Learning Context Modulates the Processing of Expectancy Violations

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Abstract

The detection of unexpected or unfavorable events is crucial for successful behavioral adaptation. There is a family of ERP components, the so-called error negativities, that has been associated with these detection processes. In the current study, we explored the functional characteristics of one of these components, the N2b which reflects the detection of unexpected events in a stream of stimuli in our environment, in more detail. In a sequence learning task, we found that the same type of deviant event elicited an N2b only when it conveyed information about the to-be-learned sequence, but not when it was rendered learning-irrelevant by means of task instruction. This supports the view that deviant events generate an error negativity in a similar way as committed errors and negative feedback. It also demonstrates that error monitoring processes are very flexible and can be tailored to the specific demands of the task at hand, i.e., expectancy violations only activate the error system when the detected mismatch is classified as relevant for the specific goals in the current learning context. Additionally, a P3 to all deviant types was found reflecting a higher-order form of performance monitoring associated with evaluation of task-relevant events and updating of working memory contents.

Keywords: sequence learning, performance monitoring, expectancy violation, event-related potentials, context dependency

1. Introduction

To flexibly adapt our behavior to changing environmental demands and to acquire new behavior, we constantly have to evaluate our performance in the light of its potential consequences. For this purpose it is important that unexpected or unfavorable events can be detected. This has been demonstrated in numerous studies and several ERP components have been associated with the detection of unexpected events like perceived and committed errors or surprising feedback (for a review, see Gehring, Liu, Orr, & Carp, 2012). These components share functional characteristics, rely on very similar neural mechanisms (cf. Folstein & Van Petten, 2008), and play an important role when the consequences of actions are processed.

In their reinforcement learning (RL) model, Holroyd and Coles (2002) suggested that if an event is worse than expected, e.g., an error is detected, the result is a dopaminergic reinforcement learning signal which can be measured in the event-related potential (ERP) in the form of an ERN (error-related negativity; Gehring, Goss, Coles, Meyer & Donchin., 1993;) or Ne (error negativity; Falkenstein, Hohnsbein, Hormann & Blanke, 1990; Falkenstein, Hohnsbein & Hormann, 1995; Gehring et al., 2012). This component can be observed over fronto-central brain regions at the time the error is made. Importantly, similar components cannot only be elicited by erroneous responses but also by stimuli signaling events that are worse than expected, e.g., by error observation (the oERN; De Bruijn & von Rhein, 2012; Bates, Patel, & Liddle, 2005; van Schie, Mars, Coles, & Bekkering, 2004), and by negative or unexpected feedback (the feedback-related negativity (FRN); e.g., Ferdinand, Mecklinger, Kray & Gehring, 2012; Gehring & Willoughby, 2002; Holroyd & Coles, 2002; Miltner, Braun & Coles, 1997; Oliveira, McDonald & Goodman, 2007).

Only recently, the N2b[1] elicited by the detection of an unexpected event, has been argued to signal that our expectations might need revision (Ferdinand, Mecklinger & Kray, 2008). In this latter ERP study, we investigated the build-up of expectancies and the detection of expectancy violations using a sequence learning paradigm and inserting deviant stimuli into an otherwise repeating sequence (Ferdinand et al., 2008). Interestingly, we observed an N2b to these deviant stimuli that developed with increasing sequence knowledge and that showed striking similarities to the learning-related changes in the response-locked ERN previously demonstrated by Holroyd & Coles (2002). We concluded that during learning deviant events acquire the status of an unexpected event, i.e., a perceived error (as opposed to a committed error), and can serve as a reinforcement learning signal. While performing the sequence learning task expectancies about upcoming events are generated, compared to the actual event, and evaluated on whether they deviate from the expectancies. The accuracy of this process improves with learning and this improvement is reflected in a gradual increase in N2b amplitude as a function of learning. Several other studies also reported enhanced N2b for stimuli that contradict participants' expectancies in learning situations. For instance, employing an incidental sequence learning task Eimer and colleagues (1996) found an N2b to stimuli that violated a learned spatial sequence (Eimer, Goschke, Schlaghecken & Stürmer, 1996; for similar results, see also Kopp & Wolff, 2000; Rüsseler, Hennighausen, Münte & Rösler, 2003; Verleger et al., 2015). Although not explicitly explored in these studies it is entirely conceivable that the N2b and the ERN reflect activity of a common neural generator (the ACC) initiated by input signaling that an event violates the participant's expectancy. Additionally, source-localization studies which show that the neural generators of the two components lie very close together in the medial frontal cortex, are consistent with a common neural source in the ACC (Holroyd, 2004; Nieuwenhuis, Yeung, van den Wildenberg & Ridderinkhof, 2003; see also Folstein & Van Petten, 2008).

The most important commonality between these components regards the fact that they all are conceptualized to index that an event differs from expectation. What remains an open question, however, is what actually defines the dimension on which events are evaluated deviating from expectancies. Previous research on the FRN indicated that this evaluation can depend on the alternative outcomes (e.g., Goyer, Woldorff, & Huettel, 2008; Holroyd, Larsen & Cohen, 2004; Nieuwenhuis, Yeung, Holroyd, Schurger & Cohen, 2004). For example, in a recent study it has been reported that feedback indicating that participants received no reward generated a FRN when the alternative outcomes were rewards. However, the same non rewarding feedback did not generate a FRN when the alternative outcomes were monetary losses (Holroyd et al., 2004). Similarly, using a gambling task it was shown that the FRN was larger if the outcome of the chosen gamble was worse than the simultaneously presented outcome of the unchosen gamble (Goyer, et al., 2008). Hence, one could infer that the event characteristics needed to elicit an FRN are context-dependent, i.e., in the above study the alternative feedback defines what is “better” and what is “worse” than expected. Crucially, Nieuwenhuis and colleagues (2004) demonstrated that this context-dependency is subject to an attentional bias. They conducted a gambling task in which participants had to choose one of two values (5 or 25). Feedback was given by adding a “–“ or “+” sign to indicate whether the chosen value indicated a loss or a gain, so the feedback stimulus conveyed two types of information: 1) absolute valence information, i.e., whether the money was lost or won, and 2) relative valence information, i.e., whether the chosen gamble led to the better or worse outcome (5 cents lost is better than 25 cents lost). By using these compound stimuli, it was found that the FRN can be elicited likewise by absolute (gain or loss) or relative (better or worse than expected) information, depending on which aspect was emphasized by the instruction, respectively.

These studies demonstrate that the task context can influence which events are assessed as expectancy violations and that this is reflected in the size of the FRN amplitude. However, they do not clarify whether all aspects of an event (e.g., absolute AND relative information in the study by Nieuwenhuis et al., 2004) are evaluated at the same time. Equally likely, this evaluation process may be flexible enough to differentially weigh several aspects of the same stimulus when the context of the evaluation changes. For instance, imagine a worker in a factory processing prawns. On one day, he works in the incoming inspection where he has to sort the prawns according to whether they should be further processed or whether they are spoiled and should be discarded (i.e., sorting according to smell or color). This same worker might be deployed to the final quality check on another day, where he has to assess whether the prawns are of sufficiently high quality to serve as gourmet food (i.e., sorting according to size). This means that he has to adapt his evaluation process to the current situation and the different properties of prawns should lead to an error signal depending on his function. This view assumes more economic evaluation processes in which only those aspects of an event are taken into account that are relevant in a specific learning situation. This differential importance of various features of one and the same stimulus to serve as a reinforcement learning signal depending on their behavioral relevance has not received much attention in the literature so far. Thus, the goal of the present study was to examine what determines the evaluation dimension on which actual events can deviate from expected ones. More specifically, we investigated what characteristics an expectancy violation must possess to elicit an N2b and whether all aspects of a stimulus or only those that are relevant in the current context are taken into account when evaluating an event as an expectancy violation.

For this purpose, we conducted two sequence learning experiments and manipulated the task context via different learning instructions. In both experiments, the participants‘ task was to respond as fast and accurately as possible to visually presented stimuli. They were also instructed that figuring out the repeating sequence would help them to speed up response times and improve their accuracy. Unpredictable deviant stimuli were inserted in the to-be-learned sequence. Since these deviants were compound stimuli including two stimulus dimensions (stimulus identity and visual form), they could violate participants’ expectancies on different levels: They could either disrupt the sequence structure or violate the perceptual characteristics of the sequence while leaving the sequence structure intact. This is an important distinction because only a disruption of the sequence structure conveys information which is relevant for the acquisition of sequence knowledge and thus future response behavior because expectancies about the stimulus order are violated. Conversely, a change in the perceptual characteristics also constitutes a deviant event but does not allow inferring any information relevant for sequence learning. Our hypothesis was that the task context (i.e., the instruction that stimuli should be treated according to their identity irrespective of their visual form) determines the evaluation dimension and by this defines the expectancy violation. Consequently, only those violations that disrupt the sequence structure and by this convey learning relevant information should elicit an N2b. They generate a mismatch on the evaluation dimension and activate the error system which can then generate a reinforcement learning signal to adjust behavior accordingly (Experiment 1). Second, we expected that changing the learning context via the task instruction in Experiment 2 (by telling participants that stimuli deviating in their visual form are irrelevant for learning because they do not belong to the to-be-learned sequence) would also change the evaluation dimension and thus which types of deviants are classified as an expectancy violation although the to-be-learned sequence and the deviant stimuli themselves were not altered. In addition to clarifying which aspects of an event can generate expectancy violations for the monitoring system and how flexible this evaluation process is, this would also further substantiate the view that perceived errors, as reflected in the N2b, contribute to learning by generating an expectancy violation as described in RL models (e.g., Alexander & Brown, 2011; Holroyd & Coles, 2002; Sutton & Barto, 1998).

In addition, we also expected to obtain a P3 to deviant events (cf. Ferdinand et al., 2008). In contrast to the N2b which is related to the fast detection of learning-related prediction errors, the P3 reflects later and higher order evaluation and monitoring processes, like the updating of working memory representations after unexpected events (e.g., Donchin & Coles, 1988; Johnson, 1986; Polich, 2004, 2007), in this study the memory representation of the regular sequence. Since all types of deviants are unexpected and surprising events, they all should elicit a P3 irrespective of how much they can potentially contribute to sequence learning.

2. Results

2.1 Experiment 1

As explained above, our hypothesis was that only those deviants that violate the structure of the repeating sequence (structural deviants) elicit an N2b because they present expectancy violations that are relevant to sequence learning, In contrast, all deviant events irrespective of their learning relevance should elicit a P3.

2.1.1 Behavioral Data

Figure 1a shows reaction times to correct answers for regular stimuli (from regular sequences only) and deviant stimuli. Since reaction times to conceptual deviants cannot directly be compared to those of the other stimulus types because for these stimuli participants had to press a new response button requiring a less frequent motor response, they were excluded from this analysis and an ANOVA with factors Structural Violation (no: regular stimuli, perceptual deviants, yes: structural deviants, perceptual/ structural deviants) and Perceptual Violation (no: regular stimuli, structural deviants, yes: perceptual deviants, perceptual/ structural deviants) was conducted (see Table 1). It was found that stimuli containing a structural violation resulted in longer reaction times than stimuli without a structural violation (Structural Violation: $F(1,15)=110.40$, $p<.01$). Because the occurrence of a structural violation can never be predicted, this effect reflects learning of the regular sequence. Additionally, stimuli containing a perceptual violation (lower case letters) resulted in longer reaction times than stimuli without a perceptual violation (Perceptual Violation: $F(1,15)=11.61$, $p<.01$). No interaction between the two factors was found ($p=.68$) suggesting independence of learning-relevant (structural) and learning-irrelevant (perceptual) violations.

The same ANOVA was conducted for error rates (Figure 1b). It revealed that stimuli containing a structural violation resulted in higher error rates than stimuli without a structural violation (Structural Violation: $F(1,15)=132.68$, $p<.01$), reflecting learning of the regular sequence. No other effects reached significance (all p-values >.45).

2.1.2 ERP Data

Our hypothesis was that the N2b is present for structural and perceptual/ structural deviants and absent to perceptual and conceptual deviants. To test this, the N2b was first measured as the difference in mean voltage between regular stimuli (mean trial number: 1140.75) and deviant stimuli separately for each deviant type (mean trial numbers: 35, 29.5, 32, 29.56)[2]. As apparent from Figure 2, the N2b was preceded by a P2 component for those deviant types that differ visually from regular stimuli (letters in small print and new letters). This was confirmed by an analysis of the P2 effects (see Supplement). To diminish the effects of component overlap, we additionally conducted a peak-to-peak analysis of the N2b only for those conditions in which a P2 was found. In contrast to the N2b, the P3b seems to be present for all types of deviants regardless of whether they are relevant for learning or not, as was expected. In the following, ERP analyses are reported in the order implied by the above considerations.

N2b

As stated above, the N2b was first analyzed by pairwise comparisons of regular stimuli and the respective type of deviant using two-way ANOVAs with factors Stimulus Type (regular/ deviant) and Electrode (FCz, Cz, CPz, Pz) in the time window from 240 to 340 ms. The ANOVA revealed that the mean amplitude for structural deviants was more negative than that for regulars (Stimulus Type: $F(1,15)=10.89$, $p<.01$). For perceptual/ structural deviants, there was a tendency for an interaction between Stimulus Type and Electrode ($F(3,45)=3.82$, $p=.06$, $\varepsilon=.40$), reflecting the fact that the mean amplitude for regular stimuli was more positive the more posterior the electrode ($F(3,45)=17.94$, $p<.01$, $\varepsilon=.40$). For perceptual deviants, again an interaction between Stimulus Type and Electrode ($F(3,45)=7.35$, $p=.01$, $\varepsilon=.41$) was found which also reflects changes in mean amplitude for regular stimuli only. Finally, for conceptual deviants, an interaction between Stimulus Type and Electrode ($F(3,45)=27.04$, $p<.01$, $\varepsilon=.38$) was obtained. This interaction was due to mean amplitudes being more positive for conceptual deviants than for regular stimuli at FCz ($F(1,15)=7.60$, $p=.01$), but more negative at Pz ($F(1,15)=5.08$, $p=.04$), in addition to the changes in regular stimuli reported above.

To summarize, the N2b was found for structural deviants and not found for perceptual and conceptual deviants, as was expected. However, in contrast to our hypotheses, the N2b could not be reliably detected for perceptual/ structural deviants when measured by mean amplitudes.

N2b Peak-to-Peak Analysis

An additional peak-to-peak analysis of the N2b was conducted for all conditions in which a P2 was found. This analysis was conducted at electrode FCz where N2b was maximal and P2 amplitude did not differ between the conditions (see Supplement). Planned comparisons confirmed our hypothesis that the N2b was larger for perceptual/ structural deviants than for perceptual and conceptual deviants ($F(1,15)=5.55$, $p=.03$; see Figure 5), while it did not differ for perceptual and conceptual deviants ($p=.29$). By this, the additional peak-to-peak analysis supports the assumption that an N2b is also present after perceptual/ structural deviants when confounding effects of the preceding P2 are controlled for.

P3

In order to estimate whether a P3 was elicited by deviant stimuli in each violation condition, ERPs in the time window from 440 to 540 ms were analyzed by pairwise comparisons of regular stimuli and the respective type of deviant in two-way ANOVAs with factors Stimulus Type (regular/ deviant) and Electrode (FCz, Cz, CPz, Pz). These analyses showed that the P3 was present for all types of deviants (structural deviants: $F(1,15)=9.85$, $p<.01$, perceptual/ structural deviants: $F(1,15)=49.65$, $p<.01$, perceptual deviants: $F(1,15)=52.92$, $p<.01$, conceptual deviants: $F(1,15)=74.52$, $p<.01$). A subsequent ANOVA with factors Deviant Type (structural, perceptual/ structural, perceptual, and conceptual deviants) and Electrode (FCz, Cz, CPz, Pz) in the P3 time window yielded a main effect for Deviant Type ($F(3,45)=33.61$, $p<.01$, $\varepsilon=.67$) and an interaction between Deviant Type and Electrode ($F(9,135)=5.05$, $p<.01$, $\varepsilon=.27$). Pairwise comparisons revealed that the main effect was due to the P3 amplitude being more positive for conceptual deviants than for perceptual deviants ($F(1,15)=20.90$, $p<.01$), did not differ between perceptual deviants and perceptual/ structural deviants (*p*=.33), and was more positive for perceptual/ structural deviants than for structural deviants ($F(1,15)=22.75$, $p<.01$).

2.2 Summary Experiment 1

This experiment aimed at investigating which characteristics an event must possess to generate an expectancy violation and to activate the error monitoring system. In line with our hypothesis that the learning context defines this dimension on which deviant events are evaluated the behavioral results of Experiment 1 demonstrated that all deviants that violate the structure of the to-be-learned sequence (structural and perceptual/ structural deviants) produced longer reaction times and larger error rates than stimuli without structural violation (i.e., regular stimuli and perceptual deviants). This effect reflects learning of the regular sequence because the only difference between the two stimulus categories is that stimuli without a structural violation can be learned and their occurrence predicted (they are part of the regular sequence), while those with a structural violation cannot be predicted. Independent of this sequence learning effect, an effect of perceptual violation was found which was reflected in slower reaction times to lower case letters (i.e., perceptual and perceptual/ structural deviants).

These findings were confirmed by the ERP analyses indicating that the N2b was elicited in response to structural deviants only. This finding is consistent with the view that structural deviants acquired the status of perceived negative prediction errors during the course of learning and were evaluated as deviating from expectancy by the monitoring system. No N2b was found for perceptual and conceptual deviants. For perceptual deviants, this is in agreement with our hypotheses because they do not violate the structure of the regular sequence (in terms of stimulus meaning and motor response). For conceptual deviants, which strictly speaking do violate the sequence in terms of stimulus meaning and motor response, this is also in accord with our hypothesis because they are classified as not relevant for sequence learning and therefore these violations are not processed by the error monitoring system to the same extend as learning-relevant structural violations. For conceptual deviants, mean amplitudes in the N2b time window were even more positive than those for regulars - probably due to the large and early onset of the P3 to these events. An N2b was also presumed to occur for perceptual/ structural deviants because they, like the purely structural deviants, should violate participants' expectancies after sequence learning had taken place. This unexpected finding could, however, be reconciled taking the temporally overlapping P2 component into account. According to Luck and Hillyard (1994), who found a P2 to pop-out stimuli in a visual search task, the P2 reflects visual feature detection (see also Liu, Perfetti & Hart, 2001). Consistent with this view, we found a P2 for all those deviants that differed perceptually from regular events, i.e., perceptual, perceptual-structural, and conceptual deviants but not for purely structural deviants. When the effects of the preceding P2 were controlled for by means of a peak-to-peak analysis, we indeed found the predicted result that the N2b was larger for perceptual/ structural deviants than for purely perceptual and conceptual deviants. Taken together, the above findings speak in favor of the hypothesis that only deviants that are relevant in the current learning context elicit an N2b by being evaluated as events that deviate from expectancy, while other deviants that also are unexpected and task-relevant (they require a specific response) but are not relevant for learning the sequence do not represent an expectancy violation and thus do not activate the error monitoring system.

In a later time window, a P3 was found for all four deviant types. It was larger for conceptual deviants than for perceptual and perceptual/ structural deviants, and smallest for structural deviants. These amplitude differences probably arise due to a combination of the deviants being unexpected events in the context of the regular sequence and to differences in their probability of occurrence (cf. Johnson, 1986). The inverse relation between P3 amplitude and subjective stimulus probability is well-established: the lower the probability of a stimulus to occur, the larger P3 amplitude (e.g., Donchin & Coles, 1988). Moreover, Mecklinger and Ullsperger (1993) showed that when stimuli can be easily assigned to categories, the P3 amplitude is not related to the probability of the individual stimuli but to the probability of the response-defined task categories. In the current experiment, it is conceivable that perceptual/ structural and perceptual deviants were grouped together into the subjective category of “lower case letters”, while conceptual deviants were classified “new letters”. Since “new letters” occur half as often as “lower case letters” they elicit the largest P3. In contrast, structural deviants obtain their deviant character only after the regular sequence has been learned and therefore are not as salient a category. Consequently, they elicit the smallest P3.

2.3 Experiment 2

The data from the first experiment indicate that the learning situation constitutes the dimension on which events are predicted and evaluated as deviating from expectancy and thus defines the event characteristics that generate an N2b. From this it follows that changing the learning situation, e.g., by instructing participants what deviant events are relevant for sequence learning, should be mirrored in an altered sensitivity of the error system to the same events. To test this assumption more directly in the second experiment, we changed the learning relevance of the four sequence violations by using an instruction that, in contrast to the first experiment, encouraged participants to additionally focus on perceptual features of the deviants to determine whether or not a deviant is relevant for learning. We achieved this by briefing the participants that lower case letters in general do not belong to the to-be-learned sequential pattern and now required a response with a different response button. By this different task instruction, perceptual/ structural deviants should alter their status from “relevant for sequence learning” in Experiment 1 to “irrelevant for sequence learning” in Experiment 2 and thus not activate the monitoring system any more, while purely structural deviants and perceptual deviants will retain their status (i.e., structural deviants should still activate the monitoring system because they constitute learning-relevant expectancy violations and perceptual deviants should still not activate the error monitoring system because they do not represent a learning-relevant expectancy violation). Importantly, all deviants in principle still possess the same informational value concerning sequence learning as in Experiment 1 (although perceptual/structural deviants are now instructed as not being learning-relevant anymore, they still violate the regular sequence). Accordingly, our hypothesis was that the change in instructions would override the stimulus characteristics and render perceptual/ structural deviants irrelevant for learning. Therefore, we would obtain an N2b for purely structural deviants only.

2.3.1 Behavioral Data

Figure 3a shows reaction times to correct answers for regular stimuli (from regular sequences only) and deviant stimuli in Experiment 2. To keep the analysis comparable to that of Experiment 1, we decided to not exclude structural and structural/perceptual deviants from the analysis and to exclude conceptual deviants, although all three deviant types require the execution of a less practiced motor response which probably influences the behavioral data. An ANOVA on reaction times with factors Structural Violation (no: regular stimuli, perceptual deviants, yes: structural deviants, perceptual/ structural deviants) and Perceptual Violation (no: regular stimuli, structural deviants, yes: perceptual deviants, perceptual/ structural deviants) revealed a main effect for Structural Violation ($F(1,15)=63.64$, $p<.01$), a main effect for Perceptual Violation ($F(1,15)=262.64$, $p<.01$), and an interaction between the two factors ($F(1,15)=69.56$, $p<.01$). This result reflects the fact that there were simple main effects of Perceptual Violation for stimuli with and without structural violation (perceptual deviants resulted in longer reaction times than regulars: $F(1,15)=289.45$, $p<.01$; perceptual/ structural deviants resulted in longer reaction times than structural deviants: $F(1,15)=49.02$, $p<.01$), while a simple main effect for Structural Violation was significant only for stimuli without perceptual violation (structural deviants resulted in longer reaction times than regulars: $F(1,15)=79.44$, $p<.01$; perceptual/ structural deviants and perceptual deviants did not differ: $p>.17$). As in Experiment 1, the difference between structural deviants and regulars can be taken to reflect sequence learning, whereas the increase in reaction times to perceptual deviants as compared to Experiment 1 might either be due to the different role of lower case letters in the second experiment or due to the separate and less frequent response button press.

The same ANOVA was conducted for error rates (Figure 3b) and showed the same pattern of results. There were main effects for Structural Violation ($F(1,15)=67.84$, $p<.01$), a main effect for Perceptual Violation ($F(1,15)=81.78$, $p<.01$), and an interaction between the two factors ($F(1,15)=102.81$, $p<.01$). The interaction was due to simple main effects of Perceptual Violation for stimuli with and without structural violation (perceptual deviants resulted in larger error rates than regulars: $F(1,15)=121.19$, $p<.01$; perceptual/ structural deviants resulted in larger error rates than structural deviants: $F(1,15)=5.23$, $p<.05$), while a simple main effect for Structural Violation was significant only for stimuli without perceptual violation (structural deviants resulted in larger error rates than regulars: $F(1,15)=111.75$, $p<.01$; perceptual/ structural deviants and perceptual deviants did not differ: $p>.14$).

2.3.2 ERP Data

Figure 4 shows the ERPs for Experiment 2. As in Experiment 1, to test the presence of the N2b in each of the violation conditions, it was first measured as the difference in mean voltage between regular stimuli (mean trial number: 1169.81) and deviant stimuli separately for each deviant type (mean trial numbers: 35.94, 32.25, 32.44, 32.38)[2]. Also analogous to Experiment 1, to ensure that these mean amplitude measures were not contaminated by component overlap with the preceding P2, we next analyzed the P2 (see Supplement) and thereafter conducted a peak-to-peak analysis of the N2b for all conditions in which a P2 of the same size was present. Again, the P3b seems to be present for all types of deviants regardless of whether they are relevant to learning or not. In the following, ERP analyses are reported in the order implied by the above considerations.

N2b

Consistent with Experiment 1, the N2b mean amplitude measures were analyzed by pairwise comparisons of regular stimuli and the respective type of deviant using two-way

ANOVAs with factors Stimulus Type (regular/ deviant) and Electrode (FCz, Cz, CPz, Pz) in the time window from 240 to 340 ms. For structural deviants, the ANOVA revealed that the mean amplitude for structural deviants was more negative than that for regulars (Stimulus Type: $F(1,15)=4.96$, $p=.04$). For perceptual/ structural deviants, no main effect or interaction containing Stimulus Type was significant (all $p>.16$). The mean amplitude of perceptual deviants was more positive than that of regulars (Stimulus Type: $F(1,15)=6.51$, $p=.02$). And for conceptual deviants, an interaction between Stimulus Type and Electrode ($F(3,45)=9.12$, $p<.01$, $\varepsilon=.48$) was obtained that was due to mean amplitudes being more positive for conceptual deviants than for regular stimuli at FCz ($F(1,15)=6.46$, $p=.02$). To summarize, the N2b was found for structural deviants but not found for perceptual/ structural, perceptual, and conceptual deviants, as was expected. Moreover, perceptual deviants and conceptual deviants at FCz were more positive than regular stimuli, probably due to component overlap with the preceding P2 for visually deviating letters in small print. The analysis of the P2 (see Supplement) confirmed that it is present at FCz for all types of deviants except for the purely structural deviants and that it does not differ in size between the different types of deviants. For this reason, in a next step the N2b was measured peak-to-peak in all conditions including a P2.

N2b Peak-to-Peak Analysis

As in Experiment 1, an additional peak-to-peak analysis of the N2b was conducted for all conditions in which a P2 of comparable amplitude was found at FCz. The same a priori comparisons as in Experiment 1 revealed that in Experiment 2 the N2b did not differ any more between perceptual/ structural deviants and the mean of perceptual and conceptual deviants, nor for perceptual and conceptual deviants (all *p-values* $>.14$; see Figure 5).

N2b Comparison between Experiment 1 and Experiment 2

To compare the N2b across the two experiments, a Monte Carlo simulation based on 10000 samples was conducted using the standard criteria as implemented in SPSS 17. This nonparametric test was chosen because it provides an accurate estimate of the sample distribution as the low subject number in the present between participants design as the prerequisites for an analysis of variance were violated. The peak-to-peak N2b of perceptual/ structural and purely perceptual deviants were chosen for this comparison for two reasons. First, perceptual/ structural and purely perceptual deviants are perceptually equal und thus both generated a P2 of the same size. Second, the status of perceptual/ structural deviants changes from “relevant for sequence learning” in Experiment 1 to “irrelevant for sequence learning” in Experiment 2, while the status of purely perceptual deviants does not. To capture this main manipulation, the difference between these two conditions was calculated separately for each participant and each experiment and subjected to the simulation. This analysis revealed that, the mean difference of Experiment 1 (2.01 µV) and of Experiment 2 (1.07 µV) do not belong to the same distribution ($p=.04$, one-tailed). This means that there is a difference in the peak-to-peak N2b between perceptual/ structural and perceptual deviants in Experiment 1 but not in Experiment 2.

P3

As in Experiment 1, the presence of the P3 was analyzed by pairwise comparisons of regular stimuli and the respective type of deviant in two-way ANOVAs with factors Stimulus Type (regular/ deviant) and Electrode (FCz, Cz, CPz, Pz) in the time window from 440 to 540 ms. These analyses showed that the P3 was present for all types of deviants (structural deviants: $F(1,15)=22.98$, $p<.01$, perceptual/ structural deviants: $F(1,15)=90.55$, $p<.01$, perceptual deviants: $F(1,15)=90.30$, $p<.01$, conceptual deviants: $F(1,15)=93.77$, $p<.01$). The subsequent ANOVA with factors Deviant Type (structural, perceptual/ structural, perceptual, and conceptual deviants) and Electrode (FCz, Cz, CPz, Pz) revealed a main effect for Deviant Type ($F(3,45)=61.63$, $p<.01$, $\varepsilon=.70$) and Electrode ($F(3,45)=6.49$, $p=.01$, $\varepsilon=.46$), and an interaction between Deviant Type and Electrode ($F(9,135)=11.27$, $p<.01$, $\varepsilon=.42$). Pairwise comparisons showed that the main effect of Deviant Type was due to a smaller P3 amplitude for structural than for perceptual/ structural deviants ($F(1,15)=89.25$, $p<.01$), while amplitude did not differ between perceptual/ structural and perceptual deviants and between perceptual and conceptual deviants (both $p>.55$).

2.3.3 Summary Experiment 2

In the second Experiment, we wanted to further corroborate the results from Experiment 1, suggesting that the learning situation defines which events are perceived as expectancy violations and elicit an N2b. By using the same stimulus material but altering solely the instruction from Experiment 1 to Experiment 2, we aimed at changing the learning context and with it the status of perceptual/ structural deviants from "relevant for sequence learning" in Experiment 1 to "irrelevant for sequence learning" in Experiment 2. A successful change of learning context was thought to be indexed by a selective attenuation of the N2b to perceptual/ structural deviants as compared to purely structural deviants.

The behavioral data demonstrated that sequence learning had taken place. There were shorter reaction times and fewer errors to regular stimuli than to structural deviants. Additionally, reaction times and error rates increased for structural/ perceptual deviants and did not differ from those to perceptual ones. A possible explanation for this is that responses to structural/ perceptual deviants (as for perceptual and conceptual deviants) were assigned to a different response button than in Experiment 1 and a less frequent response had to be carried out for them. Another possible explanation could be that due to the instruction, lower case letters had a different status in the second experiment.

Most importantly, ERP analyses revealed that an N2b was present after structural deviants, but not after perceptual/ structural, perceptual, and conceptual deviants. To take into account the interfering influence of component overlap, in addition to mean amplitude analyses, the N2b was quantified in a peak-to-peak measure. This peak-to-peak analysis yielded no difference in N2b between perceptual/ structural, perceptual, and conceptual violation conditions. Importantly, the comparison across experiments confirmed that the N2b difference between perceptual/ structural and perceptual violations was larger in Experiment 1 than in Experiment 2. This is in line with the assumption that only violations carrying relevant information in the context of the current learning situation achieve the status of a perceived error and elicit an N2b.

In addition to the N2b, a P3 was found for all four types of deviants confirming the results of Experiment 1. It was of equal size for perceptual/ structural, perceptual, and conceptual deviants, and smaller for structural deviants. As in Experiment 1, this pattern of P3 size is most likely due to the subjective probabilities of the four deviant types (cf. Mecklinger & Ullsperger, 1993). Perceptual/ structural, perceptual, as well as conceptual deviants can be assigned to the same response button and to the same unexpected and rare event of "lower case letters". Again, structural deviants comprise their own and less salient category of rare events and, by this elicit the smallest P3.

3. Discussion

3.1 Error Monitoring

In both experiments we found an N2b to deviant events that violated participants' expectancies concerning the stimulus order. These findings are in line with several other studies reporting enhanced negative ERP components at about 200 ms for stimuli that contradict participants' expectancies in learning situations (Eimer et al., 1996; Ferdinand et al., 2008; Kopp & Wolff, 2000; Rüsseler et al., 2003). Thus, they further corroborate the view that the ERN and the N2b reflect common processing mechanisms related to the detection of unexpected learning-relevant events.

Moreover, the findings from both experiments extend the considerations on error monitoring and the N2b in an important way. They show that it is the learning situation that defines the dimension on which deviant events are evaluated. Under otherwise identical testing conditions only expectancy violations that are relevant in the current learning context (in the present experiments the context of explicitly learning a regular sequence) are classified as being deviating from expectancy and consequently elicit an error negativity. Importantly, mere perceptual violations or changes in stimulus identity (which also include a violation of the motor response) are not sufficient and do not activate the error monitoring system to the same extent as learning-relevant violations. The current results are consistent with earlier studies on the FRN (Goyer et al., 2008; Holroyd et al., 2004; Nieuwenhuis et al., 2004). Although these studies used gambling tasks in which no strategy or rule can be learned to achieve a certain outcome, they clearly demonstrated that the FRN was modulated by contextual influences. However, these studies did not address the question of whether different aspects of one and the same stimulus can elicit an error signal depending on their behavioral relevance in a specific situation. Our experiments demonstrate that the N2b actually is sensitive to the relevance of specific stimulus aspects in a given learning context. One and the same type of deviant event (perceptual/ structural deviants) elicited an N2b component only when it conveyed information about the sequence structure to be learned, but not, when it was assigned a learning irrelevant status by means of task instruction. This similarity between the FRN and the N2b is an additional indication that both components may rely on a common basic mechanism. This common mechanism might reflect that the "neural error-processing system provides a scalar estimate of utility on the basis of recent environmental events" (Goyer et al., 2008, p.2067).

According to Folstein and Van Petten (2008), a frontocentral N2 elicited by visual stimuli can also be related to novelty, mismatch from a perceptual template, or response inhibition. These alternative accounts can be ruled out as we presented simple letter stimuli that were repeatedly used and hence not novel. Also, the different violation conditions were equally rare. Most importantly, the perceptual and perceptual/ structural deviants were presented with the same frequency in both experiments but showed differential N2b responses as a function of task instructions. Additionally, all deviant events were perceptually unexpected and especially the conceptual deviants (which might be the least expected stimuli because they are presented less often than the other letters) did not elicit a large N2b. Therefore, the N2b in the current experiments cannot be explained by novelty, low frequency of occurrence, or perceptual mismatch.

Note also that our results cannot simply be due to differences in response key assignments between the two experiments (sequence responses in Experiment 1 vs. less practiced different response key in Experiment 2) because the response key assignment for perceptual/structural and perceptual deviants were the same within each experiment but perceptual/structural and perceptual deviants differed with respect to their learning-relevance in Experiment 1 but not in Experiment 2. Finally, if response inhibition was the reason for N2b elicitation in the current experiments, we would have expected that conceptual deviants, for which a different response had to be carried out, would also have elicited an N2b. However, the N2b to conceptual deviants in Experiment 1 did not differ from that to perceptual deviants for which response inhibition was not required[3]. Taken all this evidence together, we feel safe to claim that the current N2b results are caused by an expectancy violation which serves as an internal feedback signal and is driven by learning-relevant aspects of the deviant stimuli. Which aspects of the stimulus are taken into account in this evaluation process is determined by the task context. Thus, our data show that the evaluation process which determines whether a given stimulus constitutes an expectancy violation and contributes to behavioral adaptation is very economic and can be flexibly tailored to a specific learning situation.

The present findings can also be discussed in the context of the dual mechanisms of control (DMC) theory (Braver, 2012). This framework proposes two control modes working in accord to achieve optimal performance in a given task. The proactive control mode includes anticipatory processes that serve to prepare for a given task, e.g., the maintenance of goal-relevant information. In contrast, the reactive control mode reflects processes occurring during task processing, e.g., stimulus-driven goal reactivation induced by interference or episodic associations. In this sense, error monitoring is usually seen as a purely reactive process that is activated during task processing only after the error or the unexpected event is detected. Our results, however, clearly demonstrate that error monitoring also includes a preparatory, proactive component because the aspects of the stimulus that are evaluated as learning-relevant expectancy violations are dependent on the task context. So the knowledge about the task context is used to fine-tune the error monitoring system for the task at hand by defining which aspects of a stimulus can possibly elicit an error signal. Therefore one and the same stimulus can lead to a learning-relevant expectancy violation in one context but not in another.

3.2 Later Evaluation Processes

In both experiments the N2b and P3 were functionally dissociated. In Experiment 1 the P3 is elicited by the presentation of all types of deviant events. Due to its sensitivity to saliency and frequency (see above) it was largest for conceptual deviants, smaller for perceptual and perceptual/ structural deviants, and smallest for structural deviants. In contrast, the N2b was only generated by deviants that violate expectancies on a learning-relevant dimension, i.e., structural and perceptual/ structural deviants. In Experiment 2 the P3 was again present for all types of deviants. Because all but the structural deviants could subjectively be assigned to the same category the P3 was of equal size for conceptual, perceptual, and perceptual/ structural deviants. For the same reasons as in Experiment 1 it was smallest for structural deviants. However, the N2b was generated by structural deviants only and was not influenced by frequency or saliency.

Based on these findings one can assume that different types of performance monitoring that are associated with different ERP components were initiated in the current task. The first monitoring process (reflected in the N2b) represents an initial and fast evaluation of an event in terms of its hedonistic value and is driven by learning-relevant events as defined by the current task context. The second monitoring process (mirrored in the P3) is a later, higher-order form of performance monitoring that is associated with an evaluation of all unexpected task-relevant events which is crucial for updating of working memory contents (Donchin & Coles, 1988; Polich, 2004, 2007). Further studies will be required to obtain a better understanding of the interaction between both monitoring systems.

3.3 Conclusion

Both experiments reveal important insights into the mechanisms underlying performance monitoring and the detection of unexpected events. First, they confirm our previous findings that changes in expectancies that are induced via learning are reflected in N2b amplitude (Ferdinand et al., 2008) as has previously been reported for the ERN (for a review, see Gehring et al., 2012). By this, our results support the view that the generation of the N2b by perceived errors relies on the same mechanism as the generation of the ERN after committed errors or the FRN after negative feedback, and that all three components reflect the adaptation of one's behavior to current task demands. Second, while being consistent with previous findings, the present results extend our knowledge on error monitoring in an important aspect. They show that error monitoring is not exclusively reactive, but also works in a proactive manner: Expectancy violations only activate the error monitoring system (as indexed by the elicitation of the N2b) when the detected mismatch is relevant for current goals and thus can potentially contribute to learning.

4 Methods and Materials

4.1 Experiment 1

Participants

16 volunteers (8 female/ 8 male, aged 20-27 years, mean age 22.4 years) participated in the experiment. All signed informed consent before the experiment and were paid 8 € per hour. All participants were right-handed and had normal or corrected-to-normal vision.

Stimuli and Procedure

Stimuli were four capital letters (A, B, D, E), which were presented in the center of a computer display (0.36° visual angle, font: Arial Rounded MT Bold). A single letter was displayed on the screen for 200 ms. A serial reaction time task (SRTT) was applied and participants were instructed to press the corresponding response button as quickly as possible. The letter A required a button press with the left middle finger, B with the left index finger, D with the right index finger, and E with the right middle finger. If they did not respond to the stimulus, an auditory time-out signal occurred 800 ms after stimulus onset. The next letter appeared 500 ms after the response to the current stimulus or after the time-out signal. A fixation cross was displayed between presentation of letters.

The order in which the letters appeared on the screen followed either a regular or irregular sequence (see Table 1). In **regular sequences**, letters were presented according to the following sequence: DBAEBDEA. In irregular sequences, one letter in the regular sequence was replaced by a letter that otherwise had not occurred at that position within the sequence. There were four different kinds of irregular sequences. In irregular sequences with a **structural violation**, a deviant stimulus could occur at each position of the sequence (e.g. DBAE**<u>A</u>**DEA). They are called irregular sequences with structural violation here to focus on the type of expectancy violation (the deviant violates the structure of the regular sequence). In irregular sequences with **perceptual violation**, a deviant was presented as a lower case letter. However, this deviant did not violate the structure of the regular sequence since only the physical appearance of the letter was changed (e.g. DBAE***b***DEA) and participants had been instructed to press the corresponding response key irrespective of whether it was an upper or lower case letter. In irregular sequences with **structural and perceptual violation**, the deviant was presented as a lower case letter and it violated the structure of the regular sequence (e.g. DBAE***a***DEA). Finally, in irregular sequences with **conceptual violation**, the deviant was an upper-case letter (X or Y) that had not appeared in one of the previous sequences (e.g. DBAE**X**DEA). For these deviants participants were instructed to press a fifth response letter with their right little finger. The different types of violations contained in the irregular sequences can be divided in two groups. Two violation types disrupt the sequence structure (structural and structural/perceptual violations) and should be relevant for sequence learning because expectancies about the stimulus order are violated. The two other violation types only violate perceptual characteristics and have no relevance for sequence learning (perceptual and conceptual violations). Although conceptual deviants also occur at a position where another stimulus is expected, they were introduced to the participants as not belonging to the regular sequence. Additionally, they differ visually very clearly from regular stimuli. On the basis of these task and stimulus characteristics, conceptual deviants have no relevance for sequence learning.

The experiment consisted of 320 sequences - 160 regular sequences and 40 irregular sequences of each type. To facilitate regular sequence learning, the first ten sequences presented were regular. Afterwards, sequences were drawn in a random order. The beginnings and ends of each sequence were not marked.

The participants' task was to respond as accurately and as fast as possible to the stimuli on the screen by pressing a response button. They were also told that the letters were mainly presented in a repeating sequence and that trying to figure out the repeating sequence would help them to respond fast and accurately.

EEG-Recording

Participants were seated in a dimly lit, electrically shielded and sound-attenuated chamber. While performing the SRTT, the electroencephalogram (EEG) was recorded from 59 Ag/AgCl electrodes embedded in an elastic cap and amplified from DC to 100 Hz at a sampling rate of 500 Hz. The left mastoid served as reference. To control for vertical and horizontal eye-movements, the electrooculogram (EOG) was recorded from the outer ocular canthi and the right sub- and supraorbital ridges. Impedances for all electrodes were kept below 10 kΩ. Further off-line data processing included a digital band-pass filter from 0.5 Hz to 30 Hz in case of low-frequency signal drifts or high-frequency noise in the EEG channels. Recording epochs including eye movements were corrected by using a linear regression approach (Gratton, Coles & Donchin, 1983), and epochs with other recording artifacts were rejected before averaging whenever the standard deviation in a 200 ms time interval exceeded 30 µV in any EOG channel.

Data Analyses

Statistical analyses of behavioral data include measures of reaction times and accuracy. For both the behavioral data and the EEG data, trials were excluded from further analyses whenever participants produced a timeout.

Selection of the time windows for ERP analyses was based on previous studies and on visual inspection of the waveforms. Consistent with previous studies, to test whether the N2b was present, it was first measured as the difference in mean voltage between regular stimuli (all stimuli from regular sequences) and deviant stimuli in a time window from 240 ms to 340 ms after stimulus presentation separately for each deviant type.

Additionally, as it is known that the mean amplitudes in the N2b time window can be contaminated by component overlap with a preceding P2 when stimuli differ visually (Luck & Hillyard, 1994; Liu, Perfetti & Hart, 2001), an additional analysis sought to identify those deviant types that elicited a P2 by analyzing the mean amplitude differences between regulars and deviants in a 150 ms to 250 ms time window (see Supplement). Subsequently, a peak-to-peak analysis of the N2b was conducted only for those conditions in which a P2 was reliably elicited at the electrode site where N2b were largest and P2 did not differ between conditions (FCz). For this purpose, the local maxima (P2) and minima (N2b) were automatically selected in the subject average waveforms. To reduce variance due to latency jitter, the time windows for the peak-to-peak analyses were chosen to be smaller (i.e., P2: 170 to 230 ms and N2b: 260 to 320 ms) than the respective windows for the mean amplitudes analyses. In the case that no local maximum/ minimum was found the largest/smallest amplitude value in the respective time window was selected.

The P3 was measured as the difference in mean voltage between regular and deviant stimuli in a time window from 440 ms to 540 ms after stimulus presentation. For all ERP analyses a 100 ms pre-stimulus baseline was used.

Behavioral and ERP data were analyzed using repeated-measures analyses of variance (ANOVAs) with an alpha level of .05. The Greenhouse-Geisser correction for non-sphericity was used whenever appropriate and epsilon-corrected p-values are reported together with uncorrected degrees of freedom and Greenhouse-Geisser epsilon values. Statistical analyses of the ERP data were restricted to the midline electrodes (N2b and P2 analysis: FCz, Cz, CPz, Pz; N2b peak-to-peak analysis: FCz, according to the international 10-20 system). For topographical analyses of the P3, data were normalized using the vector scaling procedure as described by McCarthy and Wood (1985) and electrodes F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, O1, Oz, and O2 were used for the factors Lateralization (left, middle, and right) and Anterior-posterior (frontal, central, parietal, and occipital). For reasons of clarity, only main effects and interactions including the factors of interest are reported.

4.2 Experiment 2

Participants

16 volunteers (8 female/ 8 male, aged 19-28 years, mean age 23.3 years) that had not participated in Experiment 1 took part in Experiment 2. All signed informed consent before the experiment and were paid 8 € per hour. All participants were right-handed and had normal or corrected-to-normal vision.

Stimuli and Procedure

Stimuli, stimulus presentation, participants' task and procedure were the same as in Experiment 1. Again, the order in which the letters appeared on the screen followed either a regular sequence or an irregular sequence. Irregular sequences could include a **structural**, **perceptual, perceptual/ structural**, or **conceptual violation**. The only difference between the two experiments was that in Experiment 2 participants were told that only upper case letters belonged to the to-be-learned sequence and thus required a response with the respective response button. For this reason, conceptual deviants were also presented as lower case letters here. As in Experiment 1, the letter A required a button press with the left middle finger, B with the left index finger, D with the right index finger, and E with the right middle finger. All lower case letters were instructed as not belonging to the to-be-learned sequence and as requiring a response with a different response button. This means that all lower case letters (perceptual, perceptual/ structural, and conceptual deviants) had to be responded to with a fifth response button requiring a button press with the left ring finger.

On the basis of this instruction the violations again could be sorted in two groups. One group disrupts the sequence structure (structural violations) and should be relevant for sequence learning. The other group of deviants only violates perceptual characteristics (all lower case letters, i.e., perceptual/ structural, perceptual, and conceptual violations) and, by this, has no relevance for sequence learning.

EEG-Recording and Data Analyses

The recording procedure and data analyses were the same as in Experiment 1.

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References

Alexander, W. H., & Brown, J. W. (2011). Medial prefrontal cortex as an action-outcome predictor. *Nature Neuroscience*, **14**, 2338-1344.

Bates, A.T., Patel, T.P., & Liddle, P.F (2005). External behavior monitoring mirrors internal behavior monitoring. *Journal of Psychophysiology*, **19**, 281-288.

Braver, T.S. (2012). The variable nature of cognitive control: a dual mechanisms framework. *Trends in Cognitive Sciences*, **16(2)**, 106-113.

De Bruijn, E. R., & von Rhein, D. T. (2012). Is your error my concern? An event-related potential study on own and observed error detection in cooperation and competition. *Frontiers in Neuroscience*, **6**, 8.

Donchin, E., & Coles, M.G.H. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*, **11**, 357-374.

Eimer, M., Goschke, T., Schlaghecken, F., & Stürmer, B. (1996). Explicit and implicit learning of event sequences: Evidence from event-related brain potentials. *Journal of Experimental Psychology: Learning, Memory and Cognition*, **22**, 970-987.

Falkenstein, M., Hohnsbein, J., & Hoormann, J. (1995). Event-related potential correlates of errors in reaction tasks. In Karmos, G. , Molnar, M., Csepe, V., Czigler, I. & Desmedt, J.E. (eds), *Perspectives of event-related potentials research (EEG Suppl. 44)*. Elsevier, Amsterdam, pp. 261-272.

Falkenstein, M., Hohnsbein, J., Hoorman, J., & Blanke, L. (1990). Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In Brunia, C.H.M., Gaillard, A.W.K. & Kok, A. (eds), *Psychophysiological Brain Research*. Tilburg University Press, Tilburg, pp. 192-195.

Ferdinand, N.K., Mecklinger, A., & Kray, J. (2008). Error and deviance processing in implicit and explicit sequence learning. *Journal of Cognitive Neuroscience*, **20**, 629-642.

Ferdinand, N. K., Mecklinger, A., Kray, J., & Gehring, W. J. (2012). The processing of unexpected positive response outcomes in the mediofrontal cortex. *The Journal of Neuroscience*, **32**, 12087-12092.

Folstein, J.R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology*, **45**, 152-170.

Gehring, W.J., Goss, B., Coles, M.G.H., Meyer, D.E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science*, **4**, 385-390.

Gehring, W.J., & Willoughby, A.R. (2002). The medial frontal cortex and the rapid processing of monetary gains and losses. *Science*, **295**, 2279-2282.

Gehring, W.J., Liu, Y., Orr, J.M., & Carp, J. (2012). The error-related negativity (ERN/Ne). In: Luck, S.J., & Kappenman, K. (eds), *Oxford handbook of event-related potential components*, pp 231-291. New York: Oxford UP.

Goyer, J.P., Woldorff, M.G., & Huettel, S.A. (2008). Rapid electrophysiological brain responses are influenced by both valence and magnitude of monetary rewards. *Journal of Cognitive Neuroscience*, **20**, 2058-2069.

Gratton, G., Coles, M.G.H., & Donchin, E., (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, **55**, 468–484.

Holroyd, C.B. (2004). A note on the oddball N200 and the feedback ERN. In Ullsperger, M., & Falkenstein, M. (eds), *Errors, Conflict and the Brain. Current opinions on performance monitoring*. Dresden, Sächsisches Digitaldruck Zentrum GmbH, pp. 211-218.

Holroyd, C.B. & Coles, M.G. (2002). The neural basis of human error processing: Reinforcement learning, dopamine, and the error-related negativity. *Psychological Review*, **109**, 679-709.

Holroyd, C.B., Larsen, J.T. & Cohen, J.D. (2004). Context dependence of the event-related brain potential associated with reward and punishment. *Psychophysiology*, **41**, 245-253.

Johnson, R., Jr. (1986). A triarchic model of P300 amplitude. *Psychophysiology*, **23**, 367-284.

Kopp, B., & Wolff, M. (2000). Brain mechanisms of selective learning: event-related potentials provide evidence for error-driven learning in humans. *Biol Psychol*, **51**, 223-246.

Liu, Y., Perfetti, C.A., & Hart, L. (2001). ERP evidence for the time course of graphic, phonological, and semantic information in Chinese meaning and pronunciation decisions. *Journal of Experimental Psychology: Learning, Memory, and Cognition,* **29**, 1231-1247.

Luck, S.J., & Hillyard, S.A. (1994). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology,* **31**, 291-308.

McCarthy, G., & Wood, C.C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and clinical Neurophysiology,* **62**, 203-208.

Mecklinger, A., & Ullsperger, P. (1993). P3 varies with stimulus categorization rather than probability. *Electroencephalography and Clinical Neurophysiology,* **86**, 395-407.

Miltner, W.H.R., Braun, C.H., & Coles, M.G.H. (1997). Event-related brain potentials following incorrect feedback in a time-estimation task: evidence for a "generic" neural system for error detection. *Journal of Cognitive Neuroscience*, **9**, 788-798.

Nieuwenhuis, S., Yeung, N., van den Wildenberg, W., & Ridderinkhof, K.R. (2003). Electrophysiological correlates of anterior cingulate function in a go/no-go task: Effects of response conflict and trial type frequency. *Cognitive, Affective, & Behavioral Neuroscience,* **3**, 17-26.

Nieuwenhuis, S., Yeung, N., Holroyd, C.B., Schurger, A., & Cohen, J.D. (2004). Sensitivity of electrophysiological activity from medial frontal cortex to utilitarian and performance feedback. *Cerebral Cortex,* **14**, 741-747.

Oliveira, F.T., McDonald, J.J., & Goodman, D. (2007). Performance monitoring in the anterior cingulate is not all error related: expectancy deviation and the representation of action–outcome associations. *Journal of Cognitive Neuroscience*, **19**, 1994-2004.

Polich, J. (2004). Neuropsychology of P3a and P3b: A theoretical overview. In Moore, N.C., & Arikan, K. (eds), *Brainwaves and mind: Recent developments*. Kjellberg Inc., Wheaton, pp. 15-29.

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, **118**, 2128-2148.

Rüsseler, J., Hennighausen, E., Münte, T. F., & Rösler, F. (2003). Differences in incidental and intentional learning of sensorimotor sequences as revealed by event-related brain potentials. *Cognitive Brain Research*, **15**, 116-26.

Sutton, R.S., & Barto, A.G. (1998). *Reinforcement learning: An introduction.* MIT Press.

van Schie, H.T., Mars, R.B., Coles, M.G., & Bekkering, H. (2004). Modulation of activity in medial frontal and motor cortices during error observation. *Nature Neuroscience*, **7**, 549–554.

Verleger, R., Seitz, A., Yordanova, J., & Kolev, V. (2015). Is insight a godsend? Explicit knowledge in the serial response-time task has precursors in EEG potentials already at task onset. *Neurobiology of Learning and Memory*, 125, 24-35.

Footnotes

1 “N2b” and the more general term “N200” are often used synonymously. Here we use the term “N2b” (except when citing other studies) to distinguish the component from the mismatch negativity (MMN), that is sometimes named “N2a”.

2 The trial numbers for regulars and deviants were not matched for the analyses since all types of deviants were compared to the same regular stimuli and because regular stimuli were not included in the additional peak-to-peak analyses. However, we compared the ERPs for a random sample of regular trials that was matched in trial number to deviants (Experiment 1: mean = 35.7, Experiment 2: mean =37.4) to the ERPs for all regular trials. For both experiments, this analysis revealed no difference (Experiment 1: p=.38, Experiment 2: p =.14).

3 Interestingly, the expectancy violation in a given trial could in principle be elicited by a mismatch between the predicted and the actual stimulus or by a mismatch between the predicted and the actually demanded response. However, we think it likely that the expectancy violation is elicited from a comparison between stimuli (i.e., from a preceding stimulus or a preceding response the next stimulus is predicted). The reason for this is the following: When predicting the next response from the previous stimulus or response, this should lead to preparation of this response. When the next stimulus is then presented on the screen, it has to be checked whether this stimulus indicates the same response as the one that is already being prepared. In case of a mismatch, this would have to go hand in hand with inhibition of the prepared response. However, as discussed above, inhibition does not seem to play a role for the elicitation of the N2b.

Table 1: Sequences used in Experiment 1. For better understanding, stimuli that render a sequence irregular are underlined and boldface, perceptual deviants are in italics (this was not the case in the actual experiment). Conceptual deviants served as a control for purely perceptual deviants in that they also differ visually from regular stimuli and were not relevant for sequence learning.

		Structural Violation (Learning Relevance)	
		No	**Yes**
Perceptual Violation	**No**	No Deviants / Regular Sequence	Structural Deviants
		DBAEBDEA	DBAE<u>**A**</u>DEA
	Yes	Perceptual Deviants	Perceptual /Structural Deviants
		DBAE<u>***b***</u>DEA	DBAE<u>***a***</u>DEA

Figure Captions

Figure 1. Reaction times and error rates for regular and deviant stimuli in Experiment 1. Bars denote standard errors of means (regS: regular stimuli, strD: structural deviants, perstrD: perceptual/ structural deviants, perD: perceptual deviants, conD: conceptual deviants).

Figure 2. Stimulus-locked ERPs from Experiment 1 (regS: regular stimuli, strD: structural deviants, perstrD: perceptual/ structural deviants, perD: perceptual deviants, conD: conceptual deviants). Note that for reasons of visibility, the four types of deviants are displayed in separate columns but all compared against the same regular stimuli.

Figure 3. Reaction times and error rates for regular and deviant stimuli in Experiment 2. Bars denote standard errors of means (regS: regular stimuli, strD: structural deviants, perstrD: perceptual/ structural deviants, perD: perceptual deviants, conD: conceptual deviants).

Figure 4. Stimulus-locked ERPs from Experiment 2 (regS: regular stimuli, strD: structural deviants, perstrD: perceptual/ structural deviants, perD: perceptual deviants, conD: conceptual deviants). Note that for reasons of visibility, the four types of deviants are displayed in separate columns but all compared against the same regular stimuli.

Figure 5. Peak-to-peak N2b for perceptual/ structural deviants and for perceptual deviants in Experiment 1 and 2. Bars denote standard errors of means.

Figure 1

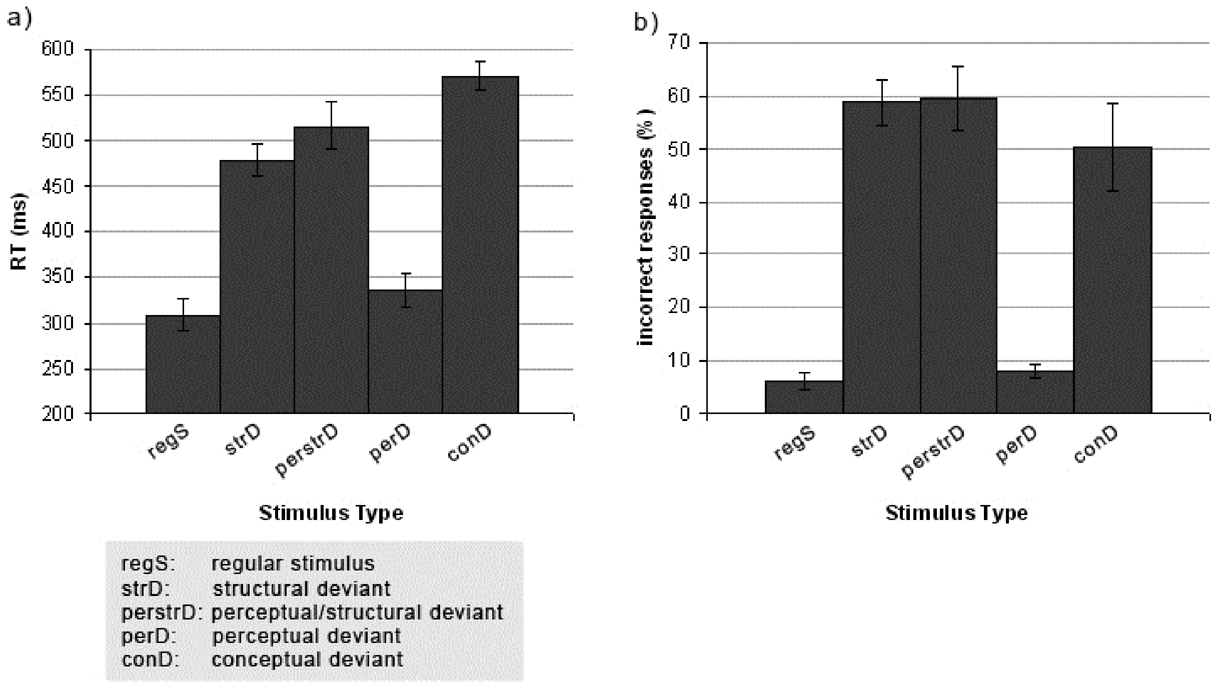

a)
RT (ms)
600
550
500
450
400
350
300
250
200
regS
strD
perstrD
perD
conD
Stimulus Type
b)
incorrect responses (%)
70
60
50
40
30
20
10
0
regS
strD
perstrD
perD
conD
Stimulus Type
regS: regular stimulus
strD: structural deviant
perstrD: perceptual/structural deviant
perD: perceptual deviant
conD: conceptual deviant

Figure 2

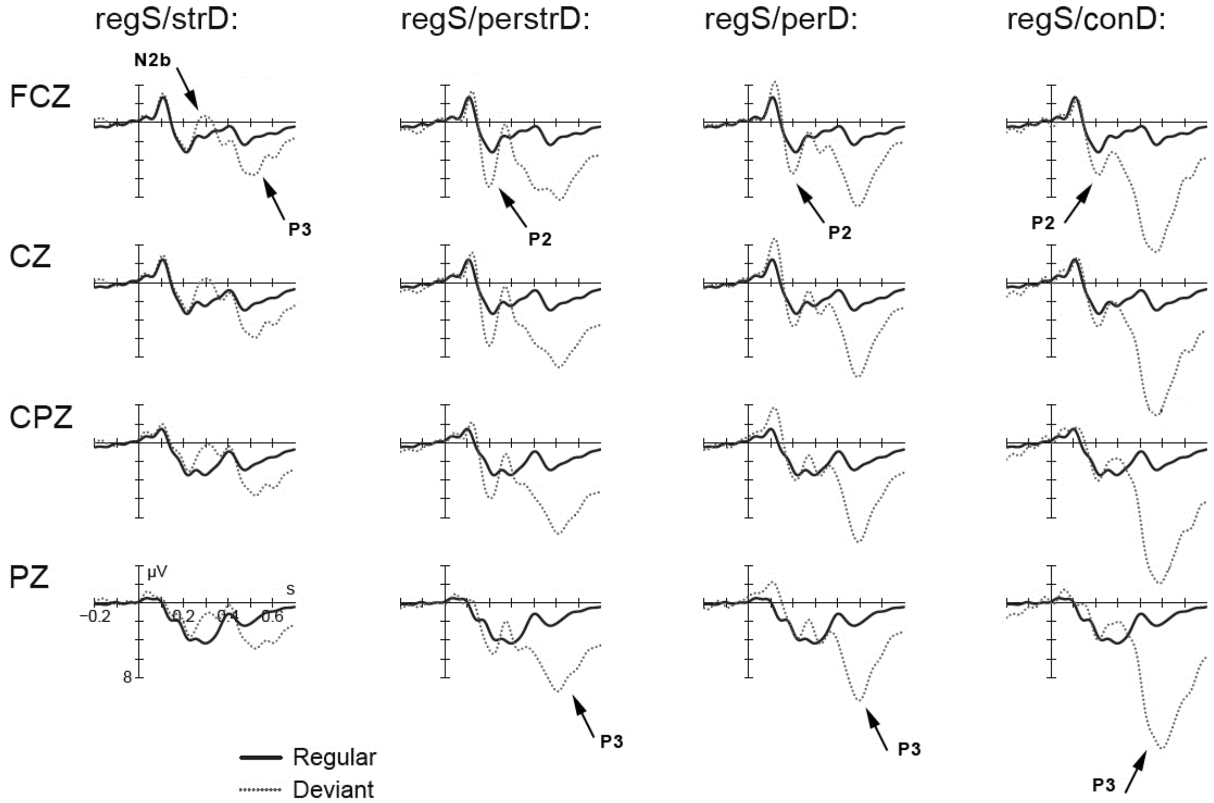
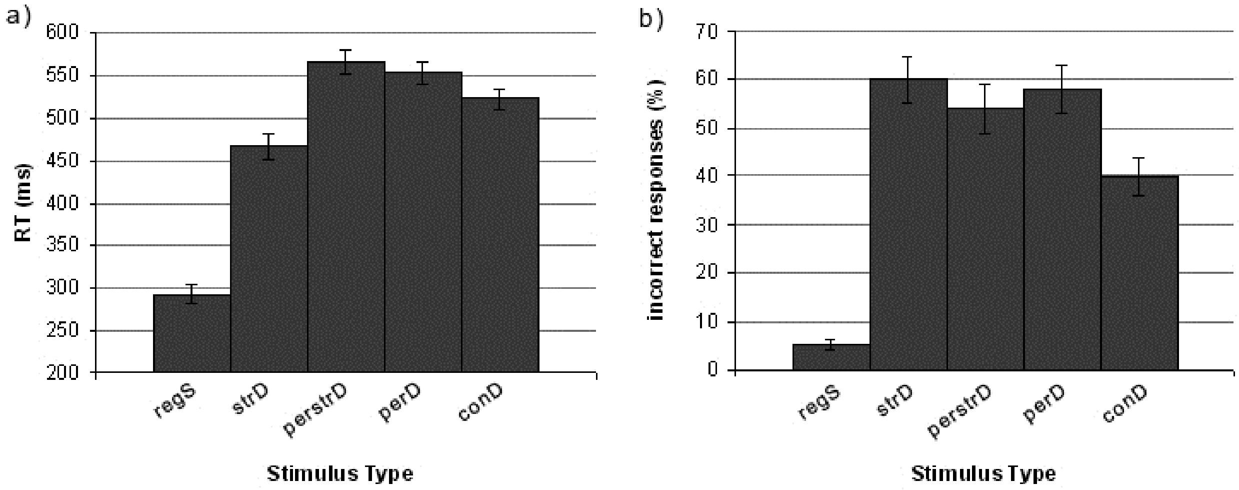

regS/strD:
regS/perstrD:
regS/perD:
regS/conD:
FCZ
CZ
CPZ
PZ
N2b
P2
P3
μV
s
−0.2
0.2
0.4
0.6
8
Regular
Deviant

Figure 3



regS: regular stimulus
strD: structural deviant
perstrD: perceptual/structural deviant
perD: perceptual deviant
conD: conceptual deviant

Figure 4

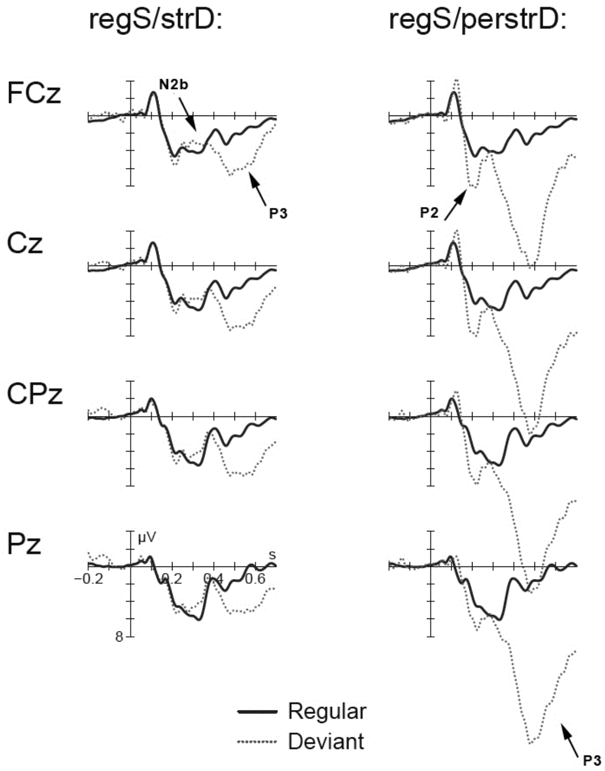
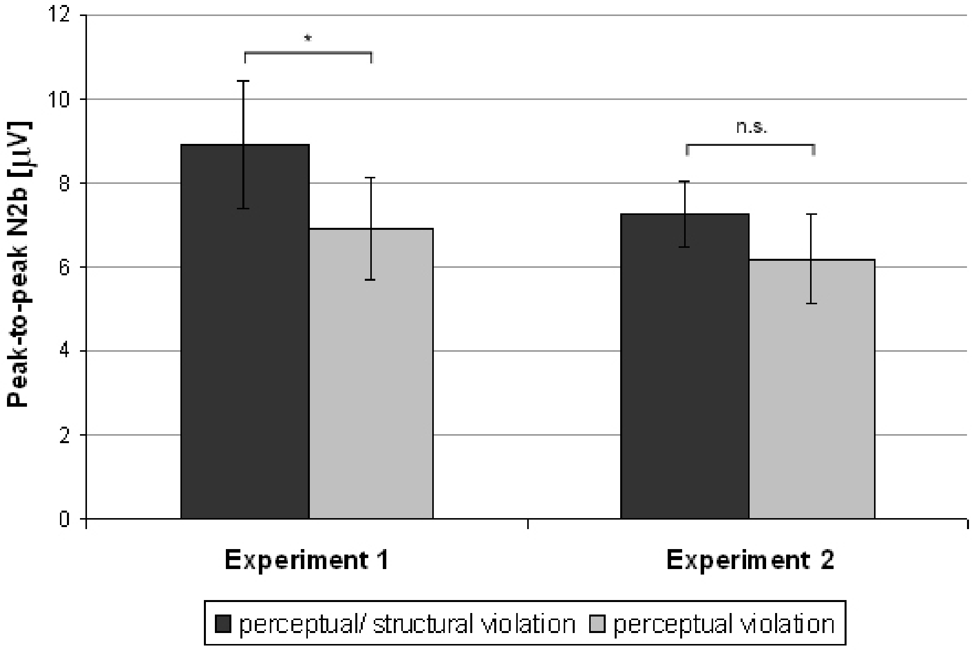

regS/strD:
regS/perstrD:
regS/perD:
regS/conD:
FCz
Cz
CPz
Pz
N2b
P3
P2
μV
s
−0.2
0.2
0.4
0.6
8
Regular
Deviant

Figure 5



12
10
8
6
4
2
0
Peak-to-peak N2b [µV]
*
n.s.
Experiment 1
Experiment 2
perceptual/ structural violation
perceptual violation

Supplement: Analysis of P2 effects

The mean amplitudes in the N2b time window might be contaminated by component overlap with a preceding P2, especially when stimuli differ visually (Luck & Hillyard, 1994; Liu, Perfetti & Hart, 2001). This probably reduces N2b mean amplitude relative to regular stimuli. For this reason, an additional analysis sought to identify those deviant types that elicited a P2 by analyzing the mean amplitude differences between regulars and deviants in a 150 ms to 250 ms time window at midline electrodes FCz, Cz, CPz, Pz.

Experiment 1:

An ANOVA with factors Stimulus Type (regular, deviant) and Electrode (FCz, Cz, CPz, Pz) in the P2 time window (150-250 ms) was conducted. While no significant main effect or interaction was found for structural deviants, for perceptual/ structural deviants mean amplitude was found to be more positive than that for regular stimuli (Stimulus Type: $F(1,15)=30.17$, $p<.01$). For perceptual deviants, there was a significant interaction (Stimulus Type x Electrode: $F(3,45)=13.88$, $p<.01$, $\varepsilon=.42$) that was caused by mean amplitudes for perceptual deviants being more positive than that for regular stimuli at FCz ($F(1,15)=6.39$, $p=.02$). For conceptual deviants, again a significant interaction (Stimulus Type x Electrode: $F(3,45)=13.06$, $p<.01$, $\varepsilon=.37$) was found, that was due to the mean amplitude for conceptual deviants being more positive than that for regular stimuli at FCz ($F(1,15)=9.90$, $p<.01$) and mean amplitudes for conceptual deviants being more positive at frontal electrode sites ($F(3,45)=5.02$, $p=.04$, $\varepsilon=.37$). An ANOVA with factor Deviant Type (perstrD, perD, conD) at FCz showed that P2 amplitude does not differ between deviant types ($p=.38$). This means, that a P2 is present at FCz for all types of deviants except for the purely structural deviants and that its size does not differ between the deviants containing a perceptual deviation.

Experiment 2:

An ANOVA with factors Stimulus Type (regular, deviant) and Electrode (FCz, Cz, CPz, Pz) in the P2 time window (150-250 ms) was conducted. While no significant main effect or interaction was found for structural deviants (all $p > .25$), for perceptual/ structural deviants mean amplitude was found to be more positive than that for regular stimuli (Stimulus Type: $F(1,15)=15.90$, $p<.01$). For perceptual deviants, there was a significant main effect for Stimulus Type ($F(1,15)=46.31$, $p<.01$) and a Stimulus Type by Electrode interaction ($F(3,45)=5.71$, $p=.02$, $\varepsilon=.42$). The interaction was due to mean amplitude of perceptual deviants being more positive than that for regular stimuli at all four electrode sites (all $p<.01$) with larger effects at anterior electrodes ($\omega2=0,61$ at FCz, $\omega2=0,60$ at Cz, $\omega2=0,57$ at CPz, and $\omega2=0,39$ at Pz). For conceptual deviants, again a significant main effect (Stimulus Type: $F(1,15)=12.47$, $p<.01$) and interaction (Stimulus Type x Electrode: $F(3,45)=10.65$, $p<.01$, $\varepsilon=.40$) was found. The interaction was due to the mean amplitude for conceptual deviants being more positive than that for regular stimuli at all electrode sites except for Pz ($p=.11$) and mean amplitudes for conceptual deviants being more positive at frontal electrode sites ($F(3,45)=5.85$, $p=.02$, $\varepsilon=.37$). In analogy to Experiment 1, an ANOVA with factor Deviant Type (perstrD, perD, conD) was conducted which showed that P2 amplitude at FCz does not differ between deviants ($p=.58$). Thus, a P2 is present at FCz for all types of deviants except for the purely structural deviants and does not differ in size between the different types of deviants.