

Error and Deviance Processing in Implicit and Explicit Sequence Learning

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Abstract

■ In this experiment, we examined the extent to which error-driven learning may operate under implicit learning conditions. We compared error monitoring in a sequence learning task in which stimuli consisted of regular, irregular, or random sequences. Subjects were either informed (explicit condition) or not informed (implicit condition) about the existence of the sequence. For both conditions, reaction times were faster to stimuli from regular sequences than from random sequences, thus supporting the view that sequence learning occurs irrespective of learning condition. Response-locked event-related potentials (ERPs) showed a pronounced ERN/Ne, thereby signaling the detection of committed errors. Deviant stimuli from irregular sequences elicited an N2b component that developed

in the course of the experiment, albeit faster for explicit than implicit learners. This observation supports the view that deviant events acquire the status of perceived errors during explicit and implicit learning, and thus, an N2b is generated resembling the ERN/Ne to committed errors. While performing the task, expectations about upcoming events are generated, compared to the actual events, and evaluated on the dimension “better or worse than expected.” The accuracy of this process improves with learning, as shown by a gradual increase in N2b amplitude as a function of learning. Additionally, a P3b, which is thought to mirror conscious processing of deviant stimuli and is related to updating of working memory representations, was found for explicit learners only. ■

INTRODUCTION

Thorndike (1911/1970) described in his law of effect that actions followed by positive reinforcement are more likely to be repeated in the future, whereas behavior that is followed by negative outcomes is less likely to recur. This implies that behavior is evaluated in the light of potential consequences, and nonreward events (i.e., errors) need to be detected in order for reinforcement learning to take place. In short, humans have to monitor their performance in order to detect and correct errors, and this detection process allows them to successfully adapt their behavior to changing environmental demands.

Of the abovementioned monitoring processes, the detection of committed errors is thought to be mirrored by the error-related negativity (ERN) or error negativity (Ne), an event-related potential (ERP) component elicited around the time an error is made (Gehring, Goss, Coles, Meyer, & Donchin, 1993; Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990). The ERN/Ne can be observed in simple reaction time tasks (e.g., Gehring et al., 1993; Falkenstein et al., 1990) as well as in recognition memory tasks (Nessler & Mecklinger, 2003). ERN/Ne onset coincides with response initiation and peaks roughly 80 msec afterward. Its topographical maximum lies over fronto-central brain regions, and is thought to be gener-

ated in the anterior cingulate cortex (ACC; e.g., Ullsperger & von Cramon, 2001). Furthermore, the ERN/Ne is sensitive to the degree of an error (Bernstein, Scheffers, & Coles, 1995) and influenced by its subjective significance (Hajcak, Moser, Yeung, & Simons, 2005; Gehring et al., 1993). It is also elicited by error observation and by feedback that signals an error was committed (Miltner, Braun, & Coles, 1997), thus emphasizing the flexibility of the underlying error processing system. The ERN/Ne is often followed by a positivity to errors (Pe), a positive wave with centro-parietal distribution.

A neural system that plays a crucial role in reinforcement learning is the mesencephalic dopamine system. Schultz (2002) and Schultz, Dayan, and Montague (1997) recorded spike activity from mesencephalic dopamine cells in conditioning experiments with monkeys. They found that the presentation of a reward elicits a phasic response in the dopamine neurons. This observation is consistent with the hypothesis that the mesencephalic dopamine system codes for the hedonic aspects of reward. During learning, the dopaminergic signal “propagates back in time” from the time the reward is delivered to when the conditioned stimulus is presented. Thus, the mesencephalic dopamine system can also become active in anticipation of a forthcoming reward. Moreover, when a reward is not given, the mesencephalic dopamine neurons decrease their firing rate at the time the reward would normally have been delivered.

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Dopaminergic activity also falls below baseline when the monkey is presented with a stimulus that predicts punishment. On the basis of these results, Schultz and colleagues have proposed that the dopamine neurons are sensitive to changes in the prediction of the hedonistic “value” of ongoing events: A positive dopamine signal is elicited when an event proves better than predicted, and a negative one when an event proves worse. Moreover, they suggested that the phasic responses seen in dopamine neurons might serve as error signals used for adjusting the associative strength of stimuli and responses in neural areas that receive input from the mesencephalic dopamine system (e.g., the prefrontal cortex).

In a model recently proposed by Holroyd and Coles (2002), ERN/Ne amplitude has been linked to the mesencephalic dopamine system. More specifically, this model assumes that when participants commit errors in reaction time tasks, the mesencephalic dopamine system conveys reinforcement learning signals to the frontal cortex. If the outcome of an event is better than expected (and thus the executed action implies reward), the result is a phasic dopamine burst. If the outcome is worse than expected (thus implying nonreward or punishment), the result is a dip in phasic dopamine. The ERN/Ne is presumably generated by disinhibiting the apical dendrites of motor neurons in the ACC when the dopamine reinforcement signal is lacking. These error signals are used to train the ACC, ensuring that control over the motor system will be released to a motor controller that is best suited for the task at hand. The response conflict hypothesis offers an alternative explanation for ERN/Ne generation. According to this theory, the ACC plays an important role in monitoring for the occurrence of conflict during response selection (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001). Response conflict occurs whenever two or more incompatible response tendencies are simultaneously active. Upon detection of such conflict, the ACC conveys a feedback signal to the brain areas involved in the execution of control, informing these areas that executive control processes must be more strongly engaged.

To test their model, Holroyd and Coles examined the response and feedback ERN/Ne as learning progressed throughout the course of a probabilistic learning task. They were able to show that in a 100% condition (the feedback to correct or wrong responses was 100% valid) negative feedback stimuli elicited a feedback ERN/Ne at the beginning of a learning block. As learning of the stimulus–response mappings progressed, the amplitude of the response ERN/Ne became larger, whereas the amplitude of the feedback ERN/Ne became smaller. They concluded that, as subjects learned the correct mappings, they tended to rely less on the feedback and more on their own representation of what the response should be to determine the outcome of each trial (better or worse than expected).

Together, the above reasoning regarding error monitoring and the mesencephalic dopamine system suggests

that the human brain learns by evaluating the results of our actions, and that this learning is driven by reward-related information carried to the ACC. However, these conclusions were derived from explicit learning experiments such as probabilistic learning studies. At present, it is unclear whether dopamine-induced modulation of ERN/Ne amplitude, as proposed by the reinforcement learning theory, can be generalized to other learning conditions, for example, implicit learning. The main goal of the present study is to investigate the role of error monitoring in implicit learning. More specifically, we examined whether the detection of committed and perceived errors (nonreward events) and their implication for learning require an intention to learn, or can occur without awareness of the to-be-learned materials.

So far there are only a few ERN/Ne studies that have distinguished between explicit and implicit error monitoring, namely, monitoring for noticed and unnoticed errors. One reason for this might be that error monitoring processes have mostly been investigated with overt response errors, often defined as inappropriate button presses, which people are typically aware of. Nieuwenhuis, Ridderinkhof, Blom, Band, and Kok (2001) used a different approach to examine whether an ERN/Ne and Pe can be observed after response errors that subjects are unaware of. They had their subjects perform an anti-saccade task, that is, subjects were instructed to generate a saccade to the opposite side of a peripheral onset cue. This task elicited many incorrect reflex-like saccades that people were not aware of. Nieuwenhuis et al. (2001) found that irrespective of error awareness, erroneous saccades were followed by an ERN/Ne, whereas the Pe was more pronounced for conscious than for unconscious errors. This means that error monitoring as reflected in the ERN/Ne seems to take place even when participants are not aware of their errors.

Capitalizing on these findings, in the present study we examined whether errors subjects are unaware of are used as feedback signals that mediate learning processes. For this purpose, we used a sequence learning paradigm with deviant stimuli inserted into an otherwise repeating sequence. Because a sequence learning task can be administered under both explicit and implicit learning conditions, it is a promising strategy for investigating the influence of conscious and unconscious errors on learning under otherwise identical testing conditions.

Implicit learning is conceptualized as the acquisition of information without intention to learn and without concurrent awareness of the underlying structure of the to-be-learned material. In contrast, explicit learning is accompanied by both an intention to learn and awareness of the learned information (Frensch, 1998; Berry, 1994; Seger, 1994; Reber, 1989; for a review on implicit learning, see Cleeremans, Destrebecqz, & Boyer, 1998). A paradigm frequently applied in implicit learning studies is the serial response time task (SRTT; Nissen & Bullemer, 1987). In its original version, a stimulus is presented on

a visual display in one of four possible locations. A specific button is assigned to each display location, and the participant's task is to quickly press the response button that corresponds to the location of the stimulus when it is displayed. When the sequence of stimulus locations follows a repeating pattern, reaction times decrease faster during the experiment than if the sequence is random. When the sequence is switched to a random sequence after prolonged training with a repeating sequence, there is usually a marked increase in reaction times. Participants showing this pattern of results do not necessarily notice the presence of a repeating sequence nor are they able to verbalize their knowledge of the sequential structure. This suggests that they acquire this knowledge incidentally and without the assistance of conscious learning processes (Rüsseler, Hennighausen, Münte, & Rösler, 2003; Rüsseler, Kuhlicke, & Münte, 2003; Destrebecq & Cleeremans, 2001; Eimer, Goschke, Schlaghecken, & Stürmer, 1996; Nissen & Bullemer, 1987).

In our study, subjects were presented with one of four different letters and had to press a corresponding key as quickly and accurately as possible. The letters followed either a regular sequence (a fixed pattern of letters often repeated during the experiment), irregular sequences (letter patterns deviating from the regular sequence by only one letter), or random sequences (cf. Eimer et al., 1996). Subjects were either informed about the presence of the regular sequence and instructed to learn it (explicit condition), or not informed about it (implicit condition).

This procedure offers the opportunity to examine two types of error monitoring: one involved in response-related processing and the other involved in stimulus-related processing. The first type focuses on the detection of wrong responses (i.e., committed errors). This type of error is likely to be noticed by all the subjects (irrespective of learning condition) and the implications of committed errors in probabilistic learning tasks are well investigated and are described elsewhere (e.g., Holroyd & Coles, 2002). It is included in this study to provide a baseline for error monitoring processes. The second type of error monitoring focuses on the detection of deviant stimuli. In the context of the regular sequence, subjects develop expectancies about the next stimulus that will occur on the screen (and in the case of the explicit learning instruction they are even requested to use their sequence knowledge for faster task processing). This formation and evaluation of expectancies is an important and for the explicit group even necessary part of sequence learning, because subjects are informed about the existence of a repeating sequence but have to find it themselves. Because a deviant stimulus in our task can never be predicted, it will always be perceived as an unfavorable event (i.e., error) in the context of sequence learning. Thus, we consider the detection of these stimuli a perceived error. This second error monitoring type is especially important because perceived errors (as opposed to committed errors) can be pro-

cessed with and without awareness and to the extent that they have the status of unfavorable events in both learning conditions, they allow us to directly compare implicit and explicit error monitoring processes and their effects on learning.

In several learning studies, enhanced negative ERP components (N200) have been reported for stimuli that violate participants' expectancies (Rüsseler, Hennighausen, et al., 2003; Rüsseler, Kuhlicke, et al., 2003; Kopp & Wolff, 2000; Eimer et al., 1996). Using a contingency judgment task, Kopp and Wolff (2000) showed that a stimulus that violated a predicted response elicited a fronto-centrally distributed N200 component. From their results, they inferred that the N200 reflects brain events which register the mismatch between actual and expected sensory stimuli. Eimer et al. (1996) reported enhanced N200 components to stimuli that violated a learned spatial sequence even when this sequence was acquired incidentally. Employing a sequence learning task, Rüsseler, Hennighausen, et al. (2003) found an N2b component to deviant events that violated either the stimulus or the motor sequence to be learned. Although not explicitly explored in these studies, it is conceivable that these N200 components and the ERN/Ne reflect activity of a common neural generator (the ACC) initiated by input signaling, that an event violates the participant's expectancy. Eimer et al. used an incidental learning paradigm and classified participants as having explicit or implicit knowledge on the basis of a postexperimental debriefing. Those having explicit knowledge showed a tendency toward larger N200s to deviants violating the sequence. Although the effect was still visible in the implicit group (Experiment 1), they concluded that it is a reflection of the amount of explicit knowledge about the stimulus sequence. Rüsseler, Hennighausen, et al. assigned their participants to an explicit and implicit experimental group based on instruction, and found no N2b at all in their implicit group. Therefore, the question of whether error monitoring takes place under implicit learning conditions remains an open issue.

An N200 component can also be found in go/no-go studies. Conducting such a study, Nieuwenhuis, Yeung, van den Wildenberg, and Ridderinkhof (2003) found the N200 to be related to the frequency of stimuli, in that it was enhanced for low-frequency stimuli, regardless of whether these stimuli required a go or a no-go response. They took this finding as evidence for the conflict monitoring hypothesis, which states that the N200 signals response conflict. Note, however, that these results can also be interpreted in terms of expectancy: The less frequent a stimulus-response type is, the less it is expected and the more the participants' expectation is violated. Nieuwenhuis et al. (2003) also compared the dipole sources of the ERN/Ne and N200 and found that the two dipoles lie very close together in the medial frontal cortex, consistent with a common neural source in the ACC. The colocalization of the N200 and ERN/Ne

sources provides further support for the assumption that these components can be explained within a single conceptual framework, in which both components are produced by a dopamine-related process (see also Holroyd, 2003).

Following the above arguments, we expected sequence learning to be evidenced by decreasing reaction times to regular stimuli over the course of the experiment, whereas reaction times for deviant stimuli should not show this pattern. Also, the reaction times to random stimuli should be longer than those to regular stimuli after subjects have learned the repeating sequence. Both effects were expected to be more pronounced for the explicit learning condition. As for the processing of committed errors, we predicted an ERN/Ne for wrong keypresses in both learning conditions, thereby signaling the occurrence of an error. However, we expected the effect to be larger for explicit learners because, under this condition, the information an error provides can be intentionally used for learning the sequence, and thus, an error might be of greater relevance for this group. With regard to the processing of deviants, we predicted that they acquire the status of perceived errors and elicit an N2b component, irrespective of whether subjects are aware of them. We further expected this component to develop over the course of the experiment. There are two reasons for assuming this. First, deviants should only be detectable if the repeating sequence is learned (implicitly or explicitly). Second, in analogy to the response ERN/Ne in the study of Holroyd and Coles (2002), deviant events should acquire the status of perceived errors during the experiment via learning, that is, when the sequence is learned (implicit or explicit), expectations about the next stimulus are formed. In case of a deviant, they are not confirmed and the deviant is perceived as an unfavorable event. The better the subjects are able to predict the upcoming stimuli (the better the sequence is learned), the larger the violation of their expectations when a deviant occurs. Thus, like the response and feedback ERN/Ne in a probabilistic learning task, N2b amplitude to deviants should be related to the gradual development of knowledge about the sequence structure. We expected the N2b component to be larger for explicit than for implicit learners because the deviants occur in opposition to the subject's explicit expectation established during sequence learning in that condition. We also supposed the N2b to exist for implicit learners, thereby indicating that error monitoring processes are at work even when a subject remains unaware of them.

METHODS

Participants

Forty volunteers (19 women/21 men, aged 18–27 years, mean age = 21.1 years) participated in the experiment.

They all signed informed consent before the experiment and were paid 8 Euros per hour. All subjects were right-handed and had normal or corrected-to-normal vision.

Stimuli and Procedure

Stimuli were four capital letters (A, B, C, D), which were presented in the center of a computer display (0.36° visual angle). The letter A required a button press with the left middle finger, B with the left index finger, C with the right index finger, and D with the right middle finger. A single letter was displayed on-screen for 200 msec. Subjects were instructed to press the corresponding response button as quickly as possible. In case they did not respond to the stimulus, an auditory timeout signal occurred 800 msec after stimulus onset. The next letter appeared 500 msec after the response to the current stimulus or after the timeout signal. A fixation cross was displayed between presentation of letters.

The order in which the letters appeared on the screen followed either a regular, irregular, or random sequence. In regular sequences, letters were presented according to the following sequence: C, B, A, D, B, C, D, A. 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. Such a deviant stimulus could occur at each position of the sequence with equal probability and each of the four letters had equal probability to occur as a deviant. No immediate letter repetition was allowed if the deviant stimulus would have been the second letter in the repetition pair, to prevent priming effects in responses to deviants. Immediate repetitions were allowed if the deviant stimulus was the first letter of the pair to obtain more irregular sequences. Because the stimuli following deviants are not included in any of the analyses, priming effects are of no importance here. In the random sequences, the order of the letters was determined randomly with the following constraints: No immediate letter repetition was allowed, and irregular sequences and substrings of the regular sequence that were four or more characters long were not allowed. The probability of occurrence for each letter was the same for regular, irregular, and random sequences.

Each subject performed two blocks of 112 sequences. Sequences 1–96 were 48 regular and 48 irregular sequences, drawn in a random order. Sequences 97–112 were random sequences. Random sequences were always presented at the end of a regular/irregular block to provide a measure of sequence learning that is free from practice effects (i.e., the reaction time difference between regular stimuli at the end of a block and the following random stimuli). The beginnings and ends of each sequence were not marked.

Subjects were randomly divided into two groups and were assigned to either an explicit or an implicit sequence learning task. Participants in the explicit learning

group were told that the letters were mainly presented in a repeating sequence. They were not given the regular sequence in advance, but had to discover it themselves during the experiment and were told that learning this sequence should be used to improve performance. In contrast, the presence of a sequence was not mentioned to the implicit learning group.

To assess whether subjects in the implicit learning group became aware of the repeating sequence during the experiment, they were asked after the experiment whether they (1) had noticed anything unusual and (2) had noticed a repeating pattern in the stimulus presentation. Thereafter, subjects from the implicit as well as the explicit learning group were asked to write down the regular sequence and to complete a recognition test and a sequence production task. In the recognition test, subjects were presented with 24 four-letter strings composed of the same letters used in the experiment, and asked to determine whether these strings were part of the repeating regular sequence (one third was part of it). In the sequence production task, we adopted the process dissociation procedure (Jacoby, 1991, 1998) to identify explicitly learned sequence parts. Subjects were asked to produce eight-letter sequences under an inclusion and an exclusion condition. In the inclusion condition they were to type the repeating regular sequence, whereas in the exclusion condition they were to avoid typing it. The idea was that participants without explicit knowledge of the regular sequence should have trouble discriminating between these constraints, and therefore, would produce similar sequences in both conditions, whereas subjects with explicit sequence knowledge should have no problem following the instructions (see also Destrebecq & Cleeremans, 2001; Schlaghecken, Stürmer, & Eimer, 2000). Based on the criterion of better-than-chance performance in all three tasks, two participants from the implicit learning group were excluded from further analyses. Both subjects noticed the presence of the sequence and were able to recall two four-letter strings that together formed the complete regular sequence. They showed better than chance performance in the recognition test ($Pr = .25$, $\chi_{(\alpha = .05, df = 2)}^2 = 18.00$ and $Pr = .19$, $\chi_{(\alpha = .05, df = 2)}^2 = 6.75$, respectively; see also section data analyses). Additionally, they produced the regular sequence in 100% of cases in the inclusion condition of the sequence production task and were able to avoid it in the exclusion condition (that is, they produced no five-, six-, seven-, and eight-letter strings of the regular sequence).

EEG Recording

Subjects were seated in a dimly lit, electrically shielded, and sound-attenuated room. While performing the modified 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 for the EEG recordings. 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 k Ω .

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 subjects produced a timeout. Selection of the time windows for ERP analyses was based on previous studies and on visual inspection of the waveforms.

For analyzing the data from the recognition test, we used the *Pr* measure as described by Snodgrass and Corwin (1988). *Pr* is computed as hit rate minus false alarms rate. Data from free recall, recognition test, and sequence production task were compared to chance level.

Behavioral and ERP data were analyzed using repeated measures analyses of variance (ANOVAs) with an alpha level of .05. The Greenhouse–Geisser correction for nonsphericity was used whenever appropriate and epsilon-corrected *p* values are reported together with uncorrected degrees of freedom and Greenhouse–Geisser epsilon values.

We restricted the statistical analyses of the ERP data to the scalp electrodes that showed the maximal effect or to the electrodes that are normally used to describe the particular effect. To examine the temporal development of ERP components, we divided the experiment into four bins. For topographical analyses, data were normalized using the vector scaling procedure as described by McCarthy and Wood (1985).

For the purpose of the linear regression analysis, EEG data were interpolated. The number of trials in the reaction time data allowed us to form 12 bins over the course of the experiment each containing a maximum of 64 correct responses to regular stimuli (explicit group: mean = 55.35, implicit group: mean = 56.74). Due to the low number of deviant stimuli (96), we were only able to form four reliable bins in the EEG data containing a maximum of 24 responses to deviants (explicit group: mean = 20.87, implicit group: mean = 20.19). To ensure that there was an equal number of bins in reaction time and EEG data for the regression analysis, mean values for the missing bins were estimated by using a window of 24 trials that overlapped between bins, that is, trials 1 to 24 formed one bin, trials 9 to 32 formed the next, and so on.

In addition to the two subjects from the implicit group (see above), one subject from the explicit group had to be excluded from the analyses because of technical artifacts during EEG recording. Consequently, all

statistical analyses were based on 18 participants in the implicit and 19 participants in the explicit group.

RESULTS

Behavioral Data

Both groups learned the sequential structure of the material as reflected in reliably prolonged reaction times for random compared to regular sequences (see Figure 1A). An ANOVA with the between-subjects factor group (explicit, implicit) and the two within-subjects factors stimulus type (regular stimuli from the second half of each block, randomized stimuli) and block (block 1, block 2) shows that reaction times in the explicit group were shorter than those in the implicit group [main effect for group, $F(1, 35) = 4.11, p = .05$]. Reaction times to stimuli from random sequences were longer than those to stimuli from regular sequences [main effect for stimulus type, $F(1, 35) = 157.97, p < .0001$] and these learning effects were larger in the second half of the experiment than in the first [main effect for block, $F(1, 35) = 39.89, p < .0001$]. Reaction time gains (random vs. regular stimuli) due to sequence learning were larger for explicit versus

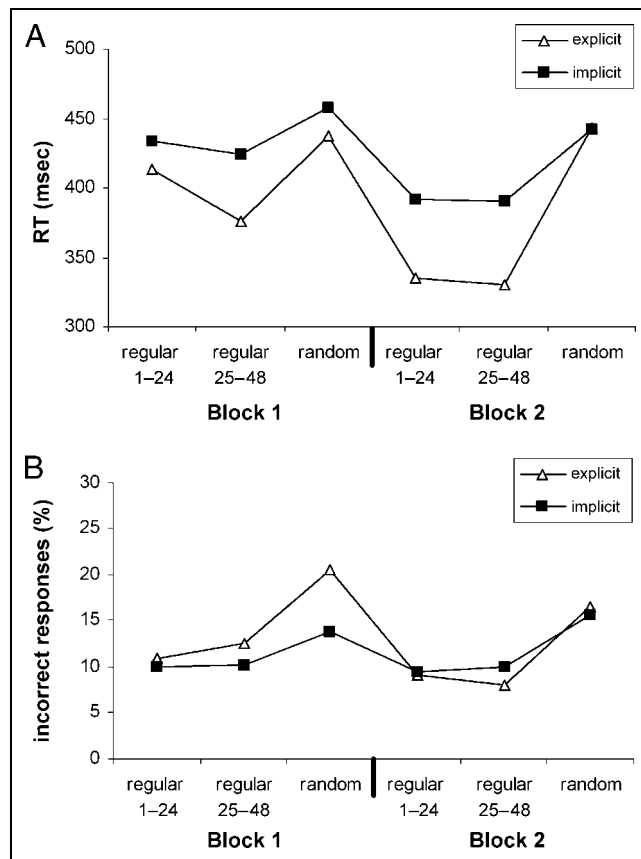


Figure 1. (A) Mean reaction times to correct responses for regular and random stimuli and for both learning groups. (B) Error rates for regular and random stimuli and for both learning groups. Irregular sequences are not included in these figures.

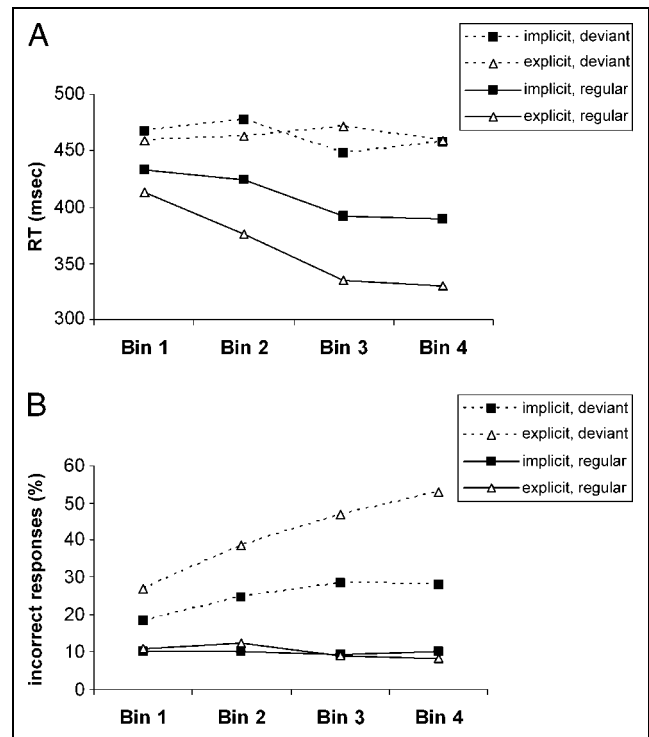


Figure 2. (A) Mean reaction times to correct responses for regular and deviant stimuli and for both learning conditions as a function of bin. (B) Error rates for regular and deviant stimuli and for both learning conditions as a function of bin. Random sequences are not included in these figures.

implicit learners [interaction between stimulus type and group, $F(1, 35) = 20.43, p < .0001$], and reaction times in block 2 were faster than those in block 1 for stimuli from regular sequences [interaction between stimulus type and block, $F(1, 35) = 28.32, p < .0001$]. The three-way interaction between group, stimulus type, and block was also significant [$F(1, 35) = 6.01, p < .02$].

Correct responses to stimuli from regular sequences became faster over the course of the experiment, whereas correct responses to deviant stimuli from irregular sequences did not show this pattern (see Figure 2A). To illustrate this effect, we divided the experiment into four bins, each containing 24 sequences. An ANOVA with factors group (explicit, implicit), stimulus type (regular stimuli, deviants), and bin (1, 2, 3, 4) shows that reaction times to deviants were longer than reaction times to regular stimuli [main effect for stimulus type, $F(1, 35) = 142.02, p < .0001$], and also that reaction times became faster over the course of the experiment [main effect for bin, $F(3, 105) = 26.95, p < .0001, \epsilon = .81$]. This learning effect was larger for explicit learners [interaction between stimulus type and group, $F(1, 35) = 12.66, p = .0011$]. Furthermore, there was an interaction between stimulus type and bin [$F(3, 105) = 20.27, p < .0001, \epsilon = .85$] and an interaction between stimulus type, bin, and group [$F(3, 105) = 7.50, p = .0004, \epsilon = .85$], indicating that the reaction times to regular stimuli

became faster during the experiment, and especially so for explicit learners.

To examine the extent to which learning was also visible in the error rates, we conducted the same analyses for the performance data. An ANOVA with the between-subjects factor group (explicit, implicit) and the two within-subjects factors stimulus type (regular stimuli from the second half of each block, randomized stimuli) and block (block 1, block 2) shows that there were more errors in the first half of the experiment than in the second half [main effect for block, $F(1, 35) = 4.24, p = .0470$] and more errors to random than to regular stimuli [main effect for stimulus type, $F(1, 35) = 44.15, p < .0001$], which reflects learning of the regular sequence (see Figure 1B). Additionally, there was an interaction between block and group [$F(1, 35) = 9.79, p = .0035$]. Contrasts showed that this is due to less errors in the second than in the first half for the explicit group [$F(1, 18) = 11.36, p = .0034$], which was not the case for the implicit group ($p = .41$).

An ANOVA with factors group (explicit, implicit), stimulus type (regular stimuli, deviants), and bin (1, 2, 3, 4) reveals that explicit subjects made more errors than implicit subjects [main effect for group, $F(1, 35) = 8.67, p = .0057$] and that there were more errors to deviant than to regular stimuli [main effect for stimulus type, $F(1, 35) = 110.92, p < .0001$]. Furthermore, the proportion of errors increased with bins [main effect for bin, $F(3, 105) = 13.18, p < .0001, \epsilon = .8171$]. The performance difference between regular and deviant stimuli was larger for the explicit than for the implicit group [interaction between group and stimulus type, $F(1, 35) = 13.68, p = .0007$] and it developed during the experiment [interaction between bin and stimulus type, $F(3, 105) = 22.47, p < .0001, \epsilon = .9394$]. The three-way interaction between group, bin and stimulus type was also significant [$F(3, 105) = 5.3, p = .0024, \epsilon = .9394$], reflecting the fact that erroneous responses to deviant stimuli increased over the course of the experiment, whereas errors to regular stimuli did not (see Figure 2B) and that this pattern was more pronounced for the explicit group.

ERP Data

The ERN/Ne and Pe

As can be seen in Figure 3A, which shows response-locked ERP waveforms elicited by correct and erroneous responses, erroneous responses elicited a pronounced ERN/Ne with maximum amplitude at Cz. An ANOVA with the factors group (explicit, implicit), stimulus type (regular, deviant), and response (incorrect, correct) in the ERN/Ne time window (0–100 msec) revealed that the mean amplitude of incorrect responses was more negative than that for correct responses [main effect for response, $F(1, 35) = 46.60, p < .0001$] and that mean

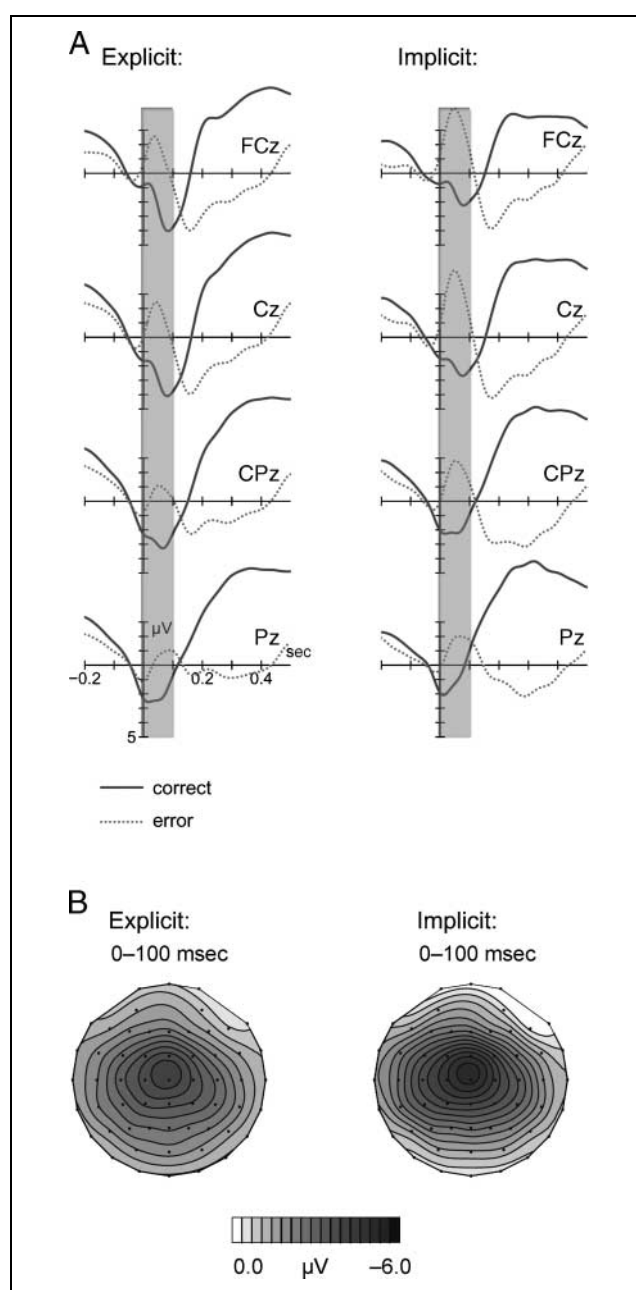


Figure 3. (A) Response-locked ERP waveforms elicited by correct and erroneous answers at electrode sites FCz, Cz, CPz, and Pz, displayed separately for implicit and explicit learners. (B) Topographic difference maps of the ERN/Ne for implicit and explicit learners (incorrect – correct answers) in the time window 0–100 msec.

amplitudes were smaller for implicit than for explicit subjects [main effect for group, $F(1, 35) = 4.60, p = .0390$]. No effects involving the factor stimulus type were found for ERN/Ne amplitude.

Topographic maps of the ERN/Ne for implicit and explicit learners (correct – incorrect answers) are depicted in Figure 3B. The topography of the ERN/Ne is highly similar for explicit and implicit learners. An ANOVA with factors group (explicit, implicit), anterior–posterior (frontal, central, parietal, and occipital electrode sites),

and lateralization (left, middle, right) confirmed that there was neither a main effect ($p = .82$) nor significant interactions involving the factor group.

The ERN/Ne was followed by a Pe, with a maximum at central recording sites. Mean amplitude at Cz in the Pe time window (120–220 msec) was larger for erroneous than for correct responses [main effect for response, $F(1, 35) = 27.07, p < .0001$] and there was no difference between the two groups.

The N2b

An ANOVA with the factors group (explicit, implicit), stimulus type (regular, deviant), and bin (1, 2, 3, 4) revealed that the mean amplitude in the N2b range (220–320 msec) was significantly more negative for deviant than for regular stimuli at electrode FCz [main effect for stimulus type, $F(1, 35) = 25.57, p < .0001$]. As apparent from Figure 4A, which shows the ERPs elicited by regular and deviant stimuli at four midline electrode sites, the N2b to deviants was most pronounced at electrode site FCz. Additionally, we found an interaction between stimulus type and bin [$F(3, 105) = 3.84, p = .0152, \epsilon = .89$]. In contrast to our expectations, the factor group failed to reach significance ($p = .12$). Although there was no interaction with the factor group, based on the clear between-group differences in the learning effects, we examined the two experimental groups in separate ANOVAs. These analyses showed that there was a change in mean amplitude for deviants in the implicit condition. In this condition, the N2b became more negative over bins [$F(3, 51) = 3.42, p = .03, \epsilon = .83$], whereas the N2b to regular stimuli did not vary across bins. In the explicit condition, neither deviant nor regular stimuli were modulated by the bin factor [$F(3, 54) < 1$; see Figure 5]. Because the changes in mean N2b amplitude to deviant events as well as response times to regular events for the implicit group both followed a linear trend [$F(1, 17) = 11.35, p = .0036$ and $F(1, 17) = 64.13, p < .0001$, respectively], we tried to assess whether there was an interrelation between the two variables. We conducted a linear regression analysis and found a significant relation [$R^2 = .91, F(1, 11) = 46.94$]. The faster the reaction times to regular stimuli, the larger the N2b component, that is, the smaller the absolute amplitude to deviant stimuli (see Figure 6). This relation was not found for the explicit group [$R^2 = .19, F(1, 11) = 0.39$].

The lack of a similar relationship between response time and N2b to deviant events for the explicit group might be due to faster sequence learning in that condition. This would also be consistent with the pattern of results we obtained in the response time analysis. To further explore this possibility, we analyzed the time course of the N2b to deviants within the first bin in the explicit group by subdividing these trials into three parts (bin1_1, bin1_2, bin1_3; see Figure 7). An ANOVA with factors stimulus type (regular, deviant) and bin (bin1_1,

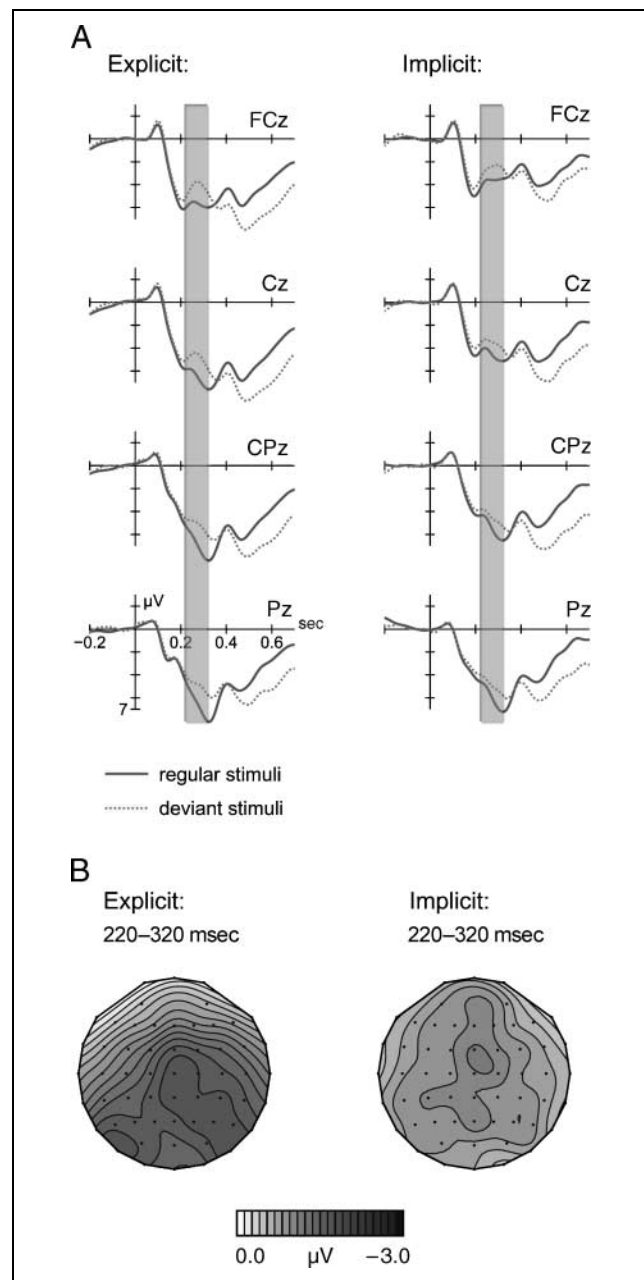


Figure 4. (A) Stimulus-locked N2b waveforms elicited by regular and deviant stimuli at electrode sites FCz, Cz, CPz, and Pz, displayed separately for implicit and explicit learners. (B) Topographic difference maps of the N2b for implicit and explicit learners (deviants – regulars) in the time window 220–320 msec.

bin1_2, bin1_3) showed a main effect for stimulus type [$F(1, 16) = 4.37, p = .05$] and an interaction between stimulus type and bin [$F(2, 32) = 4.38, p = .02, \epsilon = .84$]. The latter interaction reflects the fact that a difference between regular and deviant stimuli was present in bin1_3 [$F(1, 16) = 11.67, p = .0035$], but not in the other two bins.

Topographic maps of the N2b for implicit and explicit learners (regulars – deviants) show a broad scalp distribution with a central maximum in both groups (see

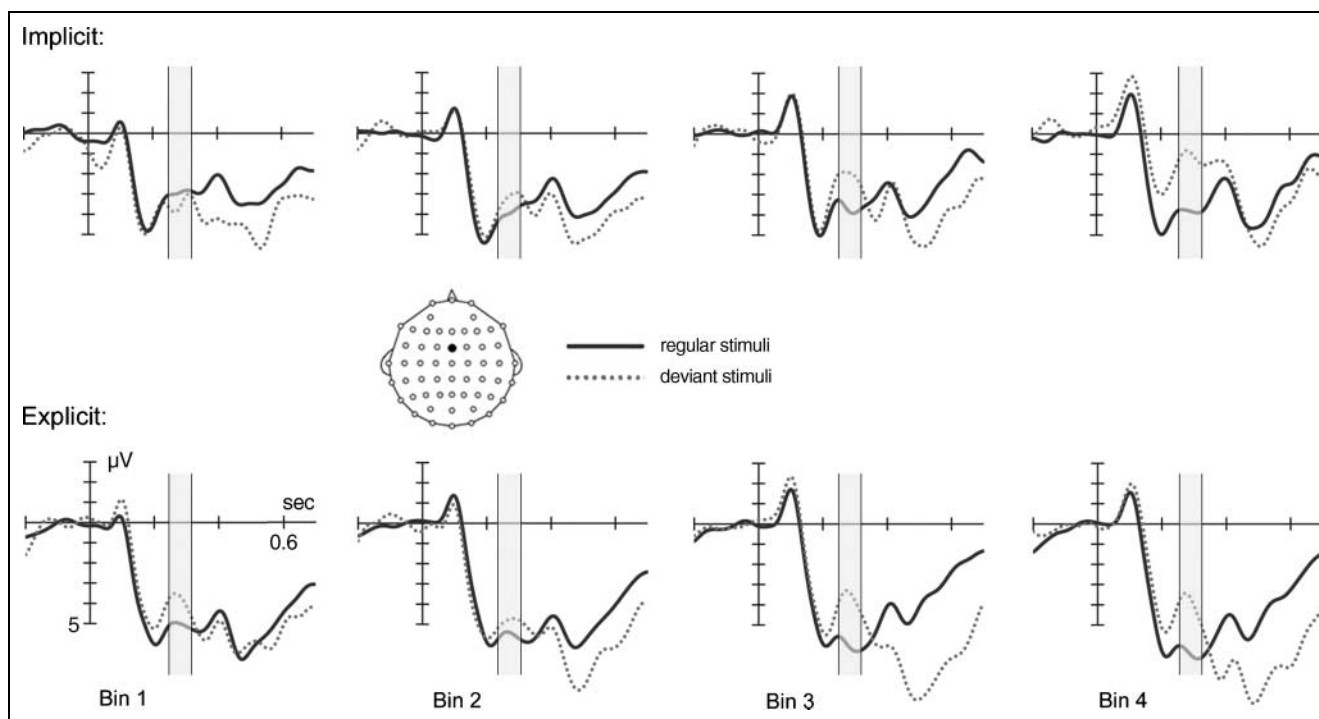


Figure 5. Development of stimulus-locked N2b waveforms elicited by regular and deviant stimuli over the course of the experiment at electrode site FCz, displayed separately for implicit and explicit learners.

Figure 4B). An ANOVA with factors group (explicit, implicit), anterior–posterior (frontal, central, parietal, occipital), and lateralization (left, middle, right) confirmed that there was no significant main effect ($p = .94$) and no significant interaction including the group factor.

To compare the scalp topography of the N2b and the ERN/Ne, both components were subjected to an ANOVA with factors component (ERN, N2b), anterior–posterior (frontal, central, parietal, occipital), and lateralization (left, middle, right). There were main effects for anterior–posterior [$F(3, 108) = 16.70, p < .0001, \epsilon = .5351$] and for lateralization [$F(2, 72) = 12.74, p < .0001, \epsilon = .8024$].

The interactions between component and anterior–posterior [$F(3, 108) = 10.33, p < .0001, \epsilon = .6821$], component and lateralization [$F(2, 72) = 5.10, p = .0120, \epsilon = .8621$], anterior–posterior and lateralization [$F(6, 216) = 9.77, p < .0001, \epsilon = .6639$], and between component, anterior–posterior, and lateralization [$F(6, 216) = 3.01, p = .0216, \epsilon = .6454$] were significant. Contrast showed that this was due to the fact that the ERN/Ne was larger at central midline electrodes [$F(1, 36) = 4.07, p = .0216$] and the N2b was more pronounced than the ERN/Ne at occipital electrodes [$F(1, 36) = 6.83, p = .0130$].

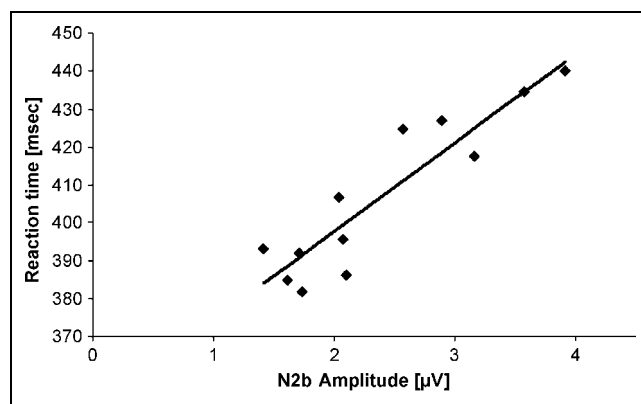
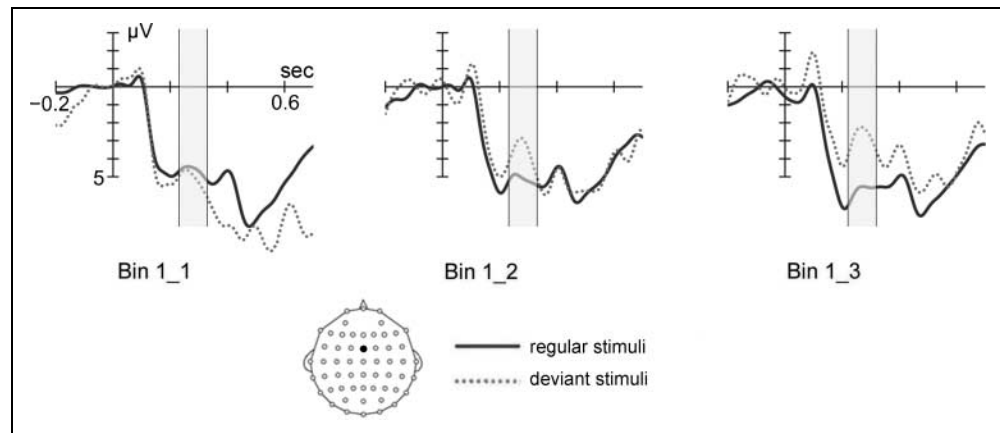


Figure 6. Linear regression for implicit learning condition: The faster the reaction times to regular stimuli, the smaller the mean amplitude to deviant stimuli.

The P3b

An ANOVA with factors group (explicit, implicit), bin (1, 2, 3, 4), and stimulus type (regulars, deviants) in the time window from 450 to 550 msec at the Pz electrode showed a main effect for stimulus type [$F(1, 35) = 20.83, p < .0001$]. The interactions between stimulus type and bin and between stimulus type, bin, and group were only marginally significant ($p = .09$ and $p = .14$, respectively). On the basis of the latter analysis and the clear behavioral differences between the two groups, we examined the two experimental groups in separate ANOVAs. There was a main effect for stimulus type for both groups [$F(1, 18) = 23.55, p = .0001$ and $F(1, 17) = 7.13, p = .02$, respectively]. Only for explicit learners did we find an interaction between stimulus type and bin [$F(3, 54) = 3.97, p = .02$] that was due to larger

Figure 7. Development of the stimulus-locked N2b component elicited by deviant stimuli in bin 1 of the experiment at electrode site FCz for explicit learners.



P3b components for deviants than for regulars in bin 3 [$F(1, 18) = 25.40, p < .0001$] and bin 4 [$F(1, 18) = 6.95, p < .02$].

The Late Posterior Component

In addition to the N2b, we found a late posterior component to deviant stimuli in the time window from 280 to 360 msec. In contrast to the fronto-central maximum of the N2b, this negativity had a clear maximum at parietal recording sites, measured at Pz. An ANOVA with factors group (explicit, implicit), stimulus type (regular, deviant), and bin (1, 2, 3, 4) revealed that the mean amplitude for deviant stimuli was more negative than that for regulars [main effect for stimulus type, $F(1, 35) = 27.93, p < .0001$]. Moreover, it revealed a main effect for bin [$F(3, 105) = 9.54, p < .0001, \epsilon = .78$] and an interaction between stimulus type and bin [$F(3, 105) = 6.61, p = .0019, \epsilon = .70$]. There was no main effect for group ($p = .71$). Further ANOVAs showed that the interaction was due to a gradually developing negativity to deviants over the course of the experiment that was present in both groups [explicit group: $F(3, 54) = 5.82, p = .0086, \epsilon = .60$; implicit group: $F(3, 51) = 4.57, p = .01, \epsilon = .85$]. This development followed a linear trend in both groups [explicit group: $F(1, 18) = 14.65, p = .0012$; implicit group: $F(1, 17) = 12.50, p = .0025$], whereas no such pattern was obtained for regular stimuli (see Figure 8A).

DISCUSSION

The main goal of this study was to investigate error monitoring processes during implicit and explicit sequence learning, that is, we wanted to examine the role of errors people are unaware of on learning and compare it to the effect of errors people are aware of. In more detail, we examined whether perceived and committed errors possess the status of unfavorable events and by this are used as feedback signals that mediate learning even under

implicit learning conditions. In order to do so, we conducted an SRTT under an explicit and implicit learning condition. Subjects in both conditions displayed slower reaction times to random than to regular sequences. Additionally, correct responses to stimuli from regular sequences became faster over the course of the experiment, whereas reaction times to deviant stimuli from irregular sequences showed no such decrease. Although both effects were larger for the explicit group, they were also present for the implicit group. Thus, we infer that sequence learning took place under both conditions, albeit to a larger extent in the explicit group.

Learning of the regular sequence was also visible in the accuracy data. All in all, subjects made fewer errors in response to stimuli from the regular sequence than from random sequences. Additionally, errors to deviant stimuli increased from the first to the second half of the experiment, whereas errors to regular stimuli did not show this pattern (see Figure 2B). This might also partly be due to a speed-accuracy tradeoff across regular and deviant events. The more the regular sequence is learned, the faster the responses to regular stimuli. At the same time, deviant stimuli are less expected and that makes it harder to respond correctly to them. This pattern was more pronounced for the explicit group, which might reflect better learning in that group.

Erroneous responses elicited an ERN/Ne with maximum amplitude at Cz for explicit as well as implicit learners, signaling the detection of a committed error. Furthermore, the mean amplitude for the explicit group was smaller than that for the implicit group. A reason for this could be that the explicit learning group had to perform two tasks, namely, applying the stimulus-response mapping rule and detecting and learning the regular sequence, whereas the implicit group had to perform only the former task. This leads to enhanced time pressure and also may have compromised the representation of the stimulus-response mappings in the explicit group, which both are known to reduce the ERN/Ne (Coles, Scheffers, & Holroyd, 2001). This is supported by the finding that the overall error rate was larger in the explicit group. In

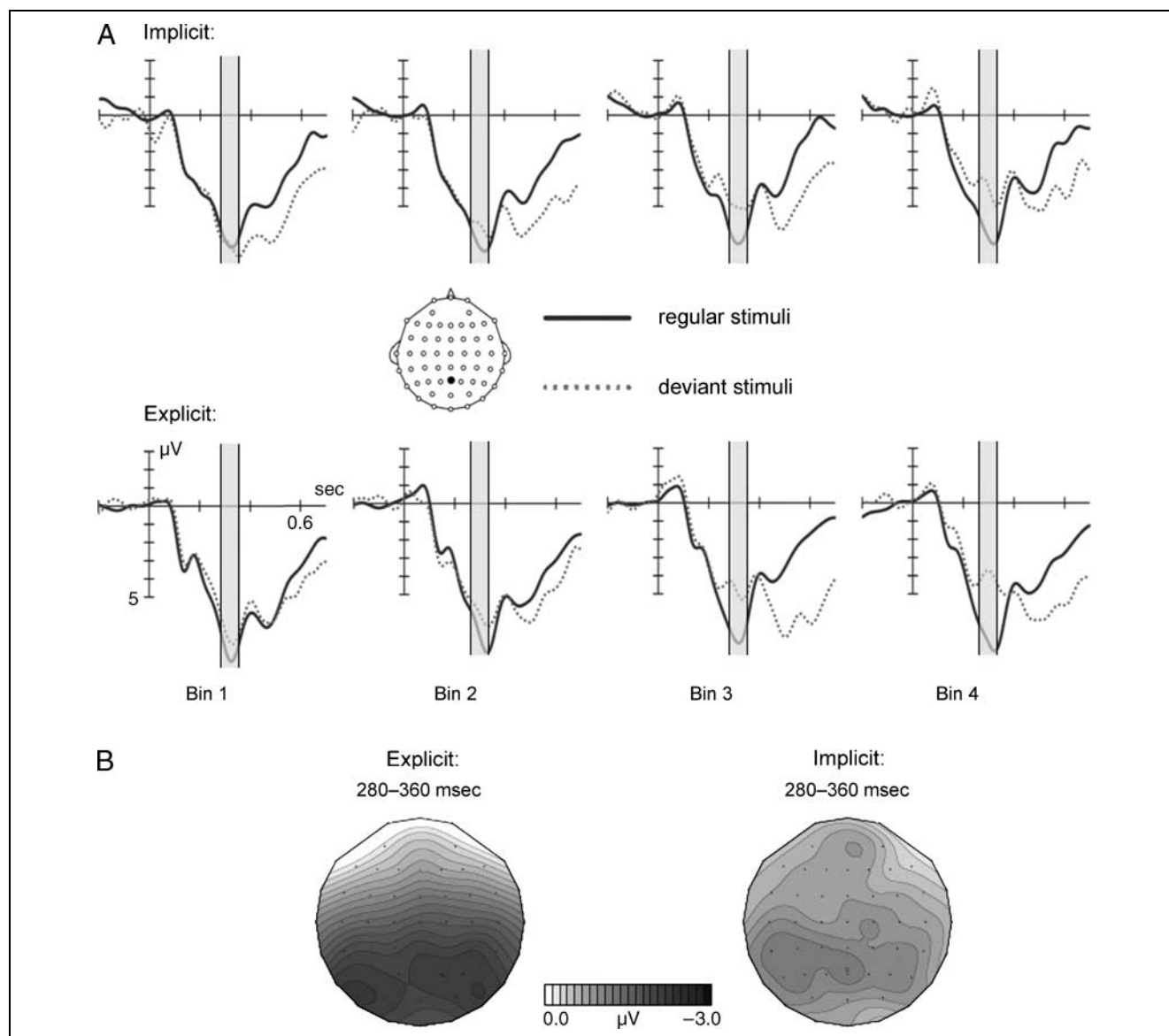


Figure 8. (A) Development of the stimulus-locked late posterior component elicited by regular and deviant stimuli over the course of the experiment at electrode site Pz, displayed separately for implicit and explicit learners. (B) Topographic difference maps of the late posterior component for implicit and explicit learners (deviants – regulars) in the time window 280–360 msec.

a similar vein, Gehring et al. (1993) showed that ERN amplitude is reliably smaller for speed as compared to accuracy instructions (see also Yeung, Botvinick, & Cohen, 2004; Falkenstein et al., 1990). Because the ERN/Ne topography did not differ between groups, the component seems to be generated by the same brain mechanisms in both cases. No effects of stimulus type were found for ERN/Ne amplitude; a finding that cannot be explained by the conflict monitoring hypothesis. Because there is more response conflict to deviants than to regular stimuli, as indexed by a larger error rate to deviants, according to the conflict monitoring hypothesis, the ERN/Ne should be larger for responses to deviant stimuli than for those to regular stimuli, which was not the case.

Using a similar sequence learning experiment, Rüsseler, Kuhlicke, et al. (2003) found a larger ERN/Ne in explicit than in implicit learners. They concluded that explicit learners searched for the sequence embedded in the stimulus material to be able to anticipate the upcoming response, and that this requires holding an ongoing model of the sequence in working memory. Thus, for explicit but not implicit learners, an error would be a relevant event with respect to sequence learning. This discrepancy to our results might be due to differences in the experimental design of the two studies. In the study by Rüsseler, Kuhlicke, et al., stimuli were flanked by two irrelevant letters to induce response conflict. Thus, enhanced response conflict may have enhanced the error relevance in the explicit group in the latter study as

compared to our study, in which there was no response conflict due to irrelevant flankers. Furthermore, the study by Rüsseler, Kuhlicke, et al. aimed to examine the influence of learning mode (explicit or implicit) on the ERN/Ne. For this purpose, regular and random sequences were compared. However, there were no irregular sequences with deviant letters as in the present study.

The ERN/Ne was followed by a Pe that was the same for both learning groups. According to Nieuwenhuis et al. (2001), who found a larger Pe for conscious than for unconscious errors in an antisaccade task, the Pe amplitude is sensitive to error awareness. If this holds true, the same Pe amplitude in both groups may reflect the fact that subjects from both groups have been equally aware of their committed errors. This finding emphasizes the importance of introducing a different error type that subjects are not necessarily aware of to address the question of whether errors subjects are unaware of can influence learning.

Consistent with our prediction, that deviants acquire the status of perceived errors, we found a larger N2b for deviant stimuli. This component was present for the implicit and the explicit learning groups and its topography did not differ between groups. This means that regardless of whether subjects learn a sequence explicitly or implicitly, deviants are used as feedback signals that mediate sequence learning. Moreover, for the implicit group, the N2b gradually increased during the course of the experiment. This effect cannot be explained by reference to the different response latencies for deviant and standard stimuli because no such effect was visible when the ERP waveforms obtained for standard stimuli were compared with the ERPs measured in the random blocks, although reaction times were considerably slower in the latter case. Although we found no topography difference for the two groups and no significant interaction with factor group in the overall design, for the implicit group there was a linear relationship between the acceleration of response times to regular stimuli and the development of the N2b to deviants; the faster the reaction times became, the more negative was the N2b amplitude to deviant stimuli. No such effect was obtained for the explicit group. This result might reflect the fact that the N2b is related to a gradual development of knowledge about the sequence structure and accompanied by the formation of expectancies about the next stimulus. The expected and actual stimulus are then compared, and the event is evaluated on the dimension “better or worse than expected” to avoid future prediction errors, and thus, enable learning. The absence of a similar relationship for the explicit group is due to faster sequence learning in that condition. In fact, when we enhanced the temporal resolution of the time-course analyses by subdividing the bins into smaller parts, there was a developing negativity in the first quarter of the experiment for explicit learners, too. Taken together, we found that not only do error monitoring process take

place in implicit learning, but they also might play a crucial role in the process of learning itself. Errors are detected and used as feedback signals that allow the build-up of expectations, and this may be one of the basic mechanisms that drives learning, even when people learn implicitly, and thus, are not aware of errors.

Previous ERP studies on implicit sequence learning have also reported an enhanced N2b approximately 250 msec after stimulus presentation that was larger for deviant stimuli interspersed in a regular stimulus sequence (Rüsseler, Hennighausen, et al., 2003; Rüsseler & Rösler, 2000; Schlaghecken et al., 2000; Eimer et al., 1996). Eimer et al. (1996) found an N2b after an incidental learning phase. However, in their study, participants who reported that they were unaware of a structured sequence showed no reliable N2b effect. The authors inferred that the degree to which participants became aware of the sequence structure was reflected in N2b amplitude. In other sequence learning studies, the N2b was present only for subjects who were able to verbally reproduce parts of the sequence after performing the SRTT, and it was therefore concluded that the N2b seems to be related to a conscious detection of a stimulus deviation (Rüsseler, Hennighausen, et al., 2003; Rüsseler & Rösler, 2000). The present results, however, are not consistent with the view that explicit knowledge is required for the elicitation of the N2b. Because we controlled for the presence of explicit knowledge in the implicit learning condition, our results support the view that deviants acquire the status of perceived errors and initiate dopamine-related processes that mediate sequence learning.

On the basis of these findings, we propose that the underlying mechanism for deviant processing might be the same as for error processing in reinforcement learning tasks, which is reflected in modulations of the response and feedback ERN in probabilistic learning tasks (Holroyd & Coles, 2002). By this, our results favor a unified framework for N2b and ERN/Ne. When the sequence is learned (implicit or explicit), expectancies about the next stimulus can be formed. In case of a deviant stimulus, these expectancies are not confirmed (i.e., the outcome is worse than expected) and this may generate the N2b in a similar way as the ERN/Ne to committed errors in probabilistic learning tasks. This view is further supported by the finding that latency and scalp distribution of the N200 and the feedback ERN are comparable (Holroyd, 2003) and by studies that investigated the neural sources of the N200 and ERN/Ne and found that the two dipoles lie very close together in the medial frontal cortex (Nieuwenhuis et al., 2001). When comparing ERN/Ne and N2b topography, we found that the ERN/Ne was larger than the N2b at central midline electrodes and smaller at occipital electrodes. A possible explanation for this might be that ERN/Ne and N2b reflect the same error monitoring process (detection of an expectation mismatch), but are modified by

the particular demands of what is monitored. In the case of the ERN/Ne, incorrect motor responses, and in the case of the N2b, deviant visual stimuli, cause an expectancy mismatch. This would be in line with neuropsychological evidence for a functional specialization within the ACC for different types of information (Banich et al., 2000) and different response modalities (Swick & Turken, 1999).

The N2b is usually followed by an enlarged P3b, elicited by deviant, unexpected, or surprising events. It is thought to mirror conscious processing of deviant stimuli and is often linked to updating of working memory representations (Mecklinger & Ullsperger, 1995; Donchin & Coles, 1988). In line with this view, we found an interaction between stimulus type and bin in the P3b time window only for explicit learners, which was due to a larger P3b for deviants than for regulars in bins 3 and 4. Thus, in this component different processing of deviant stimuli for the two learning conditions can be seen. Whereas the N2b might reflect the detection of deviants, the P3b might reflect conscious processing, such as evaluating incoming information and updating contextual representations in working memory (cf. Donchin & Coles, 1988).

In addition to the ERN/Ne and N2b components, we found a late posterior negativity to deviant stimuli that was maximal at parietal recording sites. This component also developed over the course of the experiment in both learning conditions. In analogy to the N400 component in studies on language (Kutas & Federmeier, 2000; Federmeier & Kutas, 1999) and music processing (Gunter, Schmidt, & Besson, 2003), this negativity might reflect the cognitive effort that is necessary to integrate a deviant stimulus into the context of a developing representation of a to-be-learned sequence. The more the sequential regularities are learned (explicitly or implicitly), the harder it is to reconcile deviant stimuli with the regular sequence.

In sum, our main goal was to investigate the role of error monitoring processes during implicit learning. We showed that not only does error monitoring take place during implicit learning, but that it also influences sequence learning. Deviant events acquire the status of perceived errors during explicit as well as implicit learning. While performing the task, expectations about upcoming events are generated and evaluated on the dimension “better or worse than expected.” The accuracy of this process improves with learning and this is reflected in gradual increases in N2b amplitude as a function of learning. Interestingly, this implies that perceived errors contribute to sequence learning even if subjects are not aware of them. Additionally, our findings also imply that the processing of committed and perceived errors (as shown by the ERN/Ne and N2b, respectively) may rely on the same neural mechanism albeit specialized for different input. The human brain learns by evaluating the results of our actions and this learning is driven by reward-related information carried

to the ACC, initiating the cognitive control of motor and learning behavior.

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