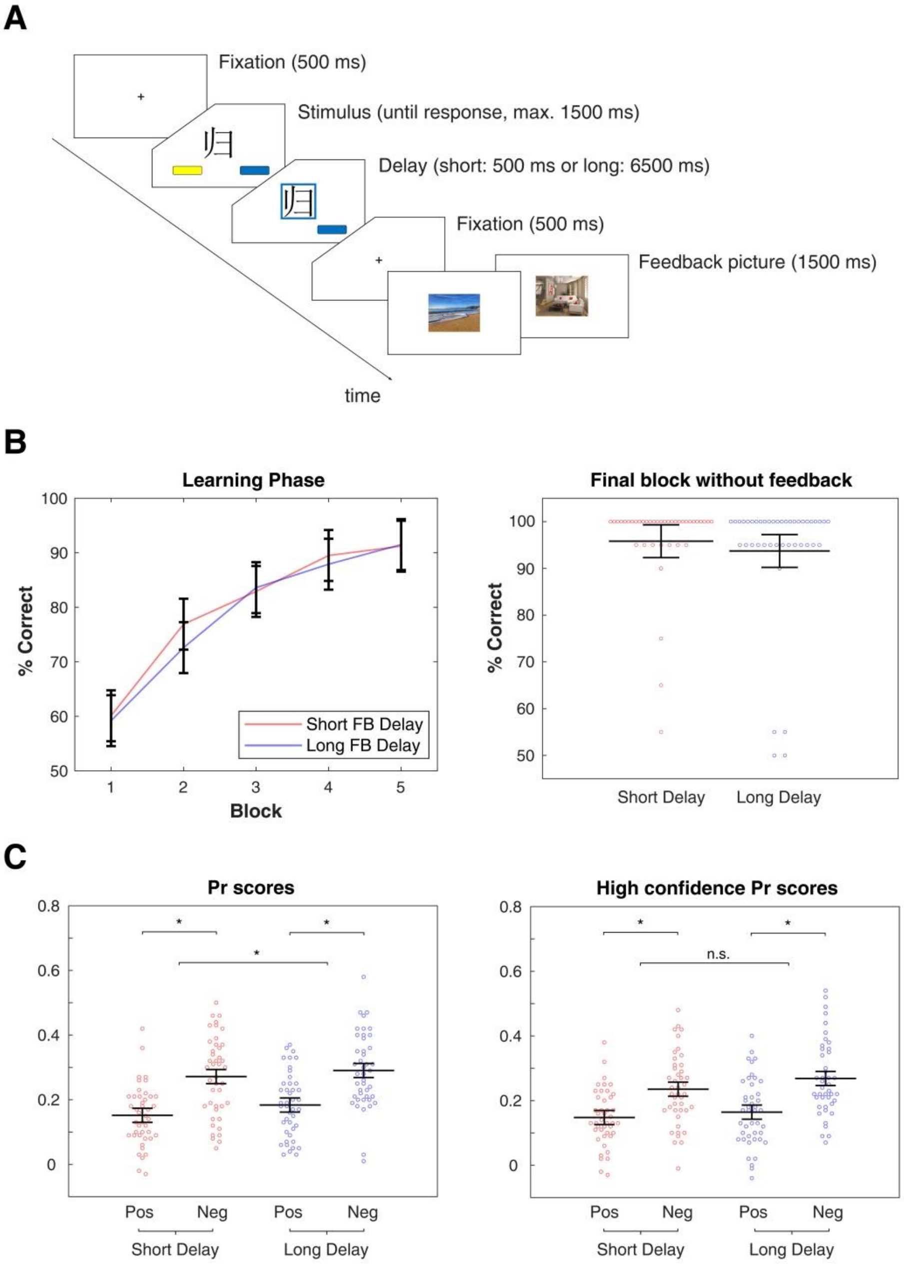

Figure 3.1: Trial procedure in the probabilistic learning task (A): At the beginning of each trial, one of four Chinese characters was presented. As soon as the participant made a choice, it was displayed for a duration defined by the delay condition (short: 500 ms, long: 6500 ms). Outdoor (indoor) scene pictures were presented as positive (negative) feedback. Behavioral results in the learning phase (B) and in the test phase (C). Beeswarm plots show individual datapoints in addition to means and confidence intervals.

3.3.2 Recognition Memory in the Test Phase

Pr scores and high-confidence Pr scores are given as a function of Delay and Valence in Figure 3.1C. Pr scores were analyzed in a two (Delay: Short, long) by two (Valence: Positive, negative) ANOVA. There was a significant main effect of Delay, $F(1,42) = 5.08$, $p < .05$, η_p^2

= .11, driven by higher Pr scores for long delayed feedback pictures. The main effect of Valence was also significant, $F(1,42) = 40.72$, $p < .001$, $\eta_p^2 = .49$, reflecting higher Pr scores for negative (indoor) than for positive (outdoor) feedback pictures. The Delay by Valence interaction was not significant, $F(1,42) < 1$, $p = .56$, $\eta_p^2 = .01$.

The analysis of the high-confidence Pr scores did not yield a significant main effect of Delay, $F(1,42) = 3.49$, $p = .07$, $\eta_p^2 = .08$, but only a strong main effect of Valence, $F(1,42) = 40.23$, $p < .001$, $\eta_p^2 = .49$, reflecting higher scores for negative (indoor) than for positive (outdoor) feedback pictures. The Delay by Valence interaction was not significant, $F(1,42) < 1$, $p = .41$, $\eta_p^2 = .02$.

3.3.3 ERPs in the Learning Phase

3.3.3.1 FRN$_{peak}$ and FRN$_{diff}$

Feedback-locked ERPs in the learning phase are shown at electrode FCz as a function of Delay, Valence, and Memory in Figure 3.2A. The corresponding FRN$_{peak}$ amplitudes were analyzed in a two (Delay: Short, long) by two (Valence: Positive, negative) by two (Memory: Hit, miss) ANOVA. This analysis yielded a significant main effect of Valence, $F(1,35) = 9.93$, $p < .01$, $\eta_p^2 = .22$, driven by more negative amplitudes for negative feedback pictures than for positive feedback pictures. Notably, a significant Delay by Memory interaction was obtained, $F(1,35) = 4.40$, $p < .05$, $\eta_p^2 = .11$. Long delayed feedback pictures that were subsequently forgotten elicited more negative FRN$_{peak}$ amplitudes than those that were subsequently remembered, $t(35) = 2.16$, $p < .05$, $d = 0.14$. In contrast, no difference was found between subsequently remembered and forgotten feedback pictures that were presented with a short delay, $t(35) = -1.28$, $p = .21$, $d = -0.10$. No further ANOVA effects reached significance, all p-values > .40.

Negative minus positive feedback difference waves are shown as a function of Delay and Memory in Figure 3.2B. FRN$_{\text{diff}}$ peak amplitudes were analyzed in a two (Delay: Short, long) by two (Memory: Hit, miss) ANOVA that yielded a significant main effect of Delay, $F(1,35) = 8.53$, $p < .01$, $\eta_p^2 = .20$, driven by more negative amplitudes for shortly delayed feedback pictures than for long delayed feedback pictures. No significant main effect of Memory, $F(1,35) < 1$, $p = .50$, $\eta_p^2 = .01$, and no Delay by Memory interaction, $F(1,35) < 1$, $p = .41$, $\eta_p^2 = .02$, were obtained.

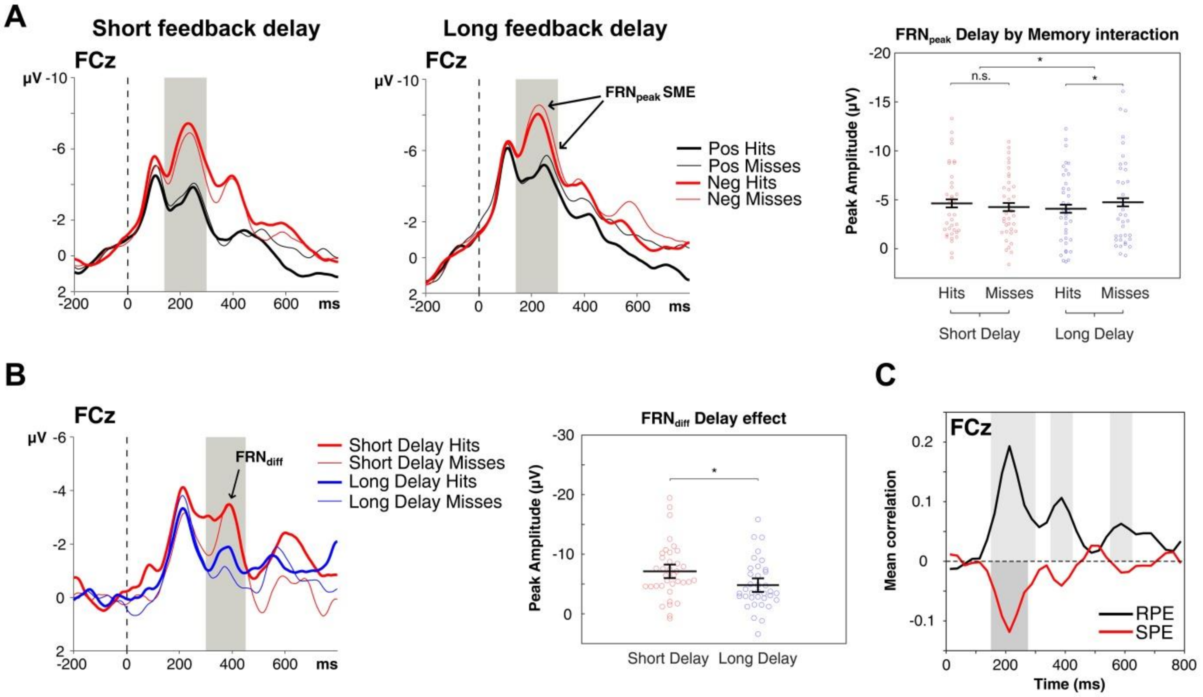

Figure 3.2: FRN and single trial EEG results in the learning phase. Feedback-locked ERP waveforms (A) and negative minus positive feedback difference waves (B) at electrode FCz. Shaded areas indicate the time windows used for the detection of P200/N200 peak amplitudes (140 – 300 ms) and FRN$_{\text{diff}}$ peak amplitudes (300 – 450 ms). Mean correlations between reward and salience prediction errors (RPE/SPE) and single trial EEG mean amplitudes at electrode FCz (C). Shaded areas indicate the time windows in which significant correlations between single trial EEG mean amplitudes and RPE (150 – 300 ms, 350 – 425 ms, 550 – 625 ms) and SPE (150 – 275 ms) estimates were obtained. Beeswarm plots show individual datapoints in addition to means and confidence intervals.

3.3.3.2 N170

Feedback-locked waveforms at electrodes P7 and P8 are depicted in Figure 3.3A. N170 amplitudes were analyzed in a two (Delay: Short, long) by two (Memory: Hit, Miss) by two

(Electrode: P7, P8) ANOVA that yielded a significant main effect of Delay, $F(1,35) = 9.13$, $p < .01$, $\eta_p^2 = .21$, reflecting larger N170 amplitudes elicited by long delayed than by shortly delayed feedback pictures. No further effects reached significance, all *p*-values > .16.

3.3.3.3 P300

Feedback-locked waveforms at electrode Pz are shown in Figure 3.3B. Mean amplitudes in the 450 – 600 ms time window were analyzed in a two (Delay: Short, Long) by two (Valence: Positive, Negative) by two (Memory: Hit, miss) by two (Electrode: Fz, Pz) ANOVA that yielded significant main effects of Delay, $F(1,35) = 5.25$, $p < .05$, $\eta_p^2 = .13$, and Valence, $F(1,35) = 5.41$, $p < .05$, $\eta_p^2 = .13$, qualified by a Delay by Valence by Electrode interaction, $F(1,35) = 8.28$, $p < .01$, $\eta_p^2 = .19$. No further effects involving the experimental factors reached significance, all *p*-values > .09. To disentangle the significant triple interaction, mean amplitudes at electrodes Fz and Pz were analyzed in separate ANOVAs including the factors Delay, Valence, and Memory. At electrode Fz, a significant main effect of Valence was obtained, $F(1,35) = 9.76$, $p < .01$, $\eta_p^2 = .22$, reflecting more positive amplitudes elicited by positive than by negative feedback pictures. No further effects reached significance, all *p*-values > .08. At electrode Pz, more positive amplitudes were elicited by shortly delayed than by long delayed feedback pictures, $F(1,35) = 4.46$, $p < .05$, $\eta_p^2 = .11$. No further effects reached significance, all *p*-values > .10.

3.3.4 Correlations Between Prediction Error Estimates and EEG Activity in the Learning Phase

The analysis of FRN amplitudes in the learning phase were complemented by a model-based single trial EEG analysis that was aimed at validating models of the functional significance of the FRN_{peak} and FRN_{diff} measures used in the present study. High correlations between EEG amplitudes and trial-by trial estimates of reward prediction errors (RPEs) in time windows in which $\mathrm{FRN}_{\mathrm{peak}}$ and $\mathrm{FRN}_{\mathrm{diff}}$ effects were present would confirm that EEG activity in these time windows reflects the processing of RPEs. High correlations between EEG amplitudes and salience prediction errors (SPEs) in the $\mathrm{FRN}_{\mathrm{peak}}$ and $\mathrm{FRN}_{\mathrm{diff}}$ time windows would indicate that EEG activity in these time windows is sensitive to general expectancy violations irrespective of valence.

Mean correlations between model-derived trial-by-trial RPE and SPE estimates and feedback-locked single trial EEG amplitudes at electrode FCz are depicted as a function of time in Figure 3.2C. Correlations between RPEs and EEG activity were marked by two distinctive positive peaks around 200 and 400 ms, indicating that large negative RPEs (as elicited by unexpected negative feedback) were associated with more negative EEG amplitudes around these time points. Correlations between SPEs and EEG activity showed a pronounced negative peak around 200 ms, suggesting that unexpected feedback, irrespective of valence, was associated with more negative EEG amplitudes around this time point. These observations were confirmed by a series of *t*-tests testing the significance of the mean correlations between RPEs/SPEs and EEG activity in each of the 32 time bins. When correcting for multiple comparisons ($\alpha = 0.0016$), significant correlations between EEG amplitudes and RPE estimates were obtained in the 150 – 300 ms and the 350 – 425 ms time intervals in which $\mathrm{FRN}_{\mathrm{peak}}$ and $\mathrm{FRN}_{\mathrm{diff}}$ effects were present, and in a later (550 – 625 ms) time interval. Significant correlations between EEG amplitudes and SPEs were only present in the 150 – 275 ms time window in which the $\mathrm{FRN}_{\mathrm{peak}}$ was measured.

Taken together, EEG activity in the $\mathrm{FRN}_{\mathrm{peak}}$ and $\mathrm{FRN}_{\mathrm{diff}}$ time windows reflected the processing of RPEs, as evidenced by high correlations between EEG amplitudes and RPE estimates. In contrast, significant correlations between EEG amplitudes and SPEs were confined to the early $\mathrm{FRN}_{\mathrm{peak}}$ time window, which suggests that EEG activity in this time window was sensitive to general expectancy violations irrespective of whether the feedback was better (positive) or worse (negative) than expected.

3.3.5 ERPs in the Test Phase

ERPs waveforms associated with correct memory decisions in the recognition memory test are depicted in Figure 3.3C. Mean amplitudes in the 300 – 500 ms and 500 – 1100 ms time windows were analyzed in two separate four-way ANOVAs including the factors Valence (positive, negative), Item Status (short delay hits, long delay hits, correct rejections), Antpos (F = frontal, FC = frontocentral, C = central, CP = centroparietal, P = parietal), and Side (left, midline, right).

In the 300 – 500 ms time window, a significant main effect of Valence was obtained, $F(1,41) = 29.60$, $p < .001$, $\eta_p^2 = .42$, reflecting more positive amplitudes elicited by positive feedback pictures than by negative ones. The Valence by Side interaction was only marginally significant, $F(1.58,64.73) = 3.36$, $p_{corr} = .05$, $\eta_p^2 = .08$. No further effects involving the experimental factors reached significance, all *p*-values > .25.

In the 500 – 1100 ms time window, significant main effects of Valence, $F(1,41) = 45.76$, $p < .001$, $\eta_p^2 = .53$, and Item Status, $F(2,82) = 10.72$, $p < .001$, $\eta_p^2 = .21$, were obtained, qualified by significant interactions between Valence and Antpos, $F(1.27,51.90) = 4.38$, $p_{corr} < .05$, $\eta_p^2 = .10$, Item Status and Antpos, $F(2.67,109.37) = 6.80$, $p_{corr} < .01$, $\eta_p^2 = .14$, Valence and Side, $F(1.64,67.24) = 6.67$, $p_{corr} < .01$, $\eta_p^2 = .14$, and Valence, Antpos, and Side, $F(4.97,203.80) = 2.69$, $p_{corr} < .05$, $\eta_p^2 = .06$. No further effects involving the experimental factors reached significance, all *p*-values > .26. Because we were chiefly interested in the effect of Item Status, which did not interact with Valence, we further explored the significant Item Status by Antpos interaction and conducted separate one-way ANOVAs including the factor Item Status for each level of the Antpos factor. The main effect of Item Status was significant at each level of the Antpos factor. Effect sizes were largest over frontocentral (η_p^2 = .21) and smallest over parietal electrode sites (η_p^2 = .18). Subsidiary *t*-tests revealed that short delay hits did not differ significantly from correct rejections, all *p*-values > .07. In contrast, long delay hits were associated with more positive mean amplitudes than correct rejections at each level of the Antpos factor. Effect sizes were largest at frontal (*d* = 0.32) and smallest at parietal electrodes (*d* = 0.15). Notably, long delay hits were also associated with more positive mean amplitudes than short delay hits. These effects were obtained at each level of the Antpos factor, but here effect sizes were largest at parietal electrodes (*d* = 0.24) and smallest at frontal electrodes (*d* = 0.18).

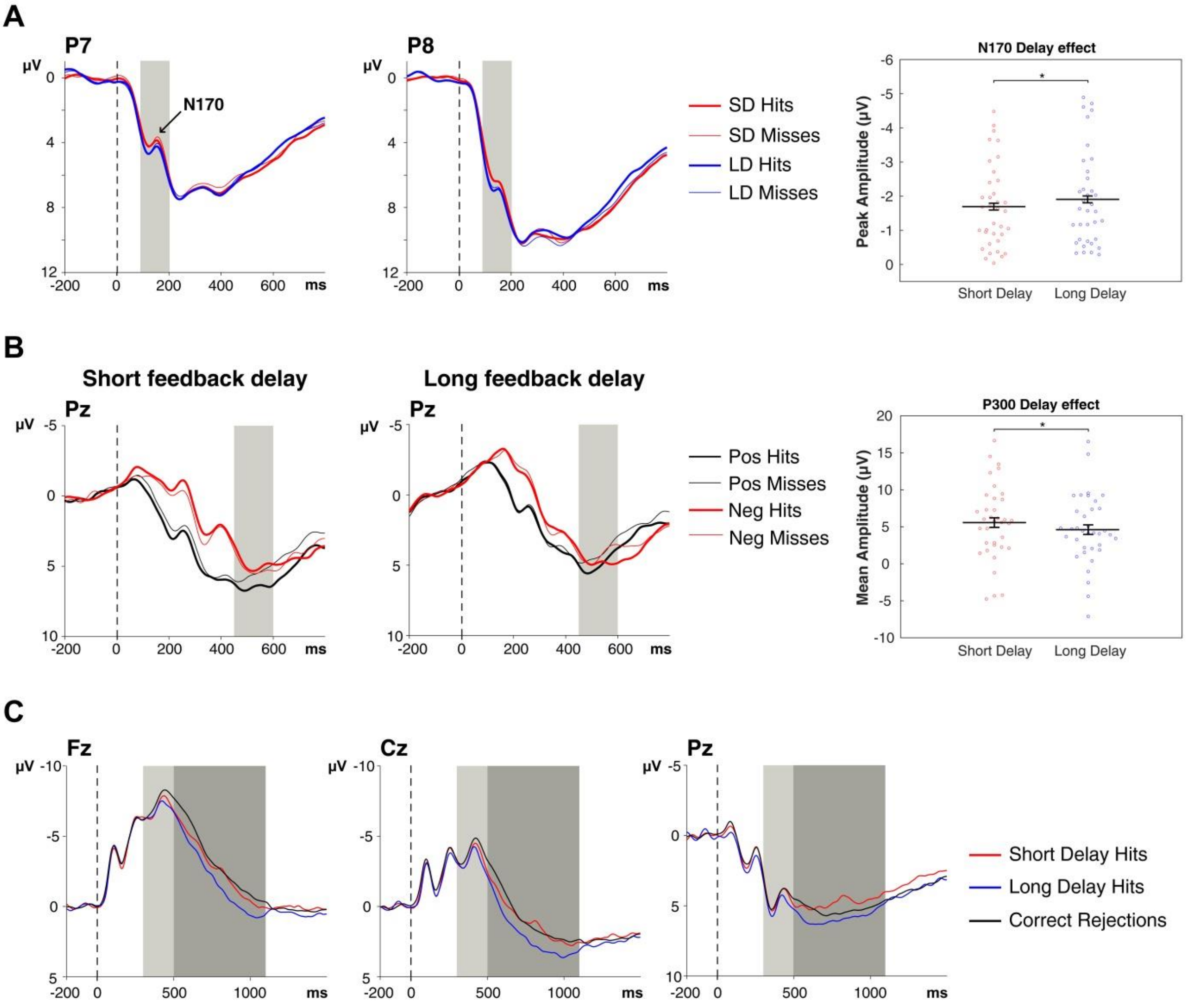

Figure 3.3: Feedback-locked waveforms in the learning phase at electrodes P7 and P8 (A). Shaded areas indicate the time window used for the detection of P100/N170 peak amplitudes (90 – 200 ms). Feedback-locked waveforms in the learning phase at electrode Pz (B). Shaded

areas indicate the 450 – 600 ms time window in which P300 mean amplitudes were analyzed. ERP waveforms associated with correct memory decisions in the test phase are shown for three representative frontal, central, and parietal electrodes (C). Shaded areas indicate the 300 – 500 ms and 500 – 1100 ms time windows used to analyze old/new effects. Beeswarm plots show individual datapoints in addition to means and confidence intervals.

3.4 Discussion

In Experiment 2, ERPs were used to investigate interactions between feedback-based learning and concurrent incidental memory encoding of feedback pictures in a probabilistic learning task. In the learning phase, participants used feedback pictures that were provided with either a short (500 ms) or long (6500 ms) temporal delay to learn associations between Chinese characters and motor responses. Based on evidence from neuroimaging studies suggesting that the processing of temporally delayed feedback engages the MTL-based declarative learning system, we used a feedback delay manipulation to establish a short delay condition in which feedback processing should strongly rely on the procedural learning system, and a long delay condition in which the declarative learning system should be more involved in feedback processing. As evidenced by the performance in the probabilistic learning task, participants were able to use the feedback for learning the stimulus-response associations and, consistent with previous studies (e.g., Foerde & Shohamy, 2011; Weismüller & Bellebaum, 2016), learned equally well in the short and long feedback delay conditions.

The major goal of Experiment 2 was to explore how feedback-based learning with long (and short) feedback delay interacts with memory encoding. In previous studies investigating the effects of feedback delay on memory for feedback pictures, delayed feedback pictures were associated with a higher proportion of correct high-confidence memory responses (Foerde & Shohamy, 2011; Lighthall et al., 2018). Consistent with these studies, and in support of the view that the involvement of the declarative memory system boosts memory for feedback events, we found that long delayed feedback pictures were remembered better than shortly delayed feedback pictures.

Of note, it has been argued that studies investigating interactions between reward learning and memory encoding need to control for motivational and attentional confounds that could affect memory encoding (Murayama & Kitagami, 2014). In the present study, these confounds were avoided by the use of an incidental learning paradigm. Furthermore, the fixed assignment of picture and feedback categories (outdoor = positive, indoor = negative) ensured that participants needed to process the picture content in order to use the feedback for learning. As these important boundary conditions were met in the present study as well in previous studies investigating the effects of feedback timing on memory (Foerde & Shohamy, 2011; Lighthall et al., 2018) we feel save to conclude that they reflect the involvement of different neural systems for immediate and delayed feedback processing.

Consistent with previous ERP studies, we analyzed FRN amplitudes in the feedback-locked ERP waveforms ($\mathrm{FRN}_{\mathrm{peak}}$) and in the negative minus positive feedback difference waves ($\mathrm{FRN}_{\mathrm{diff}}$). Whereas the $\mathrm{FRN}_{\mathrm{peak}}$ primarily captures variance related to the N200 and has been functionally related to the general violation of action-outcome relationships irrespective of their valence (Ferdinand et al., 2012), the $\mathrm{FRN}_{\mathrm{diff}}$ carries valence-related variance as reflected by the reward positivity (Holroyd et al., 2008; Proudfit, 2015). Prior studies investigating the effects of feedback timing on the FRN have found that whereas shortly delayed feedback is associated with larger $\mathrm{FRN}_{\mathrm{diff}}$ amplitudes than long delayed feedback (e.g., Höltje & Mecklinger, 2018; Peterburs et al., 2016; Weismüller & Bellebaum, 2016), the reverse applies for the $\mathrm{FRN}_{\mathrm{peak}}$ (Höltje & Mecklinger, 2018; Peterburs et al., 2016). Consistent with these studies, shortly delayed feedback elicited larger $\mathrm{FRN}_{\mathrm{diff}}$ amplitudes than long delayed feedback. This finding confirms the view that the procedural learning system was strongly involved in the processing of shortly delayed feedback. Interestingly, in the present study, $\mathrm{FRN}_{\mathrm{peak}}$ amplitudes did not differ between shortly delayed and long delayed feedback. Different from previous studies that have found increased $\mathrm{FRN}_{\mathrm{peak}}$ amplitudes for long delayed feedback (Höltje & Mecklinger, 2018; Peterburs et al., 2016), the cue (the Chinese character) and the choice (the colored button representing the response key) remained on the screen during the delay period of the feedback learning task, thereby lowering the working memory demands in the present study as compared to the aforementioned studies. It is conceivable that in the Peterburs et al. (2016) and Höltje & Mecklinger (2018) studies, higher working memory demands in the delayed feedback condition were associated with a stronger working memory-guided build-up of action-outcome expectations, the violation of which resulted in higher $\mathrm{FRN}_{\mathrm{peak}}$ amplitudes.

Comparing FRN measures for subsequently remembered or forgotten feedback pictures, we found that the $\mathrm{FRN}_{\mathrm{peak}}$ was attenuated for subsequent hit responses relative to subsequent misses in the long feedback delay condition. This finding indicates that feedback processing and incidental memory encoding competed for neural processing resources, which is in principle consistent with a similar interaction reported by Wimmer et al. (2014). As the subsequent memory effect (SME) was only found for long delayed feedback, the processing of which has been shown to engage the hippocampus (Foerde & Shohamy, 2011; Lighthall et al., 2018), it is tempting to speculate that the SME reflects a competition for hippocampal processing resources. This conjecture is supported by the finding that no SME was found in the short delay condition. In contrast, Wimmer et al. (2014) found that successful memory encoding was associated with diminished reward processing as reflected in striatal RPE signals, which could reflect a competition between memory encoding and reward learning for striatal processing resources. Importantly, Wimmer and colleagues used a reward learning task with a short reward delay (1.5 seconds) in which presumably reward learning strongly relied on the striatum. Thus, the interaction between memory encoding and delayed feedback processing in the present study most likely reflects competition for different (hippocampal) processing resources than the one reported by Wimmer et al. (2014).

Because the functional significance of the FRN is still a matter of debate, the analysis of FRN$_{\text{peak}}$ and FRN$_{\text{diff}}$ amplitudes in the learning phase was complemented by a model-based single trial EEG analysis in which we explored how the processing of reward prediction errors (RPEs) and general expectancy violations irrespective of valence was reflected in the EEG signal. Using a computational reinforcement learning model, we computed trial-by-trial estimates of RPEs and fitted them to the EEG data. Our assumption was that if the FRN reflects the processing of RPEs, best fits between RPEs and EEG amplitudes should be obtained in the time windows in which FRN effects are present in the ERP waveform. This is exactly what we found: Reliable RPE correlations were selectively observed in the FRN$_{\text{peak}}$ (140 – 300 ms) and FRN$_{\text{diff}}$ (300 – 450 ms) time windows. This finding confirms the view that the FRN reflects the processing of RPE signals on the single trial level. Notably, an exception to this pattern of results was the cluster of significant RPE correlations in the 550 – 625 ms time period. Even though this result was not predicted, it is conceivable that correlations in this late time interval were related to the P300, which peaked around 500 ms at parietal electrodes in the present study. Further research is needed to clarify the functional significance of this finding.

Different from signed RPEs, unsigned prediction errors or salience prediction errors (SPEs) distinguish between expected and unexpected outcomes without taking into account the valence of the prediction error. Based on the assumption that the FRN$_{\text{peak}}$ is sensitive to this more general type of violation of action-outcome expectations, we hypothesized that best fits between model-derived SPEs and single trial EEG amplitudes should occur in the FRN$_{\text{peak}}$ window. We found significant SPE correlations between 150 and 275 ms, where FRN$_{\text{pea}}$ effects occurred, but not in the later time windows in which correlations with the RPE dominated in the ERP waveforms. This finding confirms the view that the FRN$_{\text{peak}}$ primarily reflects variance related to the N200 and by this indicates the salience (unexpectedness) of an outcome irrespective of feedback valence. More generally, the results of the single trial EEG analysis provide further evidence in support of the view that the FRN_{peak} and the FRN_{diff} constitute functionally distinct ERP components reflecting different aspects of feedback processing, i.e., the processing of general expectancy violations and unexpected rewards, respectively.

We also analyzed two ERP components that have recently been found to be sensitive to feedback delay manipulations, i.e., the N170 and the P300. We expected that delayed feedback should elicit larger N170 amplitudes than immediate feedback. Furthermore, if the N170 reflects the involvement of declarative memory processes it is conceivable that these processes interact with memory encoding. In the present study, delayed feedback pictures elicited larger N170 amplitudes, but no effects of successful memory encoding were obtained. Based on the extant data, it is difficult to make inferences about which precise declarative memory processes the N170 delay effect reflects. It is conceivable that the N170 elicited by delayed feedback is linked to an MTL-based process that binds together the reaction given by the participants and the temporally delayed feedback stimulus (Arbel et al., 2017; Foerde & Shohamy, 2011).

Consistent with the studies by Wang et al. (2014) and Weismüller & Bellebaum (2016), we found that shortly delayed feedback pictures elicited larger P300 amplitudes than those presented with long feedback delay. Notably, in the two aformentioned studies the P300 delay effect was significant at frontal electrodes, whereas we found a significant P300 delay effect at parietal, but not at frontal electrodes. The frontal P300 effects obtained in the studies by Wang et al. (2014) and Weismüller & Bellebaum (2016) resemble frontal slow wave activity associated with the maintenance of information in working memory (Ranganath & Paller, 1999, 2000; Werkle-Bergner, Mecklinger, Kray, Meyer, & Düzel, 2005). Consistent with the recent proposal that the feedback-locked parietal P300 reflects the updating of the value assigned to an action (Fischer & Ullsperger, 2013; Ullsperger et al., 2014), the P300 delay effect obtained in the present study could reflect stronger action value updating under short feedback delay conditions for the reaction given by the participant, potentially as a downstream consequence of the more pronounced feedback evaluation process reflected in the FRN_{diff} in this condition.

Even though P300 amplitudes are often predictive of subsequent memory and reflect the encoding of item-specific details (Fabiani et al., 1986; Kamp, Bader, & Mecklinger, 2017; Karis, Fabiani, & Donchin, 1984), surprisingly no parietal subsequent memory effect (SME) was obtained in the present study. Interestingly however, as evidenced by the FRN_{peak}, an SME was obtained in the delayed feedback condition. ERPs elicited by delayed feedback pictures showed effects of successful memory encoding, albeit in an earlier time period than the P300 SME usually found during incidental encoding. Thus, it is possible that the presence of feedback stimuli and the ensuing expectancy violations speeded up memory formation in particular in the long delay condition, hereby provoking interference between feedback evaluation and memory encoding processes that relied on similar neural processing resources.

We also hypothesized that delayed feedback processing with hippocampal involvement should primarily boost the recollection of feedback pictures and give rise to a parietal old/new effects, the putative ERP correlate of recollective processing. In partial confirmation of this prediction, long delayed feedback pictures elicited a strong old/new effect between 500 and 1100 ms poststimulus. In contrast, feedback pictures that had been presented with a short feedback delay in the learning phase were not associated with an old/new effect in this late time interval. This pattern of results is consistent with the behavioral finding that feedback pictures presented with a long delay were associated with better recognition memory than those presented with a short delay.

Notably, the late old/new effect associated with long delayed feedback was more broadly distributed than typically observed in ERP studies of recognition memory. This finding is reminiscent of studies that have found more anterior topographical distributions of N400 effects for pictures as compared with words (Ganis, Kutas, & Sereno, 1996), which has been taken as evidence for partially different sets of neural generators for the N400 to verbal and pictorial stimuli (for a review, see Kutas & Federmeier, 2000). Similarly, the broad topographical distribution of the late old/new effect observed in the present study could reflect overlapping, but non-identical sets of neural generators underlying the late old/new effect for pictorial and verbal stimuli. Consistent with this view, in a recognition memory study in which scene pictures similar to those in the present study were used, young adults elicited a broadly distributed old/new effect between 300 and 900 ms that was largest over central electrode sites (Gutchess et al., 2007).

In the present study, a significant early frontal old/new effect was obtained in neither condition, indicating that there was no substantial contribution of familiarity to recognition memory. This finding contrasts with our previous study in which superior memory for pictures presented with positive feedback was associated with an early frontal old/new effect (Höltje & Mecklinger, 2018), and indicates that positive feedback valence and feedback delay benefit memory by distinct mechanisms: Whereas reward signals elicited by positive feedback strengthen a context-free and familiarity-based form of recognition, delayed feedback fosters the recollection of feedback pictures, presumably mediated by the hippocampal involvement in feedback processing.

4 Experiment 3: The Role of Explicit Outcome Expectations in Delayed Feedback Processing

4.1 Introduction

The results of Experiment 2 are broadly consistent with the view that declarative learning processes support learning from delayed feedback and benefit memory for delayed feedback events (Foerde & Shohamy, 2011). In Experiment 3, we addressed the question how these declarative learning processes get involved in delayed feedback processing initially and hypothesized that explicit outcome expectations play a pivotal role in this mechanism. It is conceivable that learners spontaneously generate explicit outcome expectations during the feedback delay period, a process that requires a mental representation of the allegedly correct stimulus-response-outcome association, which in turn is considered a hallmark feature of goal-directed or model-based learning (Daw, 2018). In particular the disconfirmation of such an explicit outcome expectation could be associated with enhanced declarative learning and memory encoding (Brod, Hasselhorn, & Bunge, 2018; Greve, Cooper, Kaula, Anderson, & Henson, 2017) and hippocampal activity reflecting the processing of expectancy mismatches (Duncan, Curtis, & Davachi, 2009; Kumaran & Maguire, 2006, 2007).

To investigate the role of explicit outcome expectations in delayed feedback processing, we contrasted a default delayed feedback condition with a “Prediction” condition in which participants were asked on each trial to indicate during the feedback delay period which type of feedback picture (indoor or outdoor scene) they expected. The configuration of the Prediction condition was intended to stimulate participants to consistently generate explicit outcome expectations, whereas this would only sporadically be the case in the default “Delay” condition. Importantly, because the probability of spontaneously generating an explicit outcome expectation could increase with the time passing until the feedback is delivered, the temporal delay between the participants' choice and the presentation of the feedback picture was kept at four seconds in both conditions. Different from previous studies investigating episodic memory for delayed feedback pictures (Foerde & Shohamy, 2011; Höltje & Mecklinger, 2020; Lighthall et al., 2018), we balanced the mapping between picture category and feedback valence. This enabled us to dissociate effects of valence on memory from differences in memory between indoor and outdoor scene pictures.

If explicit outcome expectations mediate the involvement of declarative learning processes in delayed feedback processing, the behavioral and ERP correlates of delayed feedback processing identified in Experiment 2 should be more pronounced in the Prediction condition than in the Delay condition. We also hypothesized that in particular the disconfirmation of explicit outcome expectations (i.e., negative feedback pictures) should be associated with stronger recollective processing due to the hippocampal acticity elicited by expectancy mismatches (e.g., Long, Lee, & Kuhl, 2016).

4.2 Method

4.2.1 Participants

Thirty-five native German speakers were recruited from the student population of Saarland University. Informed consent was required and participants received money (€8/h) or course credit as a compensation for their participation. All participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision and no self-reported neurological or psychiatrical problems. The experimental procedures were approved by the local ethics committee. Data from three participants had to be excluded from all analyses because there were not enough artifact-free trials (< 7) to calculate reliable ERPs in one of the conditions (see section on EEG recording and processing). Thus, all analyses are based on a data set from N = 32 participants (10 male;

median age = 21 years, range = 19-28 years) that was completely balanced regarding the assignment of experimental conditions, stimulus lists, and response keys.

4.2.2 Stimuli and Procedure

Each experimental session began with the fitting of the EEG cap (see section on EEG recording and processing). 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. All stimuli were presented in the centre of the screen on a white background.

In the learning phase of the experiment, participants learned associations between Chinese characters and two response keys with probabilistic feedback. Scene pictures were presented as feedback, and the picture category (indoor or outdoor scene) designated the valence (positive or negative) of the feedback. Feedback pictures were always presented with a temporal delay of four seconds from the participants’ response. The “Delay” condition constituted a default delayed feedback condition in which participants merely waited for the feedback picture. In the “Prediction” condition, however, participants were asked to predict the category (indoor or outdoor scene) of the upcoming feedback picture on each trial. The learning phase was followed by a retention interval of approximately five minutes during which the participants were asked to solve simple arithmetical tasks. In the ensuing test phase, recognition memory for the scene pictures was tested in a surprise memory test.

A total of 680 scene pictures were used in the experiment. Five hundred and sixty of these pictures were the same as in the Höltje and Mecklinger (2020) study, the others were collected from various free internet sources. The size of the pictures was scaled to a width of 600 pixels and a height between 350 and 450 pixels.

4.2.2.1 Learning Phase

Eight different Chinese characters, divided into two sets of four characters each (set 1: 外, 本, 归, 汉; set 2: 礼, 也, 自, 加), were used in the probabilistic feedback learning task. The two character sets were assigned to the “Prediction” and “Delay” conditions and every character was associated with one of two response keys (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. Feedback was valid in 70% of the trials, meaning that when participants responded with the correct (incorrect) button, they received positive (negative) feedback in seven out of ten times. Participants were informed that the feedback would not always be valid, but the instructions emphasized that it was possible to use the feedback for learning.

Overall, every participant completed 120 learning trials per condition, divided into three blocks of 40 trials each. The three learning blocks were followed by one block in which participants continued performing the task without feedback. Each of the four characters assigned to one condition was presented ten times per block, in pseudorandomized order, so that no character was repeated on the next trial. Participants were given ten practice trials for each condition.

The 680 scene pictures were divided into two indoor and two outdoor lists of 170 pictures each. Pictures from one indoor and one outdoor list were presented as feedback pictures in the learning phase, and pictures from the other indoor and outdoor lists served as lures in the test phase. Each picture was presented only once during learning, but not every picture from the list was necessarily used as a feedback picture. The reason for this is that the number of pictures presented from one category (indoor or outdoor scene) ultimately depended on the number of correct responses given by the participant. Importantly, even if a participant’s responses were 100% correct (incorrect), no more than 170 scene pictures from one category were presented. The reason for this is that feedback was presented with 70% validity, as stated above.

A schematic of the trial procedure is depicted in Figure 4.1A. Each trial of the probabilistic feedback learning task started with a central fixation cross (500 ms), followed by a Chinese character. The two response keys were represented by a yellow and a blue button located in the bottom left and right corners of the screen. As soon as the participant responded with a keypress, the button corresponding to the chosen key remained on the screen, whereas 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 which served to make the choice salient was shown troughout the 4000 ms long delay period less the timing of the subsequent fixation cross. 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. The delay period was followed by a central fixation cross jittered between 500 and 700 ms and a feedback picture (1500 ms). After the feedback, a blank screen was presented for 1000 ms before the next trial started.

The “Prediction” condition differed from the trial procedure in the “Delay” condition outlined above in one aspect: During the four second long delay period before the presentation of the feedback picture, participants were asked to predict the category of the upcoming feedback picture using a six-step rating scale (“sure indoor”, “probably indoor”, “maybe indoor”, “maybe outdoor”, “probably outdoor”, “sure outdoor”). The rating scale was presented in the top third of the screen, above the Chinese character.

Performance in the learning phase was assessed as the proportion of correct responses in the probabilistic feedback learning task and in the final block of the task without feedback.

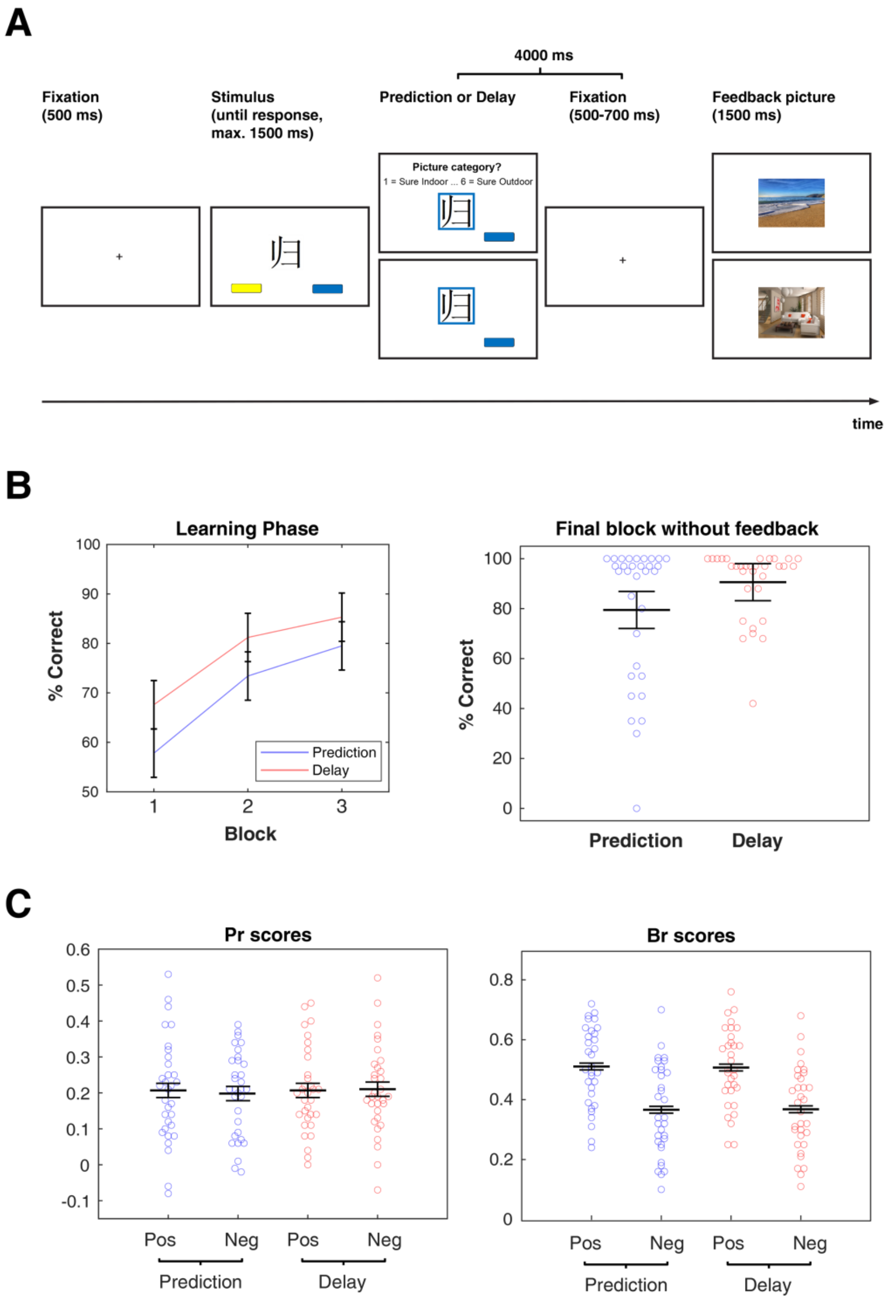

Figure 4.1: Trial procedure in the probabilistic feedback learning task (A). On each trial, a Chinese character was presented. As soon as the participants responded, their choice was displayed and participants waited passively for the presentation of the feedback picture (Delay condition) or were asked to predict the category of the upcoming feedback picture (Prediction condition). In both conditions, outdoor (indoor) scene pictures were presented as positive (negative) feedback 4000 ms after the response. Behavioral results in the learning phase (B) and in the test phase (C). Beeswarn plots show individual datapoints in addition to means and confidence intervals.

4.2.2.2 Test Phase

The 240 feedback pictures from the learning phase were presented together with 240 new scene pictures in pseudorandomized order, so that not more than three adjacent “old” or “new” pictures were presented in direct succession. Moreover, the number of pictures from each category (indoor or outdoor scene) presented as lures was the same as the number of pictures from each category presented as feedback pictures in the learning phase. Participants were admitted a short break after every 80 trials. In the beginning of each trial, a fixation cross was presented with a duration jittered between 1000 and 1500 ms, followed by a picture presented for 1500 ms. Participants were instructed to decide for every picture whether it was old or new using a six-step confidence scale („sure old“, „probably old“, „maybe old“, „maybe new“, „probably new“, „sure new“). 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. The old/new decision could be given as soon as the picture was presented. As soon as participants made a response, a blank screen was shown for 1000 ms before the next trial started.

To assess memory performance in the test phase, measures of old/new discrimination, Pr [*p*(hit) – *p*(false alarm)], and response bias, Br [*p*(false alarm) / *p*(1 – Pr)], were calculated separately for positive and negative pictures encoded in the Prediction and Delay conditions (Snodgrass & Corwin, 1988). For this purpose, the corresponding three steps of the confidence scale were collapsed into „old“- and „new“-decisions. In addition, high-confidence Pr and Br scores were calculated based on „sure“- and „probably“-decisions only.

4.2.3 EEG Recording and Processing

The EEG was recorded during the learning and test phases of the experiment 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, the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes for MATLAB (MathWorks, Inc.) were used. Electrodes were re-referenced to the average of the left and right mastoid electrodes. The data were filtered at 0.1 – 30 Hz using a second order Butterworth filter, and at 50 Hz using a Parks-McClellan notch filter. Segments were extracted from the learning phase data from 200 ms before feedback onset to 1000 ms thereafter, and segments from 200 ms before picture onset to 1500 ms thereafter were extracted from the test phase data. The segments were baseline-corrected based on activity during the 200 ms before feedback or picture onset. Independent component analysis (ICA) was applied to the segmented data to correct for ocular artifacts. Components associated with ocular artifacts were identified and rejected manually based on their activations and topographies. Segments containing artifacts were rejected using the following criteria: A minimal and maximal allowed total amplitude of ± 100 µV, a maximal difference of values of 100 µV during intervals of 200 ms (window steps of 100 ms), a maximal allowed voltage step of 15 µV/ms, and maximal 200 ms activity with a deviation of less than 0.4 µV from the maximum or minimum voltage in the segment. On average, 4.9 % and 4.3 % of all segments were rejected in the learning phase and the test phase, respectively. Grand average waveforms were low-pass filtered at 12 Hz for illustration purposes.

4.2.3.1 ERPs in the Learning Phase

ERPs were averaged for every combination of the factors Condition (Prediction, Delay), Valence (positive, negative), and Memory (hits, misses). Feedback pictures judged as being “old” or “new” in the test phase were counted as hits and misses, respectively. For this purpose, the three corresponding steps of the confidence scale were collapsed into “old”- and “new”-decisions. For the purpose of peak detection, the subject average waveforms were low-pass filtered at 10 Hz.

Because FRN effects are typically largest at frontocentral sites (Holroyd & Coles, 2002; Miltner et al., 1997), FRN measures were analyzed at electrode FCz. The FRN was quantified in two ways: The FRN_{peak} was measured according to an algorithm described in Holroyd et al. (2003; see Ferdinand et al., 2012; Holroyd et al., 2006; Peterburs et al., 2016, for studies that used a similar approach) as the difference between the N200 peak (180 – 280 ms) and the preceding P200 peak (130 – 180 ms). The FRN_{diff} was measured as the peak amplitude between 280 and 450 ms in the negative minus positive feedback difference wave (cf. Becker et al., 2014; Peterburs et al., 2016; Weismüller and Bellebaum, 2016).

As determined by an inspection of the waveforms, the feedback-locked P300 peaked around 500 ms at electrode Pz. P300 mean amplitudes between 450 and 650 ms were analyzed at electrodes FCz and Pz.

4.2.3.2 ERPs in the Test Phase

ERPs were averaged for every combination of the factors Item Status (Prediction hits, Delay hits, correct rejections) and Valence (positive, negative). Mean amplitudes were analyzed in two adjacent time windows, ranging from 300 – 500 ms and 500 – 1000 ms. The early time window is typically used for the analysis of early mid-frontal old/new effects in ERP studies of recognition memory (see Rugg & Curran, 2007, for a review). The later 500 – 1000 ms time window was chosen because, as evident from Figure 4.3A, an inspection of the waveforms suggested that the late old/new effect continued until approximately 1000 ms. In order to cover frontal electrode sites, where early mid-frontal old/new effects are largest, as well as parietal electrode sites, at which late old/new effects are typically most pronounced, mean amplitudes were analyzed at 15 electrodes broadly distributed across the scalp (F3, Fz, F4, FC3, FCz, FC4, C3, Cz, C4, CP3, CPz, CP4, P3, Pz, P4).

4.2.4 Data Analyses

All statistical analyses were conducted using IBM SPSS software. Behavioral and electrophysiological measures were analyzed using repeated measures ANOVAs and dependent *t*-tests. 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. For dependent *t*-tests, *d* was calculated according to Dunlap, Cortina, Vaslow, & Burke (1996), taking into account the correlations between measurements. Error margins in graphs represent 95% confidence intervals based on the mean square error of the depicted effect (Jarmasz & Hollands, 2009).

4.3 Results

4.3.1 Performance in the Learning Phase

Correct responses in the probabilistic feedback learning task, depicted in Figure 4.1B, were analyzed in a two (Condition: Prediction, Delay) by three (Block) ANOVA. A significant main effect of Condition was found, $F(1, 31) = 5.41$, $p < .05$, $\eta_p^2 = .15$, reflecting an overall higher proportion of correct responses in the Delay condition ($M = 0.78$, $SEM = 0.02$) as compared with the Prediction condition ($M = 0.70$, $SEM = 0.03$). The main effect of Block was also significant, $F(2, 62) = 50.21$, $p < .001$, $\eta_p^2 = .62$, indicating that the proportion of correct responses changed during the course of the learning phase. Subsidiary *t*-tests revealed that the proportion of correct responses increases from the first block ($M = 0.63$, $SEM = 0.02$) to the second block ($M = 0.77$, $SEM = 0.02$), $t(31) = 7.22$, $p < .001$, $d = 1.12$, and from the second to the third block ($M = 0.82$, $SEM = 0.03$), $t(31) = 2.75$, $p < .05$, $d = 0.35$. The interaction between Condition and Block was not significant, $F(1.49, 46.13) < 1$, $p_{\mathrm{corr}} = .57$, $\eta_p^2 = .02$. The proportion of correct responses in the block without feedback that followed the three blocks of the learning phase, depicted in Figure 4.1B, was higher in the Delay condition ($M = 0.91$, $SEM = 0.02$) than in the Prediction condition ($M = 0.79$, $SEM = 0.05$), $t(31) = 2.16$, $p < .05$, $d = 0.50$.

4.3.2 Recognition Memory in the Test Phase

Measures of old/new discrimination (Pr) and response bias (Br) in the memory test are shown in Figure 4.1C and were analyzed in separate two (Condition: Prediction, Delay) by two (Valence: Positive, Negative) ANOVAs. The analysis of Pr scores did not yield any significant effects (all *p*-values > .59). The same result was obtained in the analysis of high-confidence Pr scores (all *p*-values > .30). In the analysis of Br scores, a significant main effect of Valence was obtained, $F(1, 31) = 26.51$, $p < .001$, $\eta_p^2 = .46$, reflecting larger bias scores for positive feedback pictures ($M = 0.51$, $SEM = 0.02$) than for negative ones ($M = 0.37$, $SEM = 0.03$). The main effect of Condition was not significant, $F(1, 31) < 1$, $p = .90$, $\eta_p^2 = .00$, and neither was the Condition by Valence interaction, $F(1, 31) < 1$, $p = .72$, $\eta_p^2 = .00$. The analysis of high-confidence Br scores yielded a similar pattern of results: A significant effect of Valence was obtained, $F(1, 31) = 20.55$, $p < .001$, $\eta_p^2 = .40$, reflecting larger high-confidence bias scores for positive feedback pictures ($M = 0.27$, $SEM = 0.02$) than for negative ones ($M = 0.18$, $SEM = 0.02$). No further effects reached significance, all *p*-values > .50.

4.3.3 ERPs in the Learning Phase

4.3.3.1 FRN_{peak} and FRN_{diff}

ERPs recorded during feedback presentation in the learning phase at electrode FCz are shown in Figure 4.2A. FRN_{peak} amplitudes were analyzed in a two (Condition: Prediction, Delay) by two (Valence: Positive, Negative) by two (Memory: Hits, Misses) ANOVA that yielded a significant main effect of Condition, $F(1, 31) = 5.28$, $p <.05$, $\eta_p^2 = .15$, reflecting larger (more negative) FRN_{peak} amplitudes in the Prediction condition ($M = -4.71$, $SEM = 0.52$ µV) than in the Delay condition ($M = -4.20$, $SEM = 0.55$ µV). The main effect of Valence was also significant, $F(1, 31) = 13.20$, $p <.01$, $\eta_p^2 = .30$, reflecting larger amplitudes elicited by negative feedback pictures ($M = -3.74$, $SEM = 0.53$ µV) than by positive ones ($M = -5.17$, $SEM = 0.59$ µV). There also was a significant triple interaction between Condition, Valence, and Memory, $F(1, 31) = 5.19$, $p <.05$, $\eta_p^2 = .14$. No further effects reached significance, all *p*-values > .15.

The significant triple interaction was followed up by two ANOVAs including the factors Valence and Memory, calculated separately for the Prediction and Delay conditions. In the Prediction condition, significant main effects of Valence, $F(1, 31) = 14.34$, $p <.01$, $\eta_p^2 = .32$, and Memory, $F(1, 31) = 3.30$, $p <.05$ (one-tailed), $\eta_p^2 = .10$, were obtained. As predicted based upon prior studies, subsequently forgotten feedback pictures ($M = -4.96$, $SEM = 0.54$ µV) were associated with larger FRN_{peak} amplitudes than subsequently remembered ones ($M = -4.46$, $SEM = 0.54$ µV). The Valence by Memory interaction was not significant, $F(1, 31) < 1$, $p = .80$, $\eta_p^2 = .00$.

In the Delay condition, a significant effect of Valence was obtained, $F(1, 31) = 6.88$, $p <.05$, $\eta_p^2 = .18$, qualified by a significant Valence by Memory interaction, $F(1, 31) = 5.26$, $p < .05$, $\eta_p^2 = .15$. Subsidiary *t*-tests showed that subsequently forgotten positive feedback pictures

(M = -3.91, SEM = 0.63 µV) elicited larger FRN_{peak} amplitudes than subsequently remembered ones (M = -3.29, SEM = 0.54 µV), $t(31) = 1.93$, $p < .05$ (one-tailed), $d = 0.18$, whereas no such difference was obtained for negative feedback pictures (negative hits: M = -5.14, SEM = 0.65 µV; negative misses: M = -4.45, SEM = 0.68 µV), $t(31) = -1.43$, $p = .16$, $d = -0.18$. The main effect of Memory was nonsignificant, $F(1, 31) < 1$, $p = .91$, $\eta_p^2 = .00$.

Negative minus positive feedback difference waves at electrode FCz are shown in Figure 4.2B. FRN_{diff} amplitudes were analyzed in a two (Condition: Prediction, Delay) by two (Memory: Hits, Misses) ANOVA that did not yield any significant effects, all p-values > .15.

4.3.3.2 P300

Waveforms recorded during the learning phase at electrode Pz are shown in Figure 4.2C. P300 mean amplitudes between 450 and 650 ms were analyzed in a two (Condition: Prediction, Delay) by two (Valence: Positive, Negative) by two (Memory: Hits, Misses) by two (Electrode: FCz, Pz) ANOVA. The main effect of Condition was significant, $F(1, 31) = 7.73$, $p < .01$, $\eta_p^2 = .20$, and qualified by a Condition by Electrode interaction, $F(1, 31) = 5.02$, $p < .05$, $\eta_p^2 = .14$. The main effect of Valence did not reach significance, $F(1, 31) = 3.52$, $p = .070$, $\eta_p^2 = .10$, but there was a significant Valence by Electrode interaction, $F(1, 31) = 12.61$, $p < .01$, $\eta_p^2 = .29$. No further effects involving the experimental conditions reached significance, all p-values > .13. To follow up the significant Condition by Electrode and Valence by Electrode interactions, mean amplitudes at electrodes FCz and Pz were analyzed in two separate ANOVAs including the factors Condition, Valence, and Memory.

At the frontocentral electrode FCz, the main effect of Condition did not reach significance, $F(1, 31) = 3.18$, $p = .08$, $\eta_p^2 = .09$, and neither did any other effect, all p-values > .14. At the parietal electrode Pz, in contrast, the main effect of Condition was significant, $F(1, 31) = 10.29$, $p < .01$, $\eta_p^2 = .25$, indicating that the Prediction condition (M = 5.97, SEM = 0.90

µV) was associated with more positive mean amplitudes than the Delay condition (*M* = 4.39, *SEM* = 0.78 µV). Negative feedback pictures (*M* = 5.88, *SEM* = 0.84 µV) elicited more positive-going amplitudes than positive ones (*M* = 4.47, *SEM* = 0.80 µV), as evidenced by a significant main effect of Valence, $F(1, 31) = 8.16$, $p < .01$, $\eta_p^2 = .21$. The triple interaction between Condition, Valence, and Memory was only marginally significant, $F(1, 31) = 3.93$, $p = .06$, $\eta_p^2 = .11$.

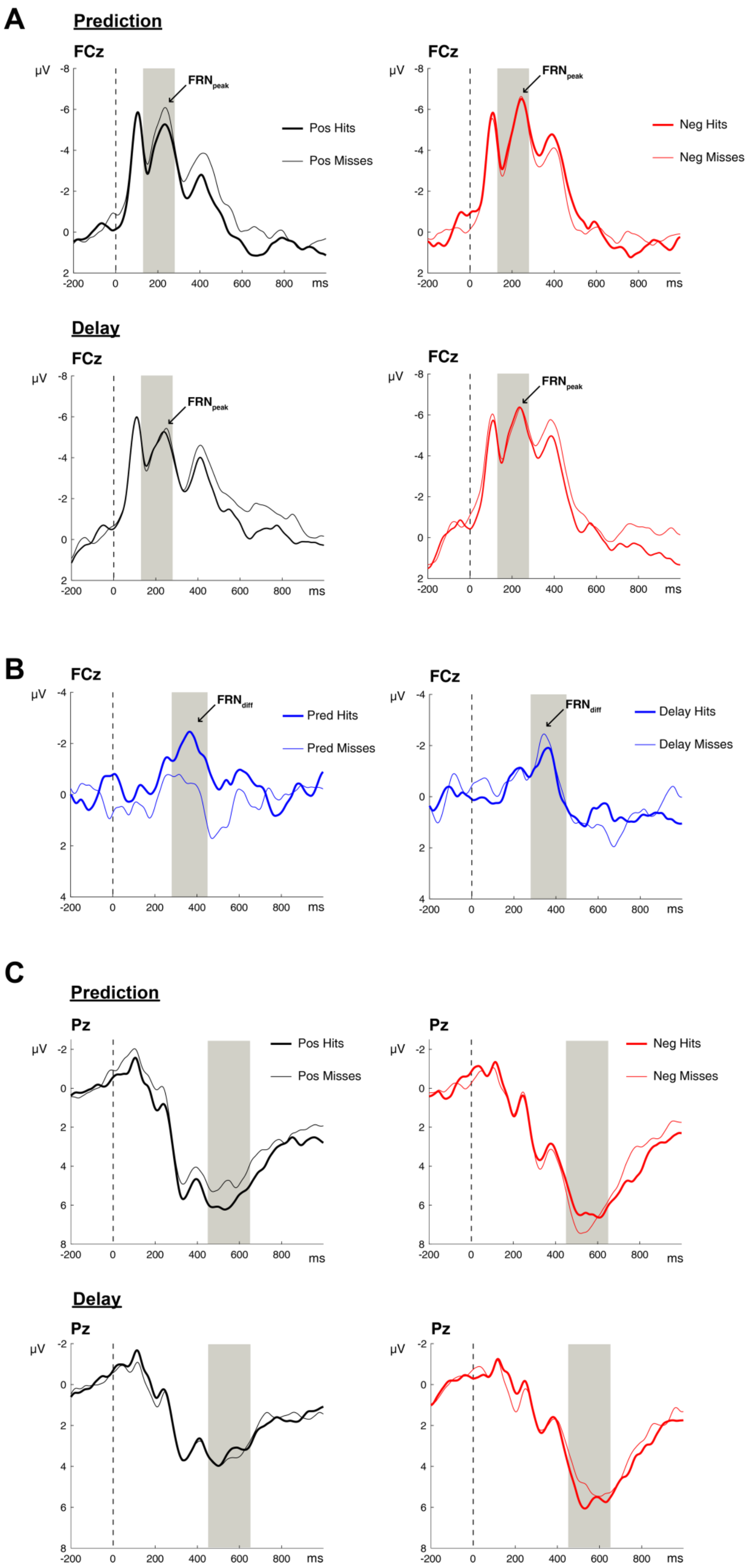
A
Prediction
FCz
FRNpeak
Pos Hits
Pos Misses
FCz
FRNpeak
Neg Hits
Neg Misses
Delay
FCz
FRNpeak
FCz
FRNpeak
B
FCz
FRNdiff
Pred Hits
Pred Misses
FCz
FRNdiff
Delay Hits
Delay Misses
C
Prediction
Pz
Pos Hits
Pos Misses
Pz
Neg Hits
Neg Misses
Delay
Pz
Pz
μV
ms
-200
0
200
400
600
800

Figure 4.2: Feedback-locked ERP waveforms recorded in the learning phase. Waveforms at electrode FCz (A), negative minus positive feedback difference waves at electrode FCz (B), and feedback-lowaveforms at electrode Pz (C). Shaded areas indicate the time windows used for the detection of P200/N200 peak amplitudes (130 – 280 ms), $\mathrm{FRN}_{\mathrm{diff}}$ peak amplitudes (280 – 450 ms), and P300 mean amplitudes (450 – 650 ms).

4.3.4 ERPs in the Test Phase

4.3.4.1 Hits and Correct Rejections

ERP waveforms associated with correct memory decisions in the recognition memory test are depicted in Figure 4.3A. Mean amplitudes in the 300 – 500 ms and 500 – 1000 ms time windows were analyzed in two separate ANOVAs including the factors Item Status (Prediction hits, Delay hits, correct rejections), Valence (positive, negative), Antpos (F = frontal, FC = frontocentral, C = central, CP = centroparietal, P = parietal), and Side (left, midline, right). Only effects involving the factor Item Status are reported, as we were mainly interested in effects of successful memory retrieval on ERP mean amplitudes.

300 – 500 ms. Mean amplitudes in this early time window showed an effect of Item Status, $F(2, 62) = 9.85$, $p < .001$, $\eta_p^2 = .24$, qualified by significant interactions between Item Status and Valence, $F(1, 31) = 4.14$, $p < .05$, $\eta_p^2 = .12$, and Item Status and Antpos, $F(2.34, 72.40) = 3.00$, $p_{\mathrm{corr}} < .05$, $\eta_p^2 = .09$. No further effects involving the factor Item Status reached significance, all p-values > .37. To follow up the Item Status by Valence and Item Status by Antpos interactions, two separate ANOVAs involving the factors Item Status and Antpos were calculated for positive and negative pictures.

Positive pictures were associated with an effect of Item Status, $F(1.62, 50.25) = 8.22$, $p_{\mathrm{corr}} < .01$, $\eta_p^2 = .21$. The Item Status by Antpos interaction was not significant, $F(2.06, 63.71) = 1.81$, $p_{\mathrm{corr}} = .17$, $\eta_p^2 = .06$. Follow-up t-tests disclosed that correct rejections ($M = -2.69$, $SEM = 0.65$ µV) were associated with more negative mean amplitudes than Prediction hits ($M = -2.22$, $SEM = 0.67$ µV), $t(31) = 2.41$, $p < .05$, $d = 0.13$, and Delay hits ($M = -1.60$, $SEM =$

0.75 µV), $t(31) = 3.81$, $p < .01$, $d = 0.26$. The difference in mean amplitudes between Prediction hits and Delay hits did not reach significance, $t(31) = 1.97$, $p = .06$, $d = 0.15$.

ERPs elicited by negative pictures were associated with a pattern of results similar to the one obtained for positive ones in this early time window: The main effect of Item Status was significant, $F(2, 62) = 6.93$, $p < .01$, $\eta_p^2 = .18$, whereas the Item Status by Antpos interaction was not, $F(2.26, 69.96) = 1.47$, $p_{corr} = .24$, $\eta_p^2 = .05$. Subsidiary *t*-tests revealed that correct rejections ($M = -3.35$, $SEM = 0.68$ µV) were associated with more negative mean amplitudes than Prediction hits ($M = -1.77$, $SEM = 0.72$ µV), $t(31) = 4.25$, $p < .001$, $d = 0.40$, and Delay hits ($M = -2.41$, $SEM = 0.76$ µV), $t(31) = 2.19$, $p < .05$, $d = 0.23$. Mean amplitudes did not differ between Prediction hits and Delay hits, $t(31) = 1.36$, $p = .19$, $d = 0.15$.

500 – 1000 ms. The analysis of mean amplitudes in this later time window yielded a main effect of Item Status, $F(2, 62) = 15.79$, $p < .001$, $\eta_p^2 = .34$, and interactions between Item Status and Valence, $F(2, 62) = 4.39$, $p < .05$, $\eta_p^2 = .12$, and Item Status and Antpos, $F(2.60, 80.60) = 4.20$, $p_{corr} < .05$, $\eta_p^2 = .12$. The triple interaction between Item Status, Valence, and Antpos was also significant, $F(2.50, 77.47) = 3.12$, $p_{corr} < .05$, $\eta_p^2 = .09$. No further effects involving Item Status reached significance, all *p*-values > .12. To further explore the triple interaction, two separate ANOVAs including the factors Item Status and Antpos were calculated for positive and negative pictures.

Positive pictures were associated with a main effect of Item Status, $F(2, 62) = 4.63$, $p < .05$, $\eta_p^2 = .13$, reflecting more negative mean amplitudes for correct rejections ($M = 1.14$, $SEM = 0.71$ µV) than for Prediction hits ($M = 1.87$, $SEM = 0.75$ µV), $t(31) = 2.20$, $p < .05$, $d = 0.18$, and Delay hits ($M = 2.08$, $SEM = 0.84$ µV), $t(31) = 2.74$, $p < .05$, $d = 0.20$. Mean amplitudes did not differ between Prediction hits and Delay hits, $t(31) = 0.71$, $p = .48$, $d = 0.05$.

Negative pictures were associated with a significant effect of Item Status, $F(2, 62) = 13.18$, $p < .001$, $\eta_p^2 = .30$, qualified by an Item Status by Antpos interaction, $F(2.63, 81.50) = 5.89$, $p < .01$, $\eta_p^2 = .16$. No further effects involving Item Status reached significance, all p-values > .23. To disentangle the significant Item Status by Antpos interaction, separate one-way ANOVAs including the factor Item Status were conducted at each level of the Antpos factor. The main effect of Item Status was significant at each level of the Antpos factor. Effect sizes were largest over frontal ($\eta_p^2 = .35$) and smallest over parietal electrode sites ($\eta_p^2 = .13$). The significant main effects of Item Status were followed up by t-tests revealing that at each level of the Antpos factor, Prediction hits ($M_F = -1.96$, SEM = 0.90 µV; $M_{FC} = -0.06$, SEM = 0.86 µV; $M_C = 2.59$, SEM = 0.86 µV; $M_{CP} = 5.06$, SEM = 0.86 µV; $M_P = 6.14$, SEM = 0.86 µV) were associated with more positive mean amplitudes than correct rejections ($M_F = -4.70$, SEM = 0.85 µV; $M_{FC} = -2.82$, SEM = 0.79 µV; $M_C = 0.12$, SEM = 0.76 µV; $M_{CP} = 2.99$, SEM = 0.70 µV; $M_P = 4.69$, SEM = 0.67 µV), all p-values < .01. Effect sizes were largest at frontocentral ($\eta_p^2 = .58$) and smallest at parietal electrodes ($\eta_p^2 = .31$). Delay hits ($M_F = -2.96$, SEM = 0.85 µV; $M_{FC} = -1.11$, SEM = 0.87 µV; $M_C = 1.52$, SEM = 0.92 µV; $M_{CP} = 4.10$, SEM = 0.90 µV; $M_P = 5.48$, SEM = 0.86 µV) were associated with more positive mean amplitudes than correct rejections at each level of the Antpos factor (all p-values < .05), except for parietal electrode sites ($p = .07$). Effect sizes were largest over frontal electrode sites ($\eta_p^2 = .36$). The difference in mean amplitudes between Prediction hits and Delay hits was significant at frontal to central electrodes (all p-values < .05), with largest effect sizes at frontal electrodes ($\eta_p^2 = .20$), whereas it did not reach significance at centroparietal ($p = .08$) and parietal electrodes ($p = .21$).

After having confirmed that both positive and negative pictures were associated with significant old/new effects (i.e., more positive mean amplitudes for hits than for correct rejections) that were most pronounced over frontal electrode sites in this late time window, we directly compared the size of the old/new effects elicited by positive and negative pictures encoded under Prediction and Delay conditions at these frontal electrodes of interest. As revealed by *t*-tests, negative pictures encoded in the Prediction condition (*M* = 2.74, SEM = 0.45 µV) elicited a larger old/new effect than when encoded in the Delay condition (*M* = 1.74, SEM = 0.50 µV), *t*(31) = 2.09, *p* < .05, *d* = 0.37, whereas the size of the old/new effect elicited by positive pictures did not differ as a function of the encoding condition (Prediction: *M* = 0.75, SEM = 0.36 µV; Delay: *M* = 1.07, SEM = 0.36 µV), *t*(31) = -1.03, *p* = .31, *d* = -0.16.

4.3.4.2 Correct Rejections and False Alarms, 300 – 500 ms

The finding that participants strongly tended to make “old” responses for positive pictures in the test phase (see section on memory results) prompted us to further explore the ERP correlates of this response bias. Similar response biases in recognition memory have previously been associated with stronger familiarity signals as reflected in the early, mid-frontal old/new effect (Azimian-Faridani & Wilding, 2006; Windmann, Urbach, & Kutas, 2002). If recognition judgements in the test phase were strongly affected by familiarity signals, new pictures judged as “old” (false alarms) should be associated with a stronger early mid-frontal old/new effect than correct rejections. Further, if positive pictures were associated with stronger familiarity signals than negative ones in the test phase, new positive pictures should elicit a stronger mid-frontal old/new effect than new negative pictures. ERP waveforms for positive and negative correct rejections and false alarms at the frontal midline electrode Fz are depicted in Figure 4.3B. Mean amplitudes in the 300 – 500 ms time window at electrode Fz were analyzed in a two (Item Status: Correct rejections, false alarms) by two (Valence: Positive, negative) ANOVA. As predicted, false alarms (*M* = -8.15, SEM = 0.93 µV) were associated with more positive mean amplitudes than correct rejections (*M* = -9.07, SEM = 0.90 µV), *F*(1, 31) = 8.54, *p* < .01, η_p^2 = .22, and positive pictures (*M* = -8.08, SEM =

0.94 µV) elicited more positive mean amplitudes than negative ones (M = -9.14, SEM = 0.91 µV), $F(1, 31) = 6.00$, $p < .05$, $\eta_p^2 = .16$. The Item Status by Valence interaction was nonsignificant, $F(1, 31) < 1$, $p = .62$, $\eta_p^2 = .01$.

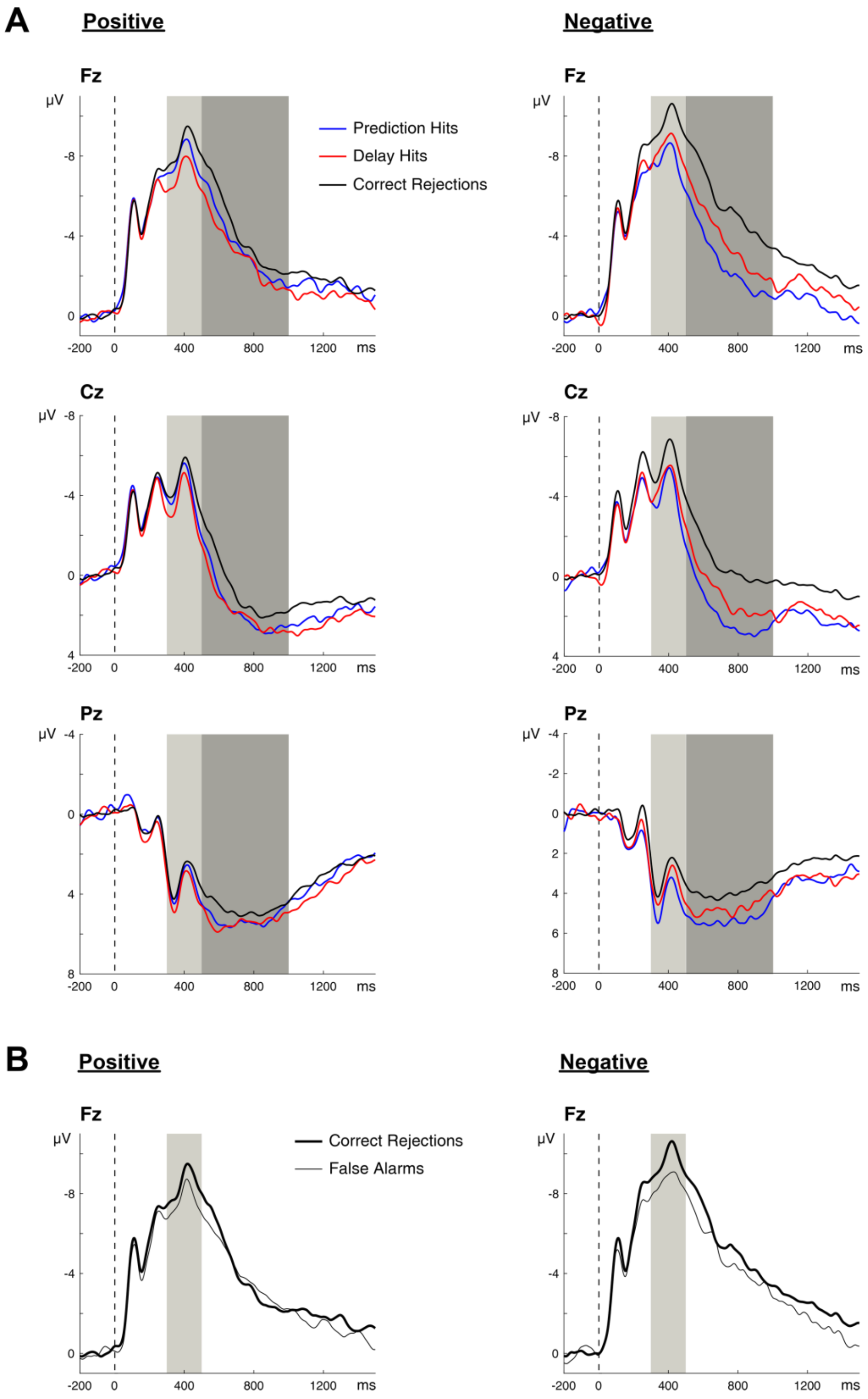

Figure 4.3: ERP waveforms recorded during picture presentation in the test phase. Waveforms associated with correct memory decisions are ahown for three respresentative frontal, central, and parietal electrodes (A). Waveforms associated with correct rejections and

false alarms are shown at the frontal midline electrode Fz (B). Shaded areas indicate the 300 – 500 ms and 500 – 1000 ms time windows used to analyze old/new effects.

4.4 Discussion

In Experiment 3, we investigated how explicit outcome expectations affect delayed feedback processing and memory for delayed feedback events. Our hypothesis was that if outcome predictions generated during the feedback delay period lead to an involvement of declarative learning processes in delayed feedback processing, the behavioral memory benefit for delayed feedback pictures (Foerde & Shohamy, 2011; Lighthall et al., 2018) and the ERP correlates associated with it (Höltje & Mecklinger, 2020) should be more pronounced under conditions that promote the generation of predictions regarding the outcome of an action. To test this hypothesis, we contrasted a Prediction condition in which participants were asked on each trial to predict the category of the upcoming feedback picture (indoor or outoor scene) with a standard delayed feedback condition in a probabilistic feedback learning task. Feedback valence and picture category were yoked so that for each participant, one picture category always coded positive feedback, and the other picture category coded negative feedback. Notably, and different from previous studies investigating memory for delayed feedback events (Foerde & Shohamy, 2011; Höltje & Mecklinger, 2020; Lighthall et al., 2018), the assignment of feedback valence and picture category was balanced across participants in the present study, which enabled us to examine effects of feedback valence on memory without confounding differences in memory between pictures categories.

As evidenced by an increase in the proportions of correct responses over the course of the learning phase, participants successfully used the feedback pictures for learning in both conditions. Performance was significantly higher in the Delay condition than in the Prediction condition, which indicates that the requirement to predict the category of the upcoming feedback picture increased task difficulty in the Prediction condition. Contrary to our expectations, feedback pictures encoded in the Prediction condition were not remembered better than those learned in the Delay condition. It is conceivable that the increased task difficulty in the Prediction condition was associated with higher attentional demands that may have counteracted the encoding of feedback pictures in this condition. Interestingly, whereas the behavioral data do not support the view that the declarative learning system was more strongly involved in the Prediction condition, the feedback-locked ERP data are suggestive of this conclusion.

As predicted based upon the results of Experiment 2, $\mathrm{FRN}_{\mathrm{peak}}$ amplitudes elicited by subsequently remembered feedback pictures were attenuated relative to subsequently forgotten ones. This finding confirms the reliability of the $\mathrm{FRN}_{\mathrm{peak}}$ subsequent memory effect observed in Exp. 2 and, beyond that, shows that this interaction between delayed feedback processing and memory encoding can be found with a feedback delay of only four seconds (vs. seven seconds in Exp. 2). In the Delay condition, the $\mathrm{FRN}_{\mathrm{peak}}$ subsequent memory effect was somewhat less pronounced than in the Prediction condition and only reached significance for positive feedback pictures. This result is consistent with our hypothesis that generating predictions about the outcome of an action leads to an involvement of the declarative learning system in delayed feedback processing: The finding that the $\mathrm{FRN}_{\mathrm{peak}}$ SME was more pronounced in the Prediction condition than in the Delay condition indicates that there was stronger interference at the electrophysiological level between feedback processing and memory encoding in the Prediction condition, which presumably reflects increased competition for similar (hippocampal) processing resources in this condition (Höltje & Mecklinger, 2020).

Feedback processing as reflected in the $\mathrm{FRN}_{\mathrm{peak}}$ was more pronounced in the Prediction condition than in the Delay condition. This finding is consistent with previous studies showing that FRN amplitudes are modulated by outcome expectations (Bismark, Hajcak, Whitworth, & Allen, 2013; Hajcak, Moser, Holroyd, & Simons, 2007). In the study by Bismark and colleagues (2013) it was found that no FRN is elicited when there is no time to develop an outcome expectation. Hajcak et al. (2007) found that unpredicted outcomes were associated with larger FRN amplitudes than predicted outcomes, but only in a task in which the outcome was predicted *after* a choice was made, and not when the prediction was made *before* the choice. However, an alternative explanation for the difference in FRN_{peak} amplitudes between the Prediction and Delay conditions is possible: The proportions of correct responses in the learning phase suggest that stimulus-response associations were learned faster in the Delay condition than in the Prediction condition, and previous studies have shown that FRN amplitudes can decrease after a stimulus-response association has been learned (Holroyd & Coles, 2002). Thus, it is conceivable that this learning-related decrease in FRN_{peak} amplitudes was on average more pronounced in the Delay condition than in the Prediction condition, whereas continued learning and feedback processing in the Prediction condition was associated with large FRN_{peak} amplitudes.

The processing of unexpected positive outcomes as reflected in FRN_{diff} amplitudes did not differ between the Prediction and Delay conditions. This result indicates that feedback processing engaged the procedural learning system to a similar extent in the two conditions.

Feedback pictures in the Prediction condition elicited larger parietal P300 amplitudes than those in the Delay condition. In ERP studies investigating feedback processing, unexpected outcomes are often associated with larger P300 amplitudes than expected outcomes (Bellebaum & Daum, 2008; Hajcak, Holroyd, Moser, & Simons, 2005; Hajcak et al., 2007; Von Borries, Verkes, Bulten, Cools, & De Bruijn, 2013). It is possible that generating predictions boosted the surprise associated with the processing of unexpected outcomes (Brod et al., 2018). Furthermore, consistent with the study by Chase et al. (2011), in which the feedback P300 was associated with feedback learning based on explicit rules, this finding could reflect a stronger reliance on declarative learning processes in the Prediction condition. It is conceivable that predicting the feedback picture category increased the amount of attentional resources allocated to processing the feedback picture and thereby boosted parietal P300 amplitudes. Negative pictures also elicited larger P300 amplitudes than positive ones; however, this valence effect most likely reflects the increased distinctiveness of negative feedback pictures resulting from the decreasing frequency of negative feedback over the course of the learning task.

ERP old/new effects revealed further evidence in support of the view that explicit outcome expectations modulate the involvement of declarative learning processes in feedback processing, which also affects memory for the feedback events. Most interestingly, negative feedback pictures that disconfirmed the expectation of a positive outcome in the feedback learning task elicited a late old/new effect in the ensuing memory test which was more pronounced for feedback pictures encoded in the Prediction condition than for those learned in the Delay condition. This finding suggests that the initial processing of unexpected negative feedback pictures in the Prediction condition during the learning phase boosted later recollective processing of these pictures in the recognition memory test. In other words, feedback pictures that disconfirmed a prediction were associated with enhanced declarative learning. This resonates with recent theoretical and empirical work suggesting that declarative learning is driven by the strength of the prediction error elicited by an event (Greve et al., 2017; Henson & Gagnepain, 2010) and could reflect a stronger involvement of declarative learning processes in predictive feedback processing.

Feedback pictures in the Prediction and Delay conditions elicited equally strong early mid-frontal old/new effects, suggesting that memory retrieval relied on episodic familiarity to a similar extent in both learning conditions.

To our surprise, participants showed a strong tendency to make incorrect “old” decisions for positive pictures in the recognition memory test. Our experimental design, carefully balanced with regard to the assignment of picture category and feedback valence, enabled us to detect this recognition bias induced by positive feedback valence which, to our best knowledge, went unnoticed in previous studies investigating memory for feedback events. A further analysis revealed that false alarms and positive pictures were associated with larger early mid-frontal old/new effects than correct rejections and negative pictures, which strongly suggests that positive pictures were often erroneously judged as “old” because they elicited strong familiarity signals in the test phase. This pattern of results is reminiscent of a study by Johansson et al. (2004) in which pictures of emotional faces were associated with a more liberal recognition bias than those of neutral faces, and correctly rejected emotional faces elicited stronger early mid-frontal old/new effects than neutral ones. The authors argued that, in order to facilitate the processing of behaviorally relevant information, the arousal associated with the processing of emotional stimuli induces a relaxation of the criterion for recognition (see Windmann and Kutas, 2001, for a similar finding with negative words). In the present study, it is conceivable that an emotional response to positive feedback pictures established in the learning phase was generalized to other pictures from the same picture category (indoor or outdoor scene) and thereby caused the recognition bias observed in the test phase. Alternatively, it is conceivable that the reward value associated with positive feedback pictures generalized to other pictures belonging to the same category, a phenomenon well known from conditioning paradigms (Miendlarzewska et al., 2016). Further research is needed to investigate how feedback valence affects memory and response bias.

5 General Discussion

The global aim of this dissertation was to investigate interactions between feedback processing and memory encoding, and how they are reflected in ERPs. One of the key questions to be answered was how the putative involvement of declarative memory processes in delayed feedback processing, as evident from hippocampal activity associated with delayed feedback processing (Foerde & Shohamy, 2011), is reflected in the ERP correlate of dopaminergic RPEs in feedback processing (i.e., the FRN). Our approach was to present feedback pictures depicting indoor and outdoor scene in a probabilistic feedback learning task in which participants learned associations between Chinese characters and two responses. In a subsequent memory test, recognition memory for the scene pictures was tested. We contrasted subsequently remembered and forgotten pictures to examine how ERPs recorded during feedback presentation were modulated by successful memory formation. Another superordinate research question was how feedback timing and valence modulate familiarity and recollection, two distinct sub-processes contributing to episodic memory retrieval. To address this question, we analyzed ERPs recorded during the presentation of “old” and “new” scene pictures in the recognition memory test. Notably, the incidental nature of the learning paradigm we employed allowed us to investigate effects of feedback timing and valence on behavioral measures of memory and ERPs associated with feedback processing and memory retrieval without motivational and attentional confounds that cannot be ruled out in intentional learning paradigms.

In the following, we will summarize the research questions and the main findings from the three experiments we conducted. Most findings were already extensively discussed in the respective chapters. We will therefore focus on the implications of our main findings and integrate them into the theoretical and empirical context provided by the literature. We will highlight the methodological advancements included in this dissertation, but also address its limitations, point out open questions, and make suggestions for future research.

5.1 Summary of Research Questions and Main Findings

5.1.1 Experiment 1

The aim of Experiment 1 was to investigate how feedback timing and valence affect memory for task-unrelated pictures presented together with performance feedback in a probabilistic learning task. Feedback was delivered either with a short (SD, 500 ms) or long (LD, 6500 ms) temporal delay. We examined how interactions between feedback processing and memory encoding are reflected in the ERP correlates of RPEs in feedback processing (i.e., the FRN) and episodic memory retrieval (i.e., early mid-frontal and late parietal old/new effects). Behaviorally, memory was better for positive than negative feedback pictures, but there was no effect of feedback delay on memory performance. In the ERPs recorded during the learning phase, subsequently remembered positive feedback pictures were associated with a subsequent memory effect that resembled in its spatiotemporal characteristics the $\mathrm{FRN}_{\mathrm{diff}}$, suggesting that positive reward prediction errors as reflected in the $\mathrm{FRN}_{\mathrm{diff}}$ contribute to successful memory encoding. Consistent with previous studies, the $\mathrm{FRN}_{\mathrm{diff}}$ was reduced for delayed feedback, but only in a condition in which feedback was useful for learning. As evidenced by behavioral and ERP estimates of familiarity and recollection, positive feedback enhanced memory mainly by boosting familiarity-based recognition.

5.1.2 Experiment 2

Experiment 2 pursued the same principal goal as Exp. 1, namely to investigate interactions between feedback processing and memory encoding under SD and LD feedback conditions, and how they are reflected in ERPs. We reasoned that the fixed assignment between picture and feedback categories (outdoor = positive, indoor = negative) employed by Foerde and

Shohamy (2011) could be an important boundary condition that enables memory for feedback pictures to benefit from delayed feedback presentation and modified the probabilistic feedback learning task accordingly. Feedback processing as reflected in the FRN_{peak} was diminished for remembered LD feedback pictures, indicating that delayed feedback processing and memory encoding competed for similar neural processing resources. As evidenced by large FRN_{diff} amplitudes in the SD condition, the evaluation of shortly delayed feedback strongly relied on the procedural learning system. A complementary model-based single trial analysis was conducted to validate models of the functional significance of the FRN. Consistent with previous studies, feedback-locked N170 and P300 amplitudes were sensitive to feedback delay. In the test phase, memory for LD feedback pictures was better than for SD pictures and accompanied by a late old/new effect, presumably reflecting extended recollective processing.

5.1.3 Experiment 3

The aim of Experiment 3 was to further explore the source of the involvement of declarative learning processes in delayed feedback processing. We reasoned that a temporal feedback delay of several seconds allows participants to spontaneously generate explicit outcome expectations, the disconfirmation of which could be associated with increased hippocampal activity and enhanced declarative learning. To test this hypothesis, we contrasted a default delayed feedback condition with Prediction condition in which the generation of explicit outcome expectations was enforced by asking participants to predict on each trial which type of feedback picture (indoor or outdoor scene) they expected. Behaviorally, there was no difference in hit rates between the two conditions, but a strong tendency to judge positive feedback pictures as “old” in the recognition memory test. A stronger FRN_{peak} SME and larger P300 amplitudes indicate that feedback processing in the Prediction condition was associated with a stronger involvement of the declarative learning system than in the Delay condition. As evidenced by ERP old/new effects, negative feedback pictures that disconfirmed an explicit outcome expectation were associated with stronger recollective processing in the Prediction condition than in the Delay condition. The behavioral response bias in the test phase was paralleled by the finding that familiarity signals elicited by “new” pictures were modulated by picture valence (positive > negative) and memory decisions (false alarms > correct rejections).

5.2 Implications

5.2.1 Insights Into the Interaction Between Delayed Feedback Processing and Memory Encoding

Recent neuroimaging research has shown that feedback timing modulates the brain systems involved in feedback learning. Learning from immediate feedback relies on the integrity of the nigrostriatal dopamine pathway, whereas the processing of feedback that is delayed by several seconds engages the hippocampus (Foerde, Race, Verfaellie, & Shohamy, 2013; Foerde & Shohamy, 2011). Furthermore, delayed feedback pictures associated with hippocampal activity are remembered better than shortly delayed ones (Foerde & Shohamy, 2011; Lighthall et al., 2018). Prima facie, these findings suggest that the involvement of declarative learning processes associated with hippocampal activity in delayed feedback processing has a beneficial effect on memory, even though it has not yet been shown that the hippocampal activity associated with delayed feedback predicts subsequent memory. One of the key findings of this dissertation is that the putative involvement of declarative learning processes in delayed feedback processing causes interference between feedback processing and memory encoding at the electrophysiological level. In Experiment 2, we replicated the behavioral effect of feedback delay on memory obtained by Foerde and Shohamy (2011) and found that long delayed feedback pictures that were subsequently remembered elicited smaller FRN_{peak} amplitudes than subsequently forgotten ones. This finding clearly shows that the memory enhancement associated with delayed feedback processing is not “for free”, but rather comes at the cost of diminished feedback processing as reflected in ERPs. In Experiment 3, we replicated the FRN_{peak} SME and found that the interference between feedback processing and memory encoding was more pronounced in a condition in which participants were asked to predict the category of the upcoming feedback picture. The latter finding indicates that the involvement of declarative learning processes in delayed feedback processing may at least to some extent be related to the spontaneous generation of explicit outcome expectations during the feedback delay period.

The FRN_{peak} SMEs obtained in Experiments 2 and 3 indicate that delayed feedback processing and incidental memory encoding compete for similar processing resources. However, even though it is tempting to speculate that this interference at the electrophysiological level reflects a competition for hippocampal processing resources, it is not possible to draw such a conclusion based on EEG data. Furthermore, the hippocampus is not the only brain structure that could cause interference between feedback processing and memory encoding. Freedberg, Toader, Wassermann, and Voss (2020) recently proposed a model for striatum-MTL interactions in learning and memory that assumes a competition for PFC processing resources early during learning as the source of competitive interactions between the striatum-based procedural learning system and the MTL-based declarative learning system. One testable prediction that can be derived from the Freedberg et al. (2020) model is that if the interference at the electrophysiological level between delayed feedback processing and memory encoding is caused by a competition for PFC processing resources, then this interference should only occur early during learning. Thus, one promising avenue for future research would be to examine learning-related changes in the interaction between delayed feedback processing and memory encoding.

Further insights into the processes reflected in the FRN_{peak} that appear to be involved both in delayed feedback processing and in declarative memory encoding could be gained by exploring the spectral characteristics of the underlying EEG activity. For instance, (frontal) theta power is associated with salience prediction errors in feedback processing (Cavanagh, Figueroa, Cohen, & Frank, 2012; Ergo, De Loof, Janssens, & Verguts, 2019; Mas-Herrero & Marco-Pallarés, 2014) and has been suggested to signal the need for cognitive control (Cavanagh & Frank, 2014). In EEG studies investigating memory formation, successful encoding is often associated with increased theta power, presumably reflecting a mechanism by which theta oscillations support the encoding of associative memories (Herweg, Solomon, & Kahana, 2020). Thus, it is conceivable that FRN_{peak} amplitudes as measured in the present work and feedback-related theta power reflect the same cognitive process that is necessary both for the processing of unexpected feedback and for memory encoding (but see Rawls et al., 2020, for a recent study indicating that the FRN and frontal midline theta reflect functionally distinct processes). Future studies should therefore examine whether interference between delayed feedback processing and memory encoding at the electrophysiological level can be localized in theta activity.

A second open question is why we found interference between delayed feedback processing and memory encoding at the electrophysiological level, but not behaviorally. In Experiment 2, feedback learning performance did not differ between the short and long feedback delay conditions, but long delayed feedback pictures were remembered better than shortly delayed ones. In the study by Wimmer et al. (2014), one of the few studies that investigated interactions between reward learning and memory encoding, behavioral interference between reward learning and memory encoding was found at the single trial level. In the Wimmer et al. (2014) study, participants performed a reward learning task with fluctuating reward probabilities. On each trial, two objects were presented surrounded by color frames representing two possible choices, each associated with drifting reward probabilities. Approximately 1.5 seconds later, participants were given “reward” or “miss” feedback. Participants were instructed to earn as much “reward” as possible in the task. One day later, a surprise recognition memory test was conducted for the objects presented together with the choice options. Wimmer et al. (2014) found that subsequent memory for the objects predicted diminished updating of choice behavior on the next trial and decreased correlations between RPE estimates derived from a computational reinforcement learning model and BOLD signals in the striatum at the time of feedback presentation. Even though the Wimmer et al. (2014) study differs in many aspects from the paradigm used in the present work, it is an intriguing question whether similar interference effects at the single trial level can be found between delayed feedback processing and memory encoding.

5.2.2 How Do Positive RPEs Affect Memory Encoding?

Our finding in Experiment 1 that the processing of positive feedback is associated with superior memory for pictures presented together with the feedback and increased reward signals as reflected in the $\mathrm{FRN}_{\mathrm{diff}}$ resonates with the results of a number of recent studies suggesting that positive RPEs strengthen memory encoding (e.g., De Loof et al., 2018; Jang, Nassar, Dillon, & Frank, 2019) and provides ERP evidence in support of this view. Interestingly, and similar to the Jang et al. (2019) study, this effect was observed after a short retention interval of only 20 minutes, which suggests that memory consolidation processes did not strongly contribute to it. In contrast, memory enhancememts associated with reward processing have often been obtained after considerably longer rentention intervals (e.g., Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Wittmann et al., 2005), and dopamine signals elicited by rewards are thought to enhance memory by facilitating the late stage of hippocampal long-term potentiation, a process that unfolds over a time scale of hours to days (Lisman et al., 2011; Shohamy & Adcock, 2010). Thus, the consolidation-independent memory enhancement for pictures presented together with positive feedback observed in Experiment 1 is most likely mediated by a distinct underlying mechanism that modulates memory encoding. In the study by Jang et al. (2019) participants were given a gambling task. On each trial, participants were first shown the value of the gamble, followed by the image of an object whose category (living or nonliving) indicated the probability of reward. Participants then made a play-or-pass decision and were shown their earnings if they played or their hypothetical trial outcome if they passed. A surprise recognition memory test for the objects presented in the gambling task was conducted either directly after a short break or on the next day. Jang et al. (2019) found that memory for the objects increased linearly as a function of the RPE elicited by the presentation of the object in the gambling task, but was unaffected by RPEs elicited by the cue signalling the value of the gamble or by the outcome. Notably, this effect was already present in the immediate memory test, indicating that it was not consolidation-dependent. Jang et al. (2019) discussed the possibility that fluctuations in anticipatory attention could have affected the encoding of the objects, even though they kept the different types of trials in the gambling task as similar as possible. In a similar vein, we cannot completely rule out the possibility that fluctuations in attention affected the encoding of the pictures presented together with the feedback in Experiment 1, although we used an incidental learning paradigm to minimize attentional and motivational influences on memory encoding. Furthermore, the Jang et al. (2019) study indicates that memory enhancements by RPEs may critically depend on the timing of the RPE. This finding highlights the utility of our learning paradigm in which memory was tested for pictures presented at the time point of feedback presentation.

Importantly, a mnemonic bias similar to the one observed in Experiment 3 cannot explain the memory enhancement associated with the processing of positive feedback in Experiment 1, since indoor and outdoor scene pictures were randomly assigned to the positive and negative feedback conditions in this study. Thus, picture category and feedback valence were independent from each other in Experiment 1, and a tendency to judge one of the picture categories as “old” more often than the other would not have systematically affected memory for positive or negative feedback pictures.

5.3 Methodological Advancements

5.3.1 Implications for ERP Studies Investigating Feedback Processing

The functional significance of the FRN has been a subject of continuous debate during the last two decades. The most prominent theory of the FRN states that it reflects dopaminergic RPEs in feedback processing (Holroyd & Coles, 2002; Sambrook & Goslin, 2015; Walsh & Anderson, 2012). However, evidence is mounting in favor of the alternative view that the FRN reflects the processing of unexpected outcomes irrespective of valence (e.g., Ferdinand et al., 2012; Hauser et al., 2014; Oliveira et al., 2007; Talmi et al., 2013; Walentowska, Severo, Moors, & Pourtois, 2019). A third branch of studies has focussed on variance in the FRN signal related to the processing of rewards or positive outcomes (for a review see Proudfit, 2015). Differences between studies regarding the measurement of the FRN certainly contributed to the divergent results in the literature: A peak-to-peak quantification of the FRN primarily captures variance related to the N200 and is more likely to reflect the processing of unexpected outcomes irrespective of valence than a quantification based on the positive minus negative feedback difference wave which by definition more strongly reflects activity differentiating between positive (rewarding) and negative (nonrewarding) outcomes. The present work contributes to a reconciliation of the divergent accounts of the FRN by acknowledging that the peak-to-peak FRN (FRN_{peak}) and the difference wave-based FRN (FRN_{diff}) are functionally dissociated and reflect the processing of unexpected outcomes irrespective of valence and rewarding outcomes, respectively. In a series of three experiments, we examined these two FRN measures and found that FRN_{peak} amplitudes were larger for negative than for positive feedback (Exp. 1 – 3), more pronounced for long delayed than for shortly delayed feedback (Exp. 1 and 2), increased by the requirement to make predictions about the feedback (Exp. 3), and sensitive to the interaction between delayed feedback processing and memory encoding (Exp. 2 and 3). In contrast, $\mathrm{FRN}_{\mathrm{diff}}$ amplitudes were consistently larger for shortly delayed feedback (Exp. 1 and 2), but not sensitive to the interaction between delayed feedback processing and memory encoding (Exp. 2) or to explicit outcome expectations (Exp. 3). Rather, ERP amplitudes in the $\mathrm{FRN}_{\mathrm{diff}}$ time window predicted subsequent memory for pictures presented together with positive feedback (Exp. 1). These results of the present work are broadly consistent with our view stated above that the $\mathrm{FRN}_{\mathrm{peak}}$ and $\mathrm{FRN}_{\mathrm{diff}}$ reflect the processing of unexpected outcomes irrespective of valence and the processing of positive outcomes, respectively. Thus, in order to avoid drawing incomplete and biased conclusions from FRN results, ERP studies investigating feedback processing should consider examining both FRN measures, for each of them provides distinct and valuable information.

5.3.2 Utility of Computational Learning Models for EEG Studies

In Experiment 2, we sought to validate the aforementioned models of the functional significance of the FRN by correlating trial-by-trial estimates of RPEs derived from a computational reinforcement learning model with EEG data recorded during feedback processing. In functional neuroimaging, similar RL models are frequently used to identify brain regions in which BOLD signals correlate with model-derived learning signals (for reviews, see Daw & Doya, 2006; O'Doherty et al., 2007). In contrast, only few studies have connected model-derived reinforcement learning parameters with EEG data at the single trial level (Chase et al., 2011; Hauser et al., 2014; Philiastides, Biele, Vavatzanidis, Kazzer, & Heekeren, 2010), even though the estimation of trial-by-trial learning parameters is one of the major advantages provided by computational RL models. We made use of this advantage and found that strong correlations between RPE estimates and EEG amplitudes were confined to those time windows in which FRN effects were present in the ERP waveforms. This finding confirms that the FRN is an ERP correlate of RPEs in feedback processing (Sambrook & Goslin, 2015; Walsh & Anderson, 2012). Furthermore, significant correlations between unsigned prediction errors (salience prediction errors, SPEs) were obtained in the earlier $\mathrm{FNR}_{\mathrm{peak}}$ time window, but not in the later $\mathrm{FRN}_{\mathrm{diff}}$ time window. This pattern of results indicates the the $\mathrm{FRN}_{\mathrm{peak}}$ measured in the original feedback-locked ERP waveforms and the $\mathrm{FRN}_{\mathrm{diff}}$ measured in the negative minus positive feedback difference wave are functionally dissociated and reflect distinct processes, namely the processing of unexpected outcome irrespective of valence ($\mathrm{FRN}_{\mathrm{peak}}$) and the processing of unexpected positive outcomes or rewards ($\mathrm{FRN}_{\mathrm{diff}}$). The results of this complementary model-based analysis further emphasize our view stated above that both FRN measures, $\mathrm{FRN}_{\mathrm{peak}}$ and $\mathrm{FRN}_{\mathrm{diff}}$, provide valuable and distinct information on feedback processing.

5.4 Concluding Remarks

Taken together, the findings obtained in this thesis provide behavioral and ERP evidence for multiple types of interactions between feedback processing and memory encoding and retrieval. Firstly, positive RPEs in feedback processing can enhance familiarity-based memory for pictures presented together with the feedback. Secondly, the putative involvement of declarative learning processes in delayed feedback processing boosts recollective memory for feedback pictures. As evidenced by ERPs, this latter interaction between delayed feedback processing and memory encoding induces a competition for neural processing resources that is intensified by the requirement to generate explicit outcome expectations. Thirdly, expectancy violations elicited by the processing of negative feedback are associated with a recollection-based memory enhancement.

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