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Research Report

Effects of learning on feedback-related brain potentials in a decision-making task

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ABSTRACT

This study investigated the neural mechanisms of feedback processing during learning. While their event-related potentials were recorded, subjects learned to make a sequence of correct choices in a decision-making task. Each choice was followed by gain or loss feedback. In subjects who learned the task, both the feedback-related negativity (FRN), the P3 and the late positivity decreased in the course of the experiment. In subjects who did not learn the task, only the FRN decreased. Moreover, from all ERPs investigated, only changes in P3 amplitude were able to predict performance. These results suggest that the motivational significance of the feedback decreased in all the subjects, but attentive processing of the feedback only decreased in subjects who learned the task. These findings support the view that learning leads to economy of effort and more efficient processing. Moreover, they show that the P3 with its close relationship to learning should be included in future studies investigating the effects of learning on ERPs.

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1. Introduction

Performance monitoring is a crucial prerequisite for adjusting and improving behaviour. One useful indicator of monitoring processes such as detecting response conflicts, errors and unexpected outcomes is the so-called feedback-related negativity (FRN, also: feedback error-related negativity). The FRN is a frontocentral negative-going deflection in the event-related potential that occurs following negative feedback. It peaks 200–300 ms after the onset of a negative feedback stimulus (Miltner et al., 1997; Gehring and Willoughby, 2002; Yeung et al., 2005). The FRN is the feedback-locked variant of the response-locked error-related negativity (ERN) which peaks around 50–60 ms after an erroneous response (Falkenstein et al., 1991; Gehring et al., 1993).

Both components have been shown to be sensitive to response or decision conflict (Yeung and Sanfey, 2004), as well as to the emotional evaluation of an outcome (Gehring et al., 1993; Hajcak et al., 2005a). As a unified account of both the ERN and FRN, the reinforcement learning theory proposed that these components occur when perceived outcomes turn out to be worse than expected (Holroyd and Coles, 2002; Nieuwenhuis et al., 2004). The negative prediction error thus generated allegedly leads to decreased activity in the mesencephalic dopamine system. This reduced dopaminergic input is believed to disinhibit the ACC which then generates the ERN/FRN. Extending this theory, recent findings suggest that positive prediction errors also elicit an ERN/FRN. Thus, these components are not only produced when outcomes are worse than expected, but whenever they are different than expected (Oliveira et al., 2007).

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Since learning changes outcome expectations, performance increases should also change the FRN. Indeed, previous studies on learning effects have found decreases in the FRN after learning compared to before having learned (Nieuwenhuis et al., 2002; Pietschmann et al., 2008; Krigolson et al., 2009; Bellebaum and Daum, 2008). Decreases in the FRN have also been observed between subjects who learned compared to those who did not learn a probabilistic reward task (Santesso et al., 2008; Krigolson et al., 2009). However, the results are not always unequivocal, since some studies either did not find any FRN at all (Groen et al., 2007), or found learning-related changes only for positive feedback, not for negative feedback (Eppinger et al., 2008, 2009).

One factor that may contribute to the inconsistencies is that the FRN is embedded into the P3, a positive-going component with a maximum at parietal sites. Importantly, the P3 is affected by factors that also influence the FRN, in particular target expectancy. The P3's most prominent feature is that it gets smaller when target probability increases (Duncan-Johnson and Donchin, 1977; Donchin and Coles, 1988), possibly due to an increased conformity to expectations (Yeung and Sanfey, 2004; Hajcak et al., 2005b). Similar to the FRN, the P3 has been reported to decrease with learning both within (e.g., Groen et al., 2007; Jongasma et al., 2006; Lindin, 2004) and between subjects (Radlo et al., 2001) across various tasks.

Despite the fact that expectancy affects both the FRN and the P3 and that therefore, learning can be assumed to affect both components, only very few studies have investigated learning-related changes in both the FRN and the P3. One exception is the study of Bellebaum and Daum (2008) in which a reduction of both the FRN and the P3 was related to having learned. Similarly, Groen et al. (2007) reported a decrease in the P3 from the first to the second section of a probabilistic learning task in children. However, changes in the FRN with learning could not be investigated in this task, since the abstract feedback stimuli failed to elicit an FRN in the first place.

A further component that can be expected to be sensitive to learning is the late positivity. The late positivity has been suggested to indicate the strength of a memory trace (formed during encoding) (Azizian and Polich, 2007). The authors of this study also tentatively suggest that the late positivity is related to cognitive shifts which are essential for set shifting, as required, for example, in the Wisconsin Card Sorting Test. It has been suggested that the late positivity and the P3 reflect similar processes (Kok, 1997). Along these lines, the late positivity evoked by emotional pictures (e.g. Diedrich et al., 1997; Amrhein et al., 2004; Cuthbert et al., 2000) may indicate "a greater allocation of perceptual processing resources to motivationally relevant input" (Cuthbert et al., 2000, p.97).

Since all these three components have been reported to change with performance improvement, it is well possible that they interact during learning. However, to our knowledge, there are no studies that systematically investigate the changes in all these three components at the same time. Therefore, the aim of the present study was to further analyse changes in feedback processing with learning by examining learning-related effects on the FRN, the P3 and the late positivity. ERPs were compared for the first half, termed

"early phase," and the second half, termed "late phase," of the experiment. We expected (1) a smaller FRN in the late phase of the experiment, when learning should have occurred, compared to the early phase of the experiment. This effect should be particularly pronounced for losses. We also expected (2) a smaller P3 and late positivity in the late than in the early phase of the experiment. Since not all of the subjects learned the given task, we also expected (3) a smaller FRN for subjects who learned the task (high learners) than for those who did not learn the task (low learners), particularly for losses, as well as (4) a smaller P3 and late positivity for high learners than for low learners.

2. Results

2.1. Behaviour

The fitted learning curves for each of the subjects are displayed in Fig. 1. Thirty-nine subjects were classified as high learners, and 23 as low learners (see Methods). High learners achieved a larger percentage of correct responses than low learners both in the early ($N=62$, $Z=-5.02$, $p<0.0001$) and the late phase ($N=62$, $Z=-6.55$, $p<0.0001$) of the experiment. Moreover, compared to low learners, high learners showed a larger increase in the mean percentage of correct responses across the two phases of the experiment, namely from 72% to 96% ($N=39$, $Z=-5.44$, $p<0.001$). The performance of low learners only increased from 55% to 59% ($N=23$, $Z=-2.37$, $p<0.05$).

For both high and low learners, response latency (see Table 1) was higher in the first than in the second phase of the experiment ($F(1,48)=18.79$, $p<0.001$). Latency was also higher for wrong than correct responses ($F(1,48)=11.49$, $p<0.01$). Moreover, an interaction between *learngroup* and *accuracy* ($F(1,48)=8.97$, $p<0.01$) showed that this effect was only due to the behaviour of high learners ($p<0.05$). Low learners had similar latencies when giving correct and wrong answers.

2.2. FRN

Grand-average ERP waveforms for the different groups are shown in Fig. 2. An ANOVA of the FRN amplitudes revealed main effects of *outcome* ($F(1,60)=28.54$, $p<0.0001$), *phase* ($F(1,60)=4.81$, $p<0.05$), and *learngroup* ($F(1,60)=6.32$, $p<0.05$), showing that the FRN was larger for losses than for gains, larger in the early than in the late phase, and larger for low learners than high learners. No further effects or interactions were observed.

2.3. P3

Similar to the FRN effects, there was a main effect of *phase* ($F(1,60)=97.63$, $p<0.0001$) and *learngroup* ($F(1,60)=31.96$, $p<0.0001$) on P3 amplitude. The P3 was both larger in the early than in the late phase and for low learners than for high learners (see Fig. 2). These main effects were further qualified by interactions of *phase* and *outcome* ($F(1,60)=6.63$; $p<0.05$) and of *phase* and *learngroup* ($F(1,60)=40.76$, $p<0.0001$). Post-hoc tests revealed that the P3 was only larger in low than high learners during the late phase, but not during the early phase ($p<0.01$).

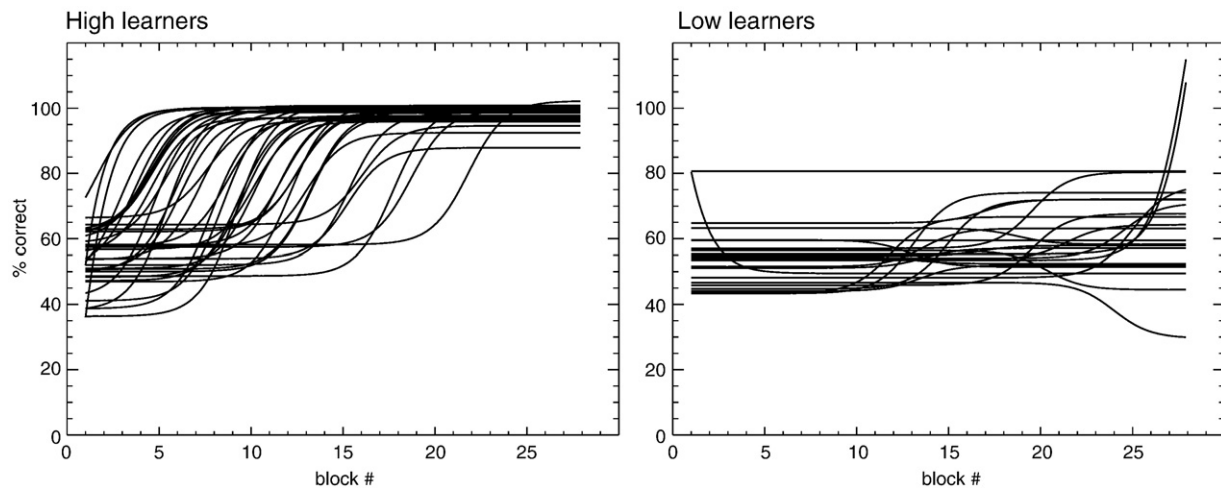


Fig. 1 – Fitted learning curves for each of the 39 high learners (left) and 19 low learners (right) across blocks.

Moreover, high learners had a larger P3 in the early than in the late phase ($p < 0.0001$), whereas low learners did not show a comparable amplitude reduction. In other words, low and high learners had a comparably large P3 in the early phase. This large P3 subsequently decreased for high learners, but not for low learners. Thus, contrary to the FRN which distinguished high and low learners during both experimental phases, their P3 was only different in the late phase. Moreover, contrary to the FRN which got smaller with learning for both high and low learners, a learning-related decrease in the P3 was only observed for high learners (Fig. 2).

2.4. Late positivity

Generally, the amplitudes at all three electrodes Fz, Cz, and Pz were larger for low learners than high learners (main effect for *learngroup*, $F(1,60) = 28.20$; $p < 0.0001$) in the early than in the late phase (main effect of *phase*, $F(1,60) = 57.10$, $p < 0.0001$), and for losses than for gains (main effect of *outcome*, $F(1,60) = 8.40$, $p < 0.01$). An additional main effect for *electrode* indicated that the amplitudes at Fz, Cz, and Pz differed from each other ($F(1.3,75.5) = 99.59$, $p < 0.0001$). These main effects were further specified by interactions of *phase* and *learngroup* ($F(1,60) = 27.79$, $p < 0.0001$), *outcome* and *learngroup* ($F(1,60) = 6.38$, $p < 0.05$), *electrode* and *learngroup* ($F(1.2,75.1) = 14.74$, $p < 0.0001$), *phase* and *electrode* ($F(1.4,81.9) = 15.10$, $p < 0.0001$), and a three-way interaction between *electrode*, *phase* and *learngroup* ($F(1.4,81.9) = 14.25$, $p < 0.0001$). Post-hoc tests indicated that Fz amplitudes were

smaller than Cz and Pz amplitudes in both high (all p 's < 0.0001) and low (all p 's < 0.0001) learners during the early phase of the experiment. During the late phase, this pattern was the same for low learners (all p 's < 0.0001). However, high learners no longer had different amplitudes at Fz than at Cz and Pz. At the same time, only high learners had smaller amplitudes in the late than in the early phase at all electrodes (all p 's < 0.0001) (Fig. 3).

2.5. Relationship between the percentage of correct answers and event-related potential changes

Five predictor variables were entered into the regression: FRN amplitude, P3 amplitude, and late positivity amplitude at each electrode Fz, Cz, and Pz. From these variables, P3 amplitude turned out to be the only valid predictor of the percentage of correct answers ($R = 0.48$), accounting for 22% of the variance ($t = -4.28$, $p < 0.0001$). This indicates that the percentage of correct responses increased with the change in P3 amplitude (Fig. 4). None of the other variables—FRN amplitude and late positivity amplitude—had additional predictive power.

3. Discussion

This study investigated how event-related potentials following feedback change with learning. Using a variant of a task that is commonly applied to elicit the feedback-related negativity (FRN), we observed modifications not only in the FRN, but also in the P3 and the subsequent late positivity.

Our data confirm and extend the findings of previous studies on learning effects on the FRN. To our knowledge, only two previous studies investigated changes with learning in both the FRN and the P3 (Bellebaum and Daum, 2008; Groen et al., 2007), and none included the late positivity. In accordance with these two studies which used a probabilistic learning task, we show comparable learning-related reductions in the FRN and P3 to also occur with a deterministic learning task. Moreover, instead of simple stimulus-response mappings (as, e.g., in Groen et al., 2007; Krigolson et al., 2009;

Table 1 – Mean response latency in seconds with standard deviation (in brackets) for correct and wrong answers in the early and late phase.

	Early phase correct	Early phase wrong	Late phase, correct	Late phase, wrong
High learners	1.49 (.58)	1.78 (.77)	1.05 (.32)	1.57 (1.13)
Low learners	1.76 (.97)	1.88 (1.11)	1.42 (.59)	1.35 (.69)

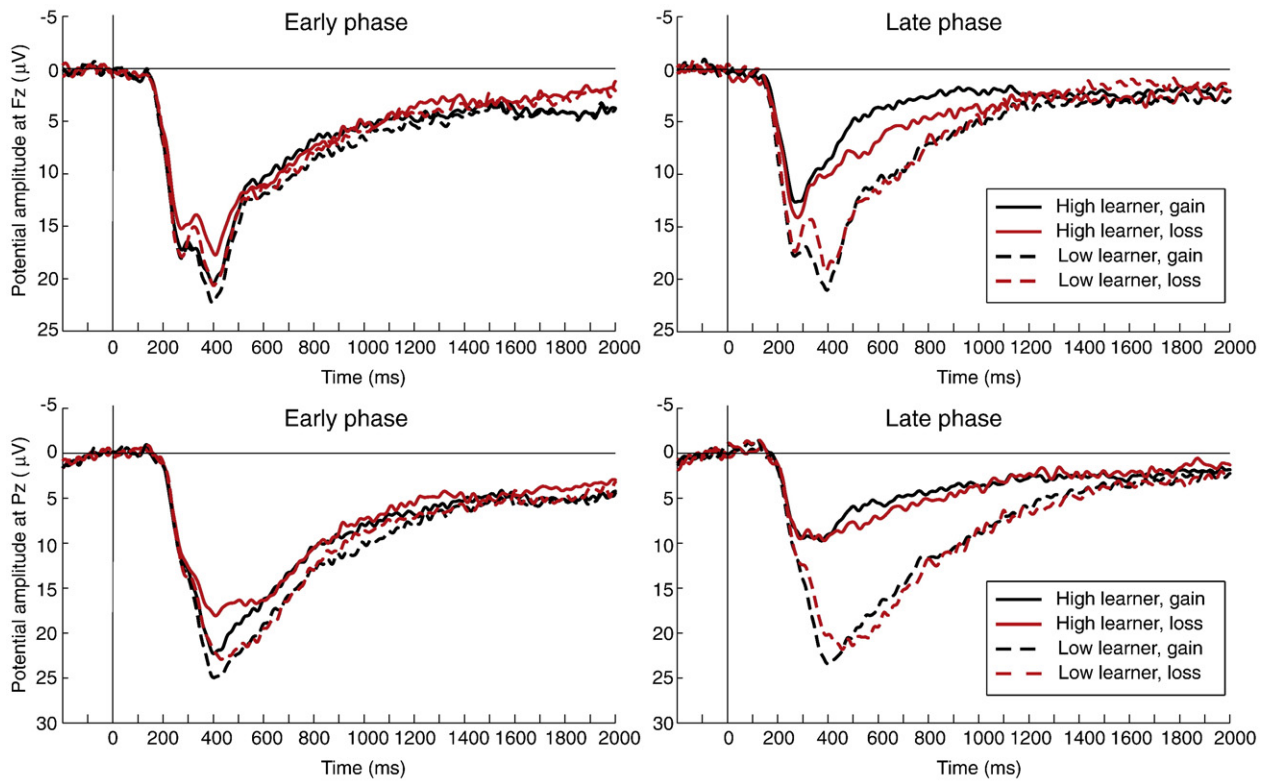


Fig. 2 – Grand averaged event-related potentials (ERPs) elicited by gains and losses in high and low learners at electrodes Fz (upper row) and Pz (lower row). The vertical line at time 0 on the x-axis marks the feedback's onset.

Pietschmann et al., 2008), the task in the present study required to deduce and reproduce a complex response sequence across a number of trials. Probing free recall instead of recognition, this task presumably relies more strongly on working memory. Therefore, in addition to FRN effects, it is particularly suited to investigate processes related to the P3 which is believed to reflect the updating of working memory (Donchin and Coles, 1988).

3.1. FRN

The results regarding the FRN were rather straightforward. As expected, the FRN was larger following losses than gains. The FRN was also generally smaller in high learners than in low learners. Moreover, throughout the experiment the FRN decreased to a similar extent in both groups, independently of the outcome type.

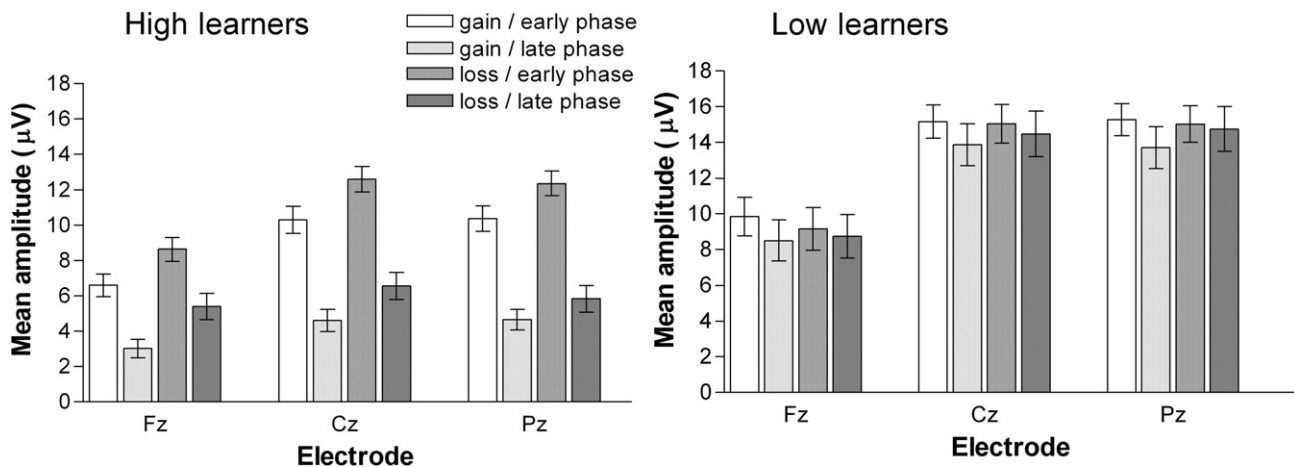


Fig. 3 – Mean amplitudes of the late positivity at electrodes Fz, Cz and Pz with standard error of the mean for each combination of outcome and phase. The amplitudes of high learners are shown on the left, those of low learners on the right.

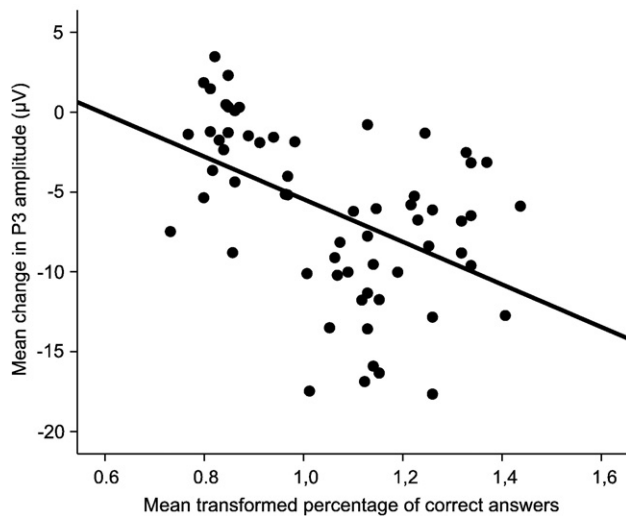


Fig. 4 – Mean transformed percentage of correct answers against mean change in P3 amplitude (amplitude in phase 2 minus amplitude in phase 1). The line shows the best-fit linear regression.

The smaller FRN amplitude in high learners as compared to low learners is consistent with findings of Santesso et al. (2008) from a probabilistic learning task in which only positive feedback was provided. Our data extend these findings by showing that the smaller FRN in learners can be observed both following positive and negative feedback. This decrease in FRN amplitude may be due to differences in outcome predictability (Holroyd and Coles, 2002). For low learners as well as for high learners in the early phase, both gains and losses were unpredictable. Gains and losses then became more predictable for high learners in the late phase. This may have led to a reduction of FRN amplitude.

However, the prediction error account does not help to explain why the FRN decreased for both high and low learners in the late phase of the experiment. Since low learners did not grasp the pattern to be learnt, outcome predictability cannot have changed for them. It is more likely that this amplitude reduction is due to a decrease in feedback saliency and motivational significance. The FRN is known to also be sensitive to the motivational significance of an outcome (Boksem et al., 2006; Pailing and Segalowitz, 2004; Falkenstein et al., 2000; Gehring et al., 1993; Hajcak et al., 2005a). Possibly, low learners got used to obtaining unpredictable losses and gains, and therefore, cared less about the outcomes of their choices. Alternatively, they may simply have lost motivation in the course of the experiment.

For high learners, a similar decrease in motivational significance may have occurred due to the specific task employed. In this task, losses were unavoidable even when all the responses were correct. Since learning was based on the performance dimension only (correct/incorrect), the high learners may have become aware in the late phase that gain and loss feedback provided no information relevant to behavioural adjustment. Therefore, feedback might have lost its motivational meaning for high learners as well. In other words, the subjects' focus may have shifted from the feedback's perfor-

mance dimension to its utilitarian dimension. Interestingly, Nieuwenhuis et al. (2004) obtained a comparable shift in dimension saliency by altering the physical characteristics of the feedback stimuli. In our experiment, such a shift in saliency seems to have been automatically triggered by learning.

3.2. P3 and late positivity

The event-related potential component that was most sensitive to learning in the present task was the P3. For example, only changes in P3 amplitude, not in FRN or late positivity amplitudes, were able to predict the percentage of correct responses. Similarly, Krigolson et al. (2009) did not find a correlation between the FRN and the percentage of correct answers. Unfortunately, they did not investigate the P3.

Our data also show evidence for a functional dissociation between the FRN and the P3. In contrast to the FRN which decreased in all subjects in the course of learning, the P3 only decreased in high learners. Moreover, the FRN was smaller in high than in low learners during both phases of the experiment, but the P3 was only smaller in high than in low learners during the late phase.

P3 amplitude is known to depend on subjective probability, effort devoted to a task (Isreal et al., 1980) and attention (cf. Johnson, 1993). All of these parameters are affected by learning and the associated increasing automatization of a task. Therefore, the decrease in P3 amplitude for high learners in the early compared to the late phase together with the smaller P3 in high learners compared to low learners in the late phase can be explained by an increase in subjective outcome probability and a reduction in effort and/or attention devoted to the task. These findings are in accordance with approaches that propose that learning leads to economy of effort and more efficient processing (e.g., Saling and Phillips, 2007).

It is of interest that the FRN, but not the P3 of low learners decreased in the late phase. This may be due to the specific role of the P3 in attention and context updating (Donchin and Coles, 1988). Despite a decrease of the feedback's motivational significance for low learners, low learners seem to have continuously paid attention to the feedback and maybe also continued to search for the correct response strategy. Thus, the sustained P3 suggests that the low learners continued to put effort into the task.

Related to these effects in the P3, learning-related differences in the amplitude of the late positivity were most evident during the late phase. Presumably as a continuation of the P3, the late positivity of high learners decreased in the late compared to the early phase at all electrodes. Both the P3 and the late positivity have been reported to be smaller for neutral than for emotional stimuli (Johnston et al., 1986; Keil et al., 2002; Cuthbert et al., 2000). Moreover, similar to Cuthbert et al. (2000) we observed a larger voltage negativity at frontal relative to central and parietal sites. Interestingly, this larger negativity disappeared in high learners in the late phase. These effects support the interpretation that high learners, but not low learners, processed the feedback less attentively in the late than in the early phase.

The differential changes in the P3 and FRN with learning could be interpreted in such a manner that the FRN reflects

more general ability or performance differences, and the P3 is more sensitive to *changes* in performance. Such an interpretation would fit the behavioural data which show general differences in performance between high and low learners during both phases, but also a larger performance increase in high as compared to low learners. Alternatively, the P3 may be sensitive to performance changes that occur later on during learning. However, the correlation of the change in P3 amplitude with the percentage of correct answers throughout the entire experiment rather supports the former interpretation. Thus, in the present task the P3 is clearly related to increases in performance, whereas the FRN may rather reflect processes that are secondary to or even underly learning, such as changes in motivation. Evidently, future studies are required to explore this issue in greater detail.

The P3 is believed to have multiple generators, the most important clusters being situated in the temporoparietal junction, i.e. supramarginal gyrus and superior temporal gyrus, and the lateral prefrontal cortex (Nieuwenhuis et al., 2005; Linden, 2005). In an fMRI-task that was identical except for a smaller number of elements per block, the most evident within- and between-subjects differences in learning could be observed in the dorsolateral prefrontal cortex, the inferior parietal cortex (precuneus and supramarginal area), and the orbitofrontal cortex (Sailer et al., 2007, 2008). Thus, the changes in the P3 observed in the present ERP study may be due to similar changes in brain activation as captured in the fMRI studies. At the same time, these fMRI studies showed no evidence of changes in ACC activation, which would be expected to underly a decrease in FRN amplitude (Miltner et al., 1997; Gehring and Willoughby, 2002; Holroyd and Coles, 2002). However, due to the inherent delay between neuronal activation and the BOLD signal changes (Moonen and Bandettini, 2000), fMRI may be more successful in measuring the slower changes of the P3 than the faster FRN fluctuations. Moreover, these data stem from different experiments with different samples, and therefore, have to be compared with caution.

The present study is limited by the fact that only women were investigated. Therefore, the results cannot be generalised to men. Furthermore, although the helplessness manipulation did not show any significant effects, it cannot be ruled out that it may nevertheless have in some way influenced the results. Further studies are required to verify the observed effects in a different context.

To conclude, our data extend previous studies which reported learning-related decreases in the FRN and the P3. Additionally, the P3 proved to be the most valuable predictor for the subjects' successful application of the learning rule. These results clearly underline the importance of including the P3 in studies of learning effects on the FRN.

4. Experimental procedures

4.1. Subjects

66 women, mostly undergraduates, took part in the EEG measurement. For one subject, the experiment had to be terminated midway because of unexpectedly occurring health

problems. Two further subjects did not complete the entire experimental session due to technical problems, and the data of one subject was not usable because it contained too many artefacts. The remaining 62 subjects were aged between 20 and 46 years (mean=24). All the subjects were right-handed, as assessed by the Edinburgh Handedness Questionnaire (Oldfield, 1971), had normal or corrected-to-normal visual acuity and no history of neurological or mental diseases.

Prior to the experiment, written informed consent was obtained from each participant according to the guidelines of the local ethics committee of the Medical University of Vienna. All the subjects received a fixed payment of € 20 for their participation.

A part of the subjects first underwent a procedure intended to induce learned helplessness, which is also why only female participants had been selected (a previous study, Fretzka et al., 1999, had revealed a larger percentage of emotionally highly reactive individuals in females than in men). However, since the groups of helpless and control subjects did not differ on any measure investigated in this manuscript, their data were pooled.

4.2. Experimental setup

Subjects were seated in a sound-attenuated and dimly lit chamber. They rested their arms on the table with the index and middle finger of the right hand on a response box. The stimuli were presented on an 18-inch (Samsung SyncMaster 181 T) LCD-monitor with a spatial resolution of 1024x768. The monitor was placed on the table at a distance of about 70 cm from the observer's eyes.

Since the data were intended to be comparable to those of an fMRI study with the same task (Sailer et al., 2007), all the subjects were submitted to a recording of MR scanner noise during the entire duration of the decision-making task.

The task was adapted from Nieuwenhuis et al. (2004; experiment 2) and Gehring and Willoughby (2002). The stimuli and their size in visual angle were largely oriented at the values reported by Nieuwenhuis et al. (2004). At the beginning of each trial, two rectangles with a central fixation spot in between appeared on the screen. After 3 s, the number 5 or 25 appeared in each of the rectangles. Each number could either appear in the right or the left rectangle, according to a non-predictable pattern. These numbers indicated points that the subjects could win or lose. One of these alternatives had to be selected by pressing the corresponding button on the response box. The choice was marked by a thickening of the black outline of the respective rectangle. If the response did not occur within 30 s, a warning was displayed on the screen. After the response occurred or another 30 s passed without response, the trial ended. One second after the button was pressed, a + or – sign was added to both the chosen and the non-chosen value which indicated whether the chosen value was gained or lost. At the same time, the thick black outline of the chosen outcome turned to red or green which indicated whether the choice was correct or incorrect. A correct choice was defined as one where the subject had chosen the larger gain or the smaller loss, an incorrect choice was defined as one where the subject had chosen the smaller gain or the greater loss (see Table 2).

Table 2 – Possible combinations of outcomes from chosen and non-chosen alternatives. “Loss” and “gain” indicate that the chosen outcome led to the loss or gain of points. “Correct” and “incorrect” indicate whether the “better” or the “worse” option had been chosen. The position of the correct and incorrect alternatives on the screen was varied.

Categories of outcomes	Outcome of chosen alternative	Outcome of non-chosen alternative
Incorrect gain	+5	+25
Correct gain	+5	–25
Correct gain	+25	+5
Correct gain	+25	–5
Incorrect loss	–5	+25
Correct loss	–5	–25
Incorrect loss	–25	+5
Incorrect loss	–25	–5

The feedback stimulus remained on the screen for 2 s, after which the empty rectangles were presented again for a variable interval of 4.7 to 6.2 s.

The task was organised as 27 blocks of 8 trials each. After each block, feedback on the total amount of points received in that particular block, the maximum number of points obtainable in the block, and the total score were presented on the screen. If a block resulted in a net loss, this amount was not subtracted from the total score.

Within each block, the sequence of correct and incorrect choices followed a pattern that the subjects could learn in order to maximise their points total. This sequence was 5, 25, 5, 5, 25, 5, 25, 25 and repeated itself in every block of the experiment. Choosing according to this sequence led to 100% correct responses. However, making 100% correct responses did not mean that no more losses occurred. Although learning reduced the occurrence of losses, losses were unavoidable. Nevertheless, learning increased the predictability of the upcoming outcomes.

The subjects were instructed that their task was to accumulate the maximal number of points and that the sequence of correct responses would follow a certain repeating pattern. They were further told that by learning and remembering this pattern they would be able to make correct responses only, and that they would maximise their total score by learning the pattern as early as possible. Completing the task took about 45 min.

4.3. Electrophysiological recording

EEG was recorded from 61 silver/silver chloride electrodes, all referenced to a sterno-vertebral site, using an elastic cap with equidistant montage (M10, EasyCap, Herrsching, Germany). Horizontal and vertical eye movements were registered by two electrodes placed at the outer canthi of both eyes and two electrodes above and below the right eye. At each recording site, the skin was slightly scratched with a sterile needle to minimise skin potential artefacts. The electrodes were filled with degassed electrode gel (Electro-Gel, ElectroCap International Inc., Eaton/OH, USA). The impedances of all electrodes were below <3 k Ω .

Signals were amplified using a DC-amplifier with high baseline stability and an input impedance of 100 G Ω (Ing. Kurt Zickler GmbH, Pfaffstätten, Austria). The data were recorded at a sampling rate of 3 kHz and downsampled to 250 Hz for digital storage.

4.4. Data processing and analysis

4.4.1. Behavioural data

For each subject, the percentage of correct responses per block was calculated and fitted with a simplified version of the generalised logistic curve (Richards' curve; Richards, 1958), $f(x) = A_0 + \frac{A_1}{1 + \exp(A_2 - x)}$, where $f(x)$ is the percentage of correct answers in block x , the constant A_0 determines the lower asymptote, $A_0 + A_1$ determines the upper asymptote, and A_2 determines the block number about which the learning curve is centred. The initial estimates were $A_0 = 50$, $A_2 = 3$ and $A_1 = 50$; that is, assuming that 50% of answers would be correct at the beginning of the experiment (by chance), that subjects would learn the sequence close to the 3rd block and that their score in the final blocks would rise (by 50%) to 100%.

Since it turned out that not all subjects were able to learn the task, they were categorised as high learners or low learners. High learners ($N = 39$) were defined according to the following two criteria: (1) a learning curve reaching a level of at least 80% correct responses, and (2) a minimum of 4 consecutive blocks with 100% correct responses. Low learners ($N = 23$) were defined as subjects with a learning curve reaching less than 80% correct responses or less, which automatically implied that they had completed less than 4 consecutive blocks with 100% correct responses.

To determine the effects of individual learning in the course of the experiment, the data were split into two halves which consisted of the first 108 and the last 108 trials of the experiment, respectively. In the following, these halves are termed “early” and “late” phase. Both the behavioural performance and the ERP data were then compared for these two phases.

To verify the classification of subjects to the groups of high and low learners, 2 two-tailed Mann–Whitney tests were performed on the percentage of correct responses. High learners were compared to low learners separately for each phase of the experiment. Additionally, the early and late phases were compared to each other separately for high and low learners by means of two Wilcoxon signed ranks tests. For these comparisons, a Bonferroni-corrected p -value of <0.01 was assumed.

As a further performance measure, response latency was calculated from stimulus onset to button press. Response latency was then submitted to a $2 \times 2 \times 2$ repeated-measures ANOVA with the within-subjects factors *phase* (early, late) and *accuracy* (correct response, wrong response) and the between-subject factor *learngroup* (high learner, low learner).

4.4.2. EEG data

Eye movement artefacts were eliminated using a linear regression approach with channel-specific correction coefficients (Vitouch et al., 1997). Blink artefacts were subtracted from the EEG with a template matching approach (Lamm et al., 2005). All trials were also visually inspected. Trials with

remaining eye or other artefacts were excluded from further analysis. Subsequently, the EEG was filtered with a low-frequency half-amplitude cutoff at 30 Hz (6dB/octave slope) for calculating mean amplitudes and generating graphs, and at 16 Hz (6dB/octave slope) for peak-picking.

Feedback-locked epochs were averaged for gain and loss trials in each phase of the experiment and separately for each subject. A baseline of 100 ms before onset of the feedback stimulus was subtracted. The FRN had a typical distribution with a maximum around 250 ms and was most pronounced for midline central scalp areas. It was quantified in the averaged ERP of each subject as the base-to-peak-to-peak voltage difference between the most negative peak and the average of the immediately preceding and following positive peaks (according to Yeung and Sanfey, 2004) at electrode Fz, all of which had to occur in the interval of 100–600 ms after feedback onset. Fz was chosen because the FRN was found to be most prominent at this recording site. For conditions with an absent FRN, a mean FRN amplitude of 0 (difference of 0 between positive and negative peaks) was employed.

The peak amplitude of the P3 was determined as the base-to-peak amplitude in the interval of 200–600 ms after feedback onset at electrode Pz. To analyse the late positivity, a slow potential change with no distinct peak, mean ERP amplitudes at the three midline electrodes Fz, Cz and Pz were extracted in the interval of 450 to 950 ms following feedback onset. This interval and the respective electrodes were chosen based on visual assessment of the grand means and on existing ERP studies (e.g., Azizian and Polich, 2007; Curran and Friedman, 2004; Cuthbert et al., 2000).

The amplitudes of the FRN and P3 were submitted to separate repeated-measures ANOVA with the two within-subjects factors *phase* (levels: early, late) and *outcome* (levels: gain, loss), and the between-subject factor *learngroup* (levels: high learner, low learner).

The amplitudes of the late positivity were submitted to a repeated-measures ANOVA with *electrode* (levels: Fz, Cz, Pz), *outcome* (levels: gain, loss), and *phase* (levels: early, late) as within-subject factors, and *learngroup* (levels: high learner, low learner) as between-subjects factor.

For all ANOVAs, the degrees of freedom were Greenhouse–Geisser-corrected when appropriate. Interaction effects were analysed with post-hoc Scheffé tests. Only post-hoc differences for comparisons of interest are reported, for example, ERP amplitudes for gains in the early versus the late phase (not for any other differences such as between gains in the early phase and losses in the late phase). A significance level of $p < 0.05$ was assumed.

4.4.3. Relationship between the percentage of correct answers and event-related potential changes

To further investigate the relationship between FRN, P3, late positivity and behaviour, a stepwise linear regression analysis was performed. Following Krigolson et al. (2009), the changes in amplitude (ERP component amplitude in the late phase minus ERP component amplitude in the early phase) were calculated for the P3, the FRN, and the mean late positivity amplitudes at each electrode Fz, Cz and Pz. These changes were entered as predictors into a regression analysis where the percentage of correct responses, following its arc sine

square root transformation, was the criterion. Regression diagnostics did not show evidence for multicollinearity among the predictors (all tolerances > 0.4).

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