Explicit and Implicit Learning of Event Sequences: Evidence From Event-Related Brain Potentials

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Event-related brain potentials (ERPs) were recorded during a serial reaction time (RT) task, where single deviant items seldom (Experiment 1) or frequently (Experiment 2) replaced 1 item of a repeatedly presented 10-item standard sequence. Acquisition of sequence knowledge was reflected in faster RTs for standard as compared with deviant items and in an enhanced negativity (N2 component) of the ERP for deviant items. Effects were larger for participants showing explicit knowledge in their verbal reports and in a recognition test. The lateralized readiness potential indicated that correct responses were activated with shorter latencies after training. For deviant items, participants with explicit knowledge showed an initial activation of the incorrect but expected response. These findings suggest that the acquisition of explicit and implicit knowledge is reflected in different electrophysiological correlates and that sequence learning may involve the anticipatory preparation of responses.

A central issue in the psychology of learning concerns the question of whether the acquisition of knowledge is accomplished by an unitary mechanism or whether functionally different types of learning have to be distinguished. In recent years, the distinction between implicit and explicit learning has generated considerable interest. The term *implicit learning* was introduced by Reber (1967) to denote a type of learning that is assumed to occur without intention to learn and without concurrent awareness of the underlying structure of the to-be-learned material (see Reber, 1989; Seger, 1994, for reviews). A paradigm that has become rather popular in the study of implicit learning is the serial reaction time (RT) task introduced by Nissen and Bullemer (1987). In this task, on each trial a stimulus is presented in one out of four possible locations arranged horizontally in a visual display, and the task of the participant is to press one of four response buttons that corresponds to the location of the stimulus. When the sequence of stimulus locations follows a repeating pattern, RTs typically decrease with practice markedly faster than in a condition in which participants respond to a random sequence. When the repeating sequence is unexpectedly switched to a random sequence after prolonged training, there is usually a

marked increase in RTs. Performance increments in this task have sometimes been observed even for participants who were not able to verbalize the sequence after training and who performed poorly in a prediction test of the sequence. This suggests that participants can acquire procedural knowledge about sequential structures incidentally and in the absence of conscious knowledge about the sequence (e.g., Cohen, Ivry, & Keele, 1990; Curran & Keele, 1993; Willingham, Nissen, & Bullemer, 1989).

In the present study, we focus on two controversial issues in the implicit-learning literature. The first issue concerns the question of whether sequence learning is actually unconscious. The second question is which role both motor and perceptual processes play with respect to learning in serial RT tasks. Two experiments are reported in which we made an attempt to further elucidate these issues by combining behavioral measures with electrophysiological indicators of participants' brain activity while they were performing a serial RT task.

Sequence Learning and Conscious Knowledge

The claim that sequence learning can occur without concurrent awareness of sequential structures has been based on dissociations between performance increments in the serial RT task and performance on measures of conscious knowledge. First, reliable performance increments in serial RT tasks have been reported for subgroups of participants who were not able to verbalize the sequence structure after training or who had not even noticed that there was a structure (e.g., Cohen et al., 1990; Curran & Keele, 1993; Lewicki, Hill, & Bizot, 1988; Reed & Johnson, 1994; Stadler, 1993; Willingham et al., 1989; Willingham, Greeley, & Bardone, 1993). Second, participants showed learning in serial RT tasks even if their performance in a subsequent prediction task in which they had to predict on each trial at which location the next stimulus would appear was

not superior to that of control participants who had been presented with a random sequence (e.g., Cohen et al., 1990; Hartman, Knopman, & Nissen, 1989; Stadler, 1989; Willingham et al., 1989). Third, sequence learning appears to be spared in amnesic patients suffering from Korsakoff's and Alzheimer's disease who show severe impairments of conscious episodic memory (Nissen & Bullemer, 1987; Nissen, Willingham, & Hartman, 1989). These findings suggest that the acquisition of skills does not necessarily start with the encoding of declarative rules (cf. Anderson, 1987) but that under certain conditions, procedural knowledge can be acquired independently from declarative knowledge (Willingham et al., 1989). Moreover, findings with neurological patients as well as recent experiments with functional brain imaging techniques like positron emission tomography have been interpreted as evidence that procedural learning may be mediated by brain structures that are distinct from the structures underlying the acquisition of conscious, declarative knowledge (e.g., Grafton et al., 1992; Schacter, 1994; Squire, 1986, 1994). For example, Grafton et al. (1992) found that procedural learning of motor skills involves modifications in various brain areas that are also involved in the execution of motor skills, including subcortical structures like the basal ganglia.

Recently, however, there has been some controversy about whether sequence learning is really unconscious (e.g., Perruchet et al., 1990; Perruchet, 1994; Shanks & St. John, 1994). In particular, Perruchet and Amorim (1992) have questioned the usefulness of prediction tasks as a measure of conscious sequence knowledge. They noted that in previous studies in which dissociations were reported between performance in serial RT tasks and prediction accuracy, participants had not been explicitly instructed to generate the same sequence as in the serial RT task. From this and other methodological arguments, Perruchet and Amorim (1992) concluded that conscious knowledge about sequential structures can be better assessed with recognition and free-recall tasks. In Perruchet and Amorim's recognition task, participants had to decide whether four-item sequences were part of the previously presented sequence or not. In their free-recall task, participants were instructed to reproduce the previously delivered sequence with the same keys as in the serial RT task. Perruchet and Amorim found remarkably high correlations between RT benefits in the serial RT task and both recognition and recall of partial sequences. They concluded that learning in the serial RT task may be mediated by the acquisition of conscious knowledge about chunks of three or four successive elements.

Although these results suggest that explicit knowledge may play a more prominent role in sequence learning than was previously thought, the issue is far from being settled. First, a dissociation between explicit knowledge and RT benefits in the serial RT task has recently been reported even though a recognition task was used (Willingham et al., 1993). Second, it is far from clear whether tasks like recognition or recall are process-pure measures of explicit knowledge or whether they tap implicit knowledge as well (Cohen & Curran, 1993; Jacoby, 1991). Moreover, all arguments in favor of or against the implicit nature of sequence learning rely on correlational evidence. However, a positive correlation between the amount of explicit knowledge and performance in the serial RT task does not necessarily indicate that performance increments were mediated by conscious knowledge. It is just as possible that explicit knowledge develops in parallel with implicit knowledge or even that conscious knowledge emerges as a consequence of the acquisition of implicit knowledge.

One general problem that underlies the controversy about the implicit nature of sequence learning results from the fact that tests of explicit knowledge are usually administered after learning. Thus, any conclusions drawn from correlations between performance in the serial RT task and explicit knowledge rely on a questionable backward inference from the later test to the earlier learning phase (Shanks & St. John, 1994). It would therefore be preferable to have an on-line measure of explicit knowledge that would allow one to observe the development of conscious knowledge unobtrusively and concurrently with performance in the serial RT task. As is argued below, we considered event-related brain potentials (ERPs) as particularly suited to serve as such an on-line measure.

The Role of Motor Processes in Sequence Learning

Another controversial issue is whether participants in serial RT tasks acquire knowledge about the sequence of stimulus events or whether they learn a sequence of specific motor responses (or both). This question has been investigated by Cohen et al. (1990) with a transfer paradigm in which participants first had to respond by pressing three response keys with three different fingers, whereas in a subsequent transfer phase, they had to respond with one finger only. Despite this change of effectors, there was almost perfect transfer of the knowledge acquired during the training phase. Positive transfer despite a change in the motor characteristics of the task was also reported by Stadler (1989) in a speeded visual-search task in which the location of a target was determined by a sequence of previously presented stimuli (cf. Lewicki et al., 1988). These studies indicate that the knowledge that participants acquired did not consist of a specific sequence of low-level motor commands coupled to specific effectors. Moreover, in a study by Howard, Mutter, and Howard (1992), participants who observed only a repeating sequence showed the same response speedup in a subsequent test phase as did participants who had been overtly responding throughout the training phase. Overt responding thus appears not to be necessary for sequence learning.

However, there is also some contrasting evidence indicating that learning of a more abstract representation of a response sequence may be involved in serial RT tasks. Willingham et al. (1989; Experiment 3) had their participants respond to the color of stimuli that appeared at one of four locations. In a *perceptual group*, the sequence of colors was random, whereas the sequence of locations followed a repeating pattern. In a *response group*, the sequence of colors followed a repeating pattern, whereas the locations were determined at random. Reliable sequence learning was obtained in the response group but not in the perceptual group (cf. also Zießler, 1994). However, one problem with this result is that the instruction to respond to the colors may have distracted participants' attention from the stimulus locations, which may account for the

lack of learning in the perceptual group (cf. Cohen et al., 1990; Curran & Keele, 1993; Nissen & Bullemer, 1987).

To further complicate the picture, Fendrich, Healy, and Bourne (1991, Experiment 2) found that both motor and perceptual sequences were learned in a task in which participants entered digit sequences with a computer keypad. When the keypad was switched between acquisition and retention, both old sequences of digits associated with new response sequences and new sequences of digits associated with old response sequences produced better performance as compared with sequences in which both digits and responses were new.

ERPs as Indicators of Sequence Learning

As this brief review shows, the experimental studies conducted so far have neither provided unambiguous evidence for the assumption that RT benefits in the serial RT task are due to implicit learning, nor answered the question of which role motor processes play in sequence learning. The present experiments served the purpose of further investigating these two issues by combining behavioral measures with electrophysiological indicators of participants' brain activity. More specifically, ERPs were recorded while participants performed a modified variant of the serial RT task where in each trial one of four letters (A, B, C, or D) was presented at fixation. The letters were mapped to four different responses (left middle finger, left index finger, right index finger, and right middle finger). A standard sequence of 10 letters was constantly repeated. To assess whether participants acquired knowledge about the sequential structure of the stimuli, deviant stimuli replaced standard items at unpredictable positions in the standard sequence. Deviant stimuli were letters that were not allowed to occur at that specific position within the regular sequence. Additionally, at the end of the first and the second halves of the experiment, participants were confronted with an unpredictable sequence in which letters appeared in a pseudo-random order and the probability of each letter was equal to that in the regular sequence. Acquisition of knowledge about the sequential structure should be reflected in faster RTs for standard as compared with deviant items as well as in an increase of RTs in random blocks as compared with regular blocks.

This paradigm allowed us to compute ERPs separately for regular and deviant items. ERPs are obtained by recording the electroencephalogram (EEG) from electrodes located at different points on the scalp. EEG waveforms obtained from a large number of trials are then averaged in a way that is time locked to the presentation of a stimulus or the execution of a response. As a result of the averaging procedure, random fluctuations of the spontaneous EEG cancel each other out and ERPs indicating the processing of a given stimulus become visible. ERPs typically consist of a sequence of positive- and negative-voltage deflections that differ in their latencies, amplitudes, and scalp topography. These ERP components are labeled according to their latency or order of occurrence and according to their polarity (e.g., P300 denotes a positive-going deflection with a peak latency of about 300 ms; N200 denotes a negative-going component peaking around 200 ms poststimu-

lus). As the exact latencies of these components may vary considerably, we use the more neutral labels P3 and N2 to denote the third positive or second negative component, respectively. It is generally assumed that ERP components reflect specific patterns of neural activity mediating perceptual, cognitive, or motor processes (cf. Hillyard & Kutas, 1983).

The present research was motivated by three distinct advantages of ERPs as compared with standard chronometric measures. First, ERPs provide an on-line measure of the time course of the brain's response to a particular stimulus event. Thus, the first purpose of the present experiments was to investigate whether the acquisition of knowledge about a sequential structure was reflected in differential modulations of ERP waveforms to deviant events as compared with regular events. Previous research has shown that stimuli deviating from a previously established context may elicit specific ERP components that are missing in the case of regular stimuli. More specifically, low-probability or unexpected events elicit an enlarged P3 component that is often preceded by an enhanced N2 (see Donchin, 1982; Ritter et al., 1984; Ruchkin, Sutton, & Tueting, 1975; Squires, Donchin, Herning, & McCarthy, 1977; Squires, Wickens, Squires, & Donchin, 1976, for reviews). In these experiments, low-frequency items and high-frequency items were delivered in a continuous stream, thus making the conscious detection of deviant stimuli rather simple (oddball paradigm). By contrast, in the present experiments, stimulus deviance was defined with respect to the relative position of an item within a more complex sequence, and participants were not informed about the presence of this sequence. Thus, whether deviations from a more complex sequential structure would also produce systematic effects on the ERP waveforms is a nontrivial question. If such effects could be established, this would add further constraints to the theoretical interpretation of ERPs and could serve as a starting point for further investigations of the neurophysiological basis of sequence learning.

Secondly, if sequential knowledge is reflected in systematic modulations of ERP waveforms, one may further ask whether these modulations indicate explicit or implicit knowledge. We therefore analyzed behavioral and electrophysiological measures of sequence learning separately for subgroups of participants who either did or did not exhibit explicit knowledge about the sequence in their verbal reports and in a recognition test. As was noted above, inferences concerning the unconscious nature of sequence learning usually rely on a problematic backward inference from a later explicit test to learning processes during the preceding serial RT task (Shanks, Green, & Kolodny, 1994; Shanks & St. John, 1994). For instance, fragmentary explicit knowledge that was available during the serial RT task may be forgotten before a direct memory test is administered after training. Moreover, probing participants' conscious knowledge has the unavoidable side effect of directing their attention to the inherent structure of the standard sequence and thereby altering their subsequent strategy in the serial RT task (Shanks et al., 1994). In contrast, ERPs may serve as a nonreactive on-line measure of the development of conscious knowledge that does not depend on the participants' overt responding and that can be obtained continuously while participants perform the serial RT task. Moreover, if one could

identify a specific ERP component that would be present only in participants showing explicit knowledge about the sequence and not in participants having no explicit knowledge, this would provide important evidence that learning in these two groups involves different brain processes during the training phase.

The third reason for using ERPs was to investigate the role of motor processes in sequence learning. Therefore, brain activity was recorded above the motor cortices to compute the *lateralized readiness potential* (LRP), which is assumed to be an index of selective response preparation and activation (cf. Coles, 1989, for an overview). The LRP reflects an asymmetric lateralization of negativity that develops prior to the execution of a left-hand or right-hand motor response over the contralateral motor cortex. If the RT improvements in the serial RT task are due to the anticipation and faster preparation of motor responses, one should expect lateralizations in the LRP waveforms for standard items to occur with shorter latencies after training, thereby indicating earlier activation of correct responses. In Experiment 2, LRPs were also computed for those deviant items that required an opposite-hand response as compared with the standard item that was to be expected at that position within the sequence. If participants generate an anticipation of the next response prior to the actual presentation of the next stimulus, one should expect in the case of these deviant items an early activation of the incorrect but expected response, which only later is replaced by the activation of the correct response.

Experiment 1

Method

Participants

Sixteen paid volunteers (nine female), aged 18–45 years (mean age: 27.3 years) participated in the experiment. All participants were right-handed and had normal or corrected-to-normal vision. On the basis of the answers regarding the presence of a sequence given by the participant at the end of the first and second half of the experiment (see below), 7 participants were classified as having explicit knowledge (Group E), whereas the remaining 9 participants were classified as having implicit knowledge (Group I).

Stimuli and Apparatus

Participants were seated in a dimly lit, electrically shielded, and sound-attenuated chamber with four response buttons, one under each left and right index and middle finger. A computer screen was placed 100 cm in front of the participant's eyes and was carefully positioned so that the stimuli (presented white on gray) occurred on the participant's horizontal straight-ahead line of sight. Stimuli were uppercase letters (A, B, C, and D), which were presented in the center of the screen and covered a visual angle of approximately 1°. Each stimulus remained on the screen until a response had been given by the participant. Response latencies were recorded for each trial. The interval between the response and the presentation of the next stimulus was 500 ms.

Procedure

Participants were instructed to respond as fast as possible to the letter stimuli without making any errors by pressing the appropriate response button. Responses were mapped to the letters in the following way: Letters A and B required a response with the left middle finger and the left index finger, respectively, and Letters C and D required a response with the right index finger and the right middle finger, respectively. The presence or absence of a sequence was not mentioned. The experiment consisted of 28 blocks, each with 120 trials. Blocks 1 to 12 and Block 14 as well as Blocks 15 to 26 and Block 28 were regular blocks (see below). Blocks 13 and 27 were random blocks. Successive blocks were separated by short rest periods, and a longer rest period was given after Block 14.

In the regular blocks, stimuli were presented in a particular 10-trial sequence (C-D-B-A-B-D-C-B-D-A). Thus, each block consisted of 12 repetitions of this sequence. The end of each sequence and the beginning of the next sequence were not marked, and each block could start at any position within this sequence. Given this sequence, left-hand and right-hand responses were equiprobable. Participants had to change the response hand on successive trials six times per sequence. On four trials, they had to respond with the same hand as in the preceding trial. In 6 out of 12 sequences of each block, one standard stimulus was replaced by a letter that otherwise had not occurred at that particular position within the sequence. Deviant stimuli were never immediate repetitions of preceding letters. After this deviant stimulus, the sequence was continued with the next standard stimulus. Thus, each block contained 6 regular stimulus sequences and 6 sequences including a deviant stimulus. In the random blocks, the sequence of the stimuli was determined randomly. The overall probability of each letter stimulus was identical to the probabilities in the regular blocks. Both in the regular and in the random blocks, identical stimuli never occurred on successive trials.

At the end of the first half of the experiment (after Block 14), participants were asked whether they had noticed anything special regarding the experimental circumstances. When the presence of a sequence was reported, the participant was asked to verbally reproduce this sequence. However, the existence of a sequence was neither confirmed nor denied. At the end of the experiment (after Block 28), participants were again asked whether anything particular had been noticed. When the presence of a sequence was not mentioned at this time, participants were informed about the existence of such a sequence. They were then asked to reproduce verbally that part of the sequence that they thought they noticed. Finally, they were asked to identify the correct sequence, which was presented to them on a sheet of paper together with five other stimulus sequences that were not used in the present experiment.

On the basis of these verbal reports, participants were classified in two categories. Participants who reported that they noticed the presence of a sequence both in the first and the second half of the experiment, who were able to reproduce at least four successive items of the letter sequence, and who correctly identified this sequence in the recognition task were classified as having some explicit knowledge with respect to this sequence (Group E). Seven participants were assigned to this group. One of them failed to recognize the correct sequence but was assigned to Group E on the basis of the other verbal reports. The remaining 9 participants who were classified as having only implicit knowledge of the sequence (Group I) did not notice the presence of a regularity in the first half of the experiment, reproduced fewer than four successive items of the sequence, and did not recognize the sequence. One of these participants identified the sequence correctly in the recognition task but was assigned to Group I on the basis of the other verbal reports. Four participants did not notice any regularity during the entire experiment.

EEG Recording

EEG was recorded with silver–silverchloride electrodes from fronto-polar, frontal, central, and parietal midline scalp sites (Fpz, Fz, Cz,

and Pz, respectively, according to the 10–20 system), as well as from left and right central scalp sites (C3' and C4', located 1 cm in front of C3 and C4, respectively). All electrodes were referenced to the right earlobe. Electrode impedance was kept below 5 kΩ. The amplifier bandpass was 0.10–70 Hz. EEG was sampled on-line every 7 ms and stored on disk.

Data Analysis

EEG was averaged off-line for epochs of 800 ms, starting 100 ms prior to stimulus onset and ending 700 ms after letter onset. Trials with eyeblinks (indicated by a voltage recorded at electrode Fpz exceeding ±50 μV) and overt response errors were excluded from analysis.

EEG was averaged separately for each half of the experiment (Blocks 1–12 and Blocks 15–26) for deviant letters, for letters immediately following the deviant, and for the remaining standard letters. Only the ERPs to deviant letters and to standard letters that were not immediately preceded by a deviant letter were further analyzed. The EEG to stimuli presented in the two random blocks was averaged separately. Additionally, separate averages were computed for deviant and standard letters for Group E and Group I.

The LRP was computed in the following way. First, the EEG was averaged separately for standard letters in the first and second halves of the experiment (Blocks 1–12 and Blocks 15–26) that required either a left or right response and that were preceded either by a same-hand or opposite-hand response. This procedure yielded one average waveform for each combination of the preceding and the present response (left/left, left/right, right/left, right/right). Next, the averaged waveforms for right-response trials were subtracted from the averages obtained for left-response trials in the following way: left/left − left/right and right/left − right/right. This specific procedure was used to ensure that the obtained difference waveforms resulted from trials that were equivalent with respect to the preceding response. The two difference waveforms were then averaged. Finally, the C3'–C4' difference potential was computed, resulting in one LRP waveform for each participant and for each half of the experiment. This procedure was conducted separately for all participants, for Group E, and for Group I.

To test whether the difference between standard and deviant letters had an effect on the ERP waveforms, repeated-measures analyses of variance (ANOVAs) were performed for N2 and P3 amplitudes for the following variables: stimulus type (standard vs. deviant), half of the experiment, half electrode location (for N2 amplitude: Fpz, Fz, Cz, C3', C4', Pz; for P3 amplitude: Fz, Cz, Pz), and participant group (E vs. I) as a between-subjects variable. When appropriate, a Geisser–Greenhouse adjustment to the degrees of freedom was performed (indicated in the results section by GG). N2 amplitude was determined as the mean amplitude within the poststimulus time window 240–340 ms. P3 amplitudes were measured separately at Fz, Cz, and Pz as the maximum positive voltage between 300 and 500 ms poststimulus. The mean amplitudes of the LRP waveforms for each half of the experiment were determined within the consecutive time windows 0–100 ms, 100–200 ms, and 200–300 ms poststimulus. For each time window, repeated-measures ANOVAs were performed on this amplitude measure for the variables experiment half and participant group (E vs. I) as a between-subjects variable. To determine when selective response preparation started as a consequence of stimulus presentation, one-tailed t tests were used to test within these time windows whether the LRP mean amplitude was significantly greater than zero.

Mean RTs were determined separately for deviant letters, for standard letters that were immediately preceded by a deviant stimulus, and for the remaining standard letters. Only the RTs to deviant letters and to standard letters that were not immediately preceded by a deviant letter were further analyzed. For these RT data, a repeated-measures ANOVA was performed for the variables time (Blocks 1–4, 5–8, 9–12, 15–18, 19–22, 23–26), stimulus type (standard vs. deviant),

and participant group (E vs. I) as a between-subjects variable. With paired t tests, it was determined whether the RT in the random blocks (Blocks 13 and 27) differed significantly from the RT to the standard letters in the preceding blocks and from the RT measured in the following regular blocks (Blocks 14 and 28).
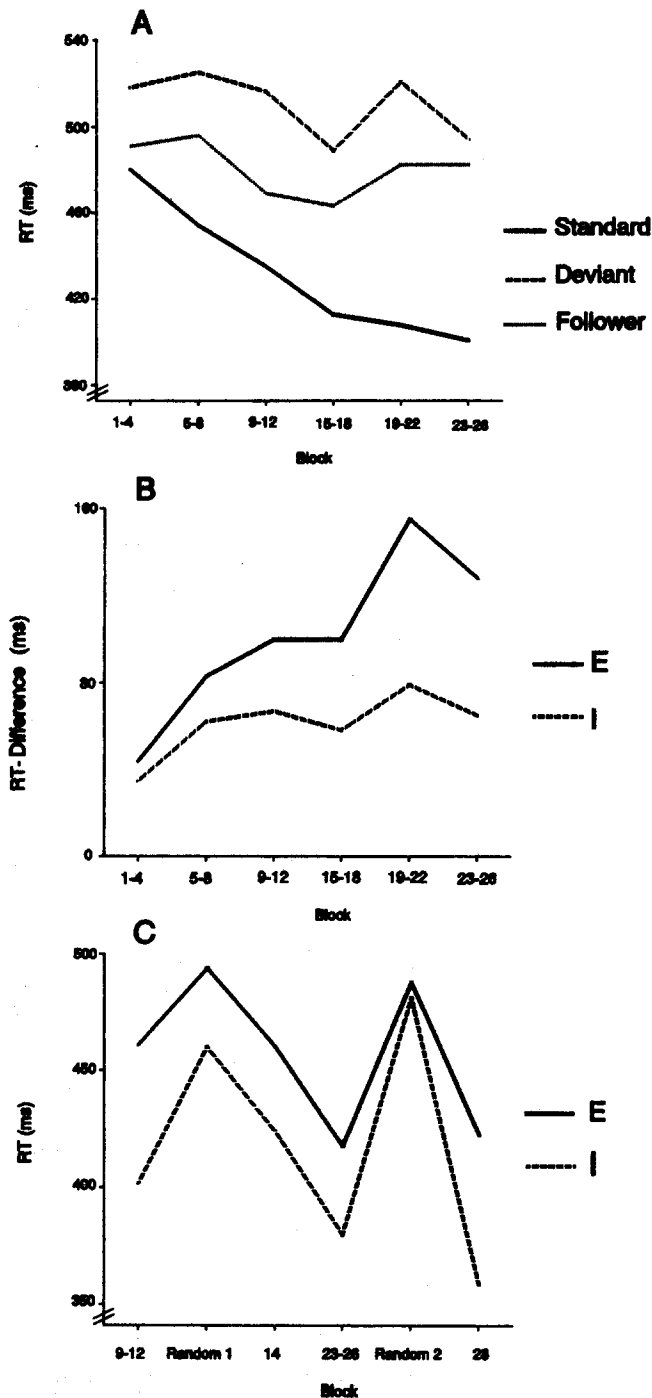
Results

Behavioral Performance

The overall RT was 432 ms for standard letters, 510 ms for deviant letters, and 480 ms for letters immediately following the deviant (see Figure 1A). The RT difference between standard and deviant stimuli was reflected in a highly significant effect of stimulus type, $F(1, 14) = 69.76, p < .001, MSE = 4,469.02$. The finding that the difference between standard and deviant stimuli affected behavioral performance was also reflected in the error rates. Only 4% of the responses to standard letters were erroneous, whereas for deviant stimuli, the error rate was 13%. The interaction between stimulus type and participant group was almost significant, $F(1, 14) = 4.37, p < .055, MSE = 4,469.02$. As can be seen in Figure 1B, the RT differences between standard and deviant letters tended to be larger for Group E than for Group I. A significant effect of time, $F(5, 70) = 12.97, p < .001, GG$, epsilon $= .590, MSE = 961.82$, indicated that responses became faster in the course of the experiment. However, as shown by a two-way Time × Stimulus Type interaction, $F(5, 70) = 7.56, p < .001, GG$, epsilon $= .482, MSE = 705.21$, these RT benefits over time were much larger for standard stimuli than for deviant stimuli (see Figure 1A).

When the participants were confronted with a random sequence (in Blocks 13 and 27), RTs were significantly delayed as compared with the RTs in the last four regular blocks and with the RTs measured in the following block (see Figure 1C). We confirmed this with separate comparisons using one-tailed paired t tests. The overall costs of switching from a regular sequence to a random sequence were 44 ms in the first and 84 ms in the second half of the experiment, $t(15) = 6.90, p < .001; t(15) = 6.45, p < .001$, respectively. The RT benefits of switching from the random block back to the regular sequence were 35 ms in the first and 90 ms in the second half of the experiment $t(15) = 2.87, p < .006; t(15) = 5.27, p < .001$, respectively. As can be seen in Figure 1C, these costs and benefits tended to be larger for Group E than for Group I.

N2 Amplitude

The mean amplitude in the N2 range was significantly more negative for deviant stimuli than for standard stimuli, $F(1, 14) = 11.59, p < .004, MSE = 20.36$. An interaction between stimulus type and experimental half was almost significant, $F(1, 14) = 4.42, p < .054, MSE = 6.18$. As can be seen in Figure 2, this effect was larger in the second half of the experiment. Moreover, the interaction between stimulus type and participant group was almost significant, $F(1, 14) = 4.21, p < .059, MSE = 20.36$, which can be interpreted as evidence for the assumption that the N2 effect elicited by deviant stimuli tended to be larger for Group E than for Group I. These tendencies are also visible in Figure 3, where the amplitude differences between standard and deviant stimuli at electrodes

A

B

C

— Standard
---- Deviant
— Follower

— E
------ I

— E
------ I

Figure 1. Reaction time (RT) results of Experiment 1. A: Mean RTs (of four succeeding regular blocks, respectively) as a function of the amount of practice, displayed separately for standard stimuli, deviant stimuli, and stimuli preceded by a deviant stimulus. B: Mean RT differences between standard and deviant stimuli as a function of the amount of practice, displayed separately for Participant Groups E and I. C: Changes in mean RT for random blocks as compared with the preceding four regular blocks and the following regular block for the first and second halves of the experiment. Changes are displayed separately for Participant Groups E and I. Group E = participants with explicit knowledge; Group I = participants with implicit knowledge.

Fz, Cz, Pz, C3', and C4' were plotted separately for each half of the experiment and each participant group. Although these amplitude differences were larger for Group E than for Group I, additional one-tailed paired *t* tests revealed that these effects differed significantly from zero not only for Participant Group E but also for Group I at all electrodes except Fpz (all $p < .05$). To test whether the negative enhancement in the N2 range as elicited by deviant stimuli can be attributed to stimulus deviance and not to the fact that the RTs to deviant stimuli were delayed, thereby possibly leading to a differential overlap of motor potentials in the ERP waveforms to standard and deviant letters, the N2 mean amplitude to standard stimuli was compared with the N2 amplitude obtained for the stimuli presented in the random blocks. The difference between the RTs measured in these random blocks and the RTs to standard stimuli was 50 ms, which is not far away from the 78-ms difference obtained between standard and deviant stimuli. However, no significant difference was present in the N2 mean amplitude for standard and for random stimuli (see Figure 4A).

P3 Amplitude

The difference between standard and deviant stimuli had no effect on the amplitude of the P3 at Fz, Cz, and Pz.

Lateralized Readiness Potential

Within each time window (0–100, 100–200, and 200–300 ms poststimulus), the LRPs for the first and second halves of the experiment were significantly different, $F(1, 14) = 5.08, p < .041, MSE = 0.20; F(1, 14) = 8.59, p < .011, MSE = 0.63;$ and $F(1, 14) = 7.86, p < .014, MSE = 0.68$, respectively, see Figure 5. Unidirectional *t* tests revealed that in the second half of the experiment, a significant lateralization to the side contralateral to the response was present within each time window, that is, already during the first 100 ms following stimulus onset, $t(15) = 2.06, p < .029; t(15) = 4.18, p < .001; t(15) = 8.99, p < .001$, for the three consecutive 100-ms time windows, respectively. In the first half, a significant lateralization was obtained only within the 200–300 ms time window, $t(15) = 6.57, p < .001$. Although Figure 5 may suggest that these differences between the two halves of the experiment were larger for Group E than for Group I, this assumption was not confirmed by statistical analysis.

Discussion

On the basis of the RT data, it is obvious that the participants acquired knowledge with respect to the stimulus sequence in the course of the experiment. First, RTs to deviant stimuli were 78 ms slower than the RTs to standard stimuli were. Second, the responses to standard stimuli became markedly faster during the experiment, whereas the RTs to deviant stimuli remained much more constant (see Figure 1A). Third, there were pronounced RT costs when participants were confronted with random sequences at the end of both the first half and the second half of the experiment.

These behavioral effects were reflected in an electrophysiological effect of stimulus deviance on N2 amplitude. The N2
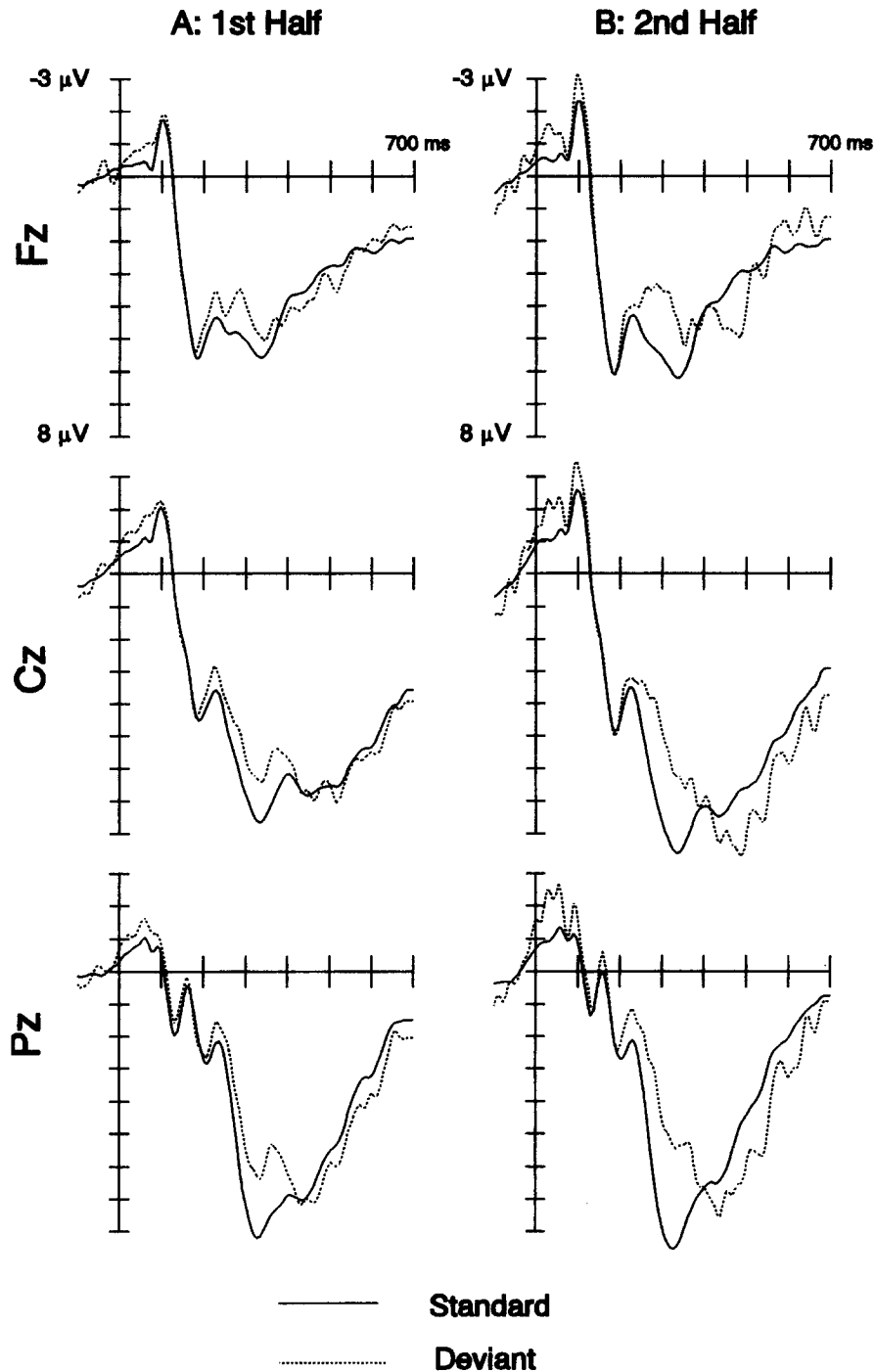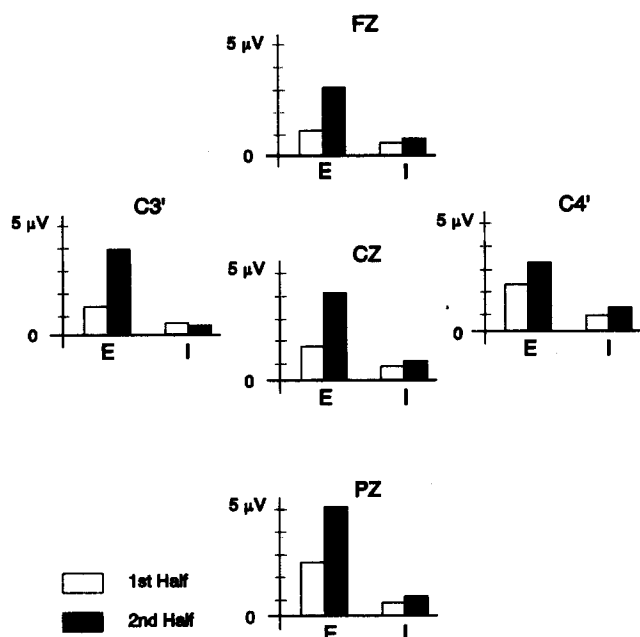
A: 1st Half   B: 2nd Half

Figure 2. Grand-averaged event-related potential waveforms elicited by standard and deviant stimuli at frontal (Fz), central (Cz), and parietal (Pz) midline scalp sites, displayed separately for the first and second halves of Experiment 1.

component was found to be more negative for deviant as compared with standard stimuli, and this effect tended to be larger in the second part of the experiment (see Figure 2). 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 RTs were considerably delayed in the latter case (see Figure 4A).

A crucial question is whether these behavioral and electrophysiological effects can be accounted for by referring to explicit sequence learning. On the basis of the participants'

Figure 3. Mean amplitude differences between event-related potential waveforms elicited by standard and deviant stimuli in the time range of the negative component (N2) in Experiment 1. Difference amplitudes at electrodes from frontal (Fz), central (Cz), and parietal (Pz) midline scalp sites and from left and right central scalp sites located 1 cm in front of C3 and C4 are displayed separately for Participant Groups E and I and for both halves of the experiment.

verbal reports, it is clear that some explicit knowledge was acquired during the experimental session. Only 4 out of 16 participants did not notice any sequence, and 7 participants were able to identify at least four successive items of the sequence at the end of the experiment. Participants classified as having explicit knowledge produced larger RT differences between deviant and standard trials than the other participant group did (see Figure 1C). Moreover, Group E also tended to produce larger N2 deviance effects than did Group I (see Figure 3). Although these effects only approached statistical significance, it may be assumed that differences in the ability to reproduce and to detect the correct stimulus sequence are reflected by corresponding differences in behavioral and in electrophysiological measures.

Given these findings, it may be hypothesized that both the RT effects and the N2 effects are a result of explicit knowledge of the stimulus sequence that has been acquired in the course of the experiment. Because both RT and electrophysiological measures are a result of averaging across a number of trials, it is possible that the behavioral and electrophysiological measures reflect the fact that when a part of the stimulus sequence is known explicitly, deviant stimuli occurring at this place will be detected. The differences between Groups E and I may thus be due to the fact—already reflected in the verbal reports—that the former group acquired explicit knowledge about larger segments of the sequence than the latter group did.

However, one finding does not readily fit with this explanation. In contrast to the N2 effect, there was no effect of stimulus deviance on P3 amplitude. Usually, an enlarged P3 is

elicited by deviant, unexpected, or surprising events. If the behavioral and electrophysiological effects discussed so far are a result of explicit knowledge, it has to be explained why the presentation of deviant stimuli did not lead to an enlarged P3. This issue is further considered in the General Discussion.

Another focus of this research is the question of whether behavioral effects in serial RT tasks are mediated primarily by knowledge about stimulus sequences or by knowledge about response sequences. This experiment gives at least some indirect information about this question. As can be seen from the LRP waveforms in Figure 5, the negative lateralization above the contralateral motor cortex that indicates the activation of the correct response started earlier during the second half of the experiment, because it was present already in the 100-ms interval following stimulus onset. This early onset of the LRP is rather remarkable, because even in the second half of the experiment, the overt response latency was beyond 400 ms. It may be assumed that these modulations of the LRP waveforms in the second half of the experiment are a reflection of the knowledge already acquired. The early onset of the LRP may be interpreted as evidence for the assumption that this knowledge has to be regarded as primarily motor. However, the possibility remains that participants primarily learned the stimulus sequence and that the expectations thus generated were communicated to the motor system at a very early stage of processing.

In Experiment 1, no LRPs could be computed for deviant stimuli, because the number of deviant trials was not sufficient to generate reliable LRP waveforms. One aim of the second experiment was to increase the number of deviant items to obtain LRPs to both standard and deviant stimuli.

Experiment 2

The results of Experiment 1 demonstrated that participants acquired knowledge of the stimulus sequence and that this knowledge is reflected both in behavioral and in electrophysiological responses to deviant stimuli. It is unclear, however, whether this knowledge has to be regarded as explicit or whether the effects found in Experiment 1 are at least partially due to implicit knowledge. In Experiment 1, the relevant interactions between stimulus type and participant group only approached statistical significance. To demonstrate more convincingly the relationship between explicit knowledge and ERP effects of stimulus deviance, additional empirical evidence is clearly needed. Experiment 2 was conducted for this purpose. In contrast to Experiment 1, where only 50% of the regular sequences were interrupted by deviant stimuli, each stimulus sequence included a deviant item in Experiment 2.[1] This manipulation should have made it even harder for the participants to consciously detect the presence of specific regularities. A second reason for increasing the number of deviant stimuli was the necessity to obtain more trials to ensure the computation of reliable LRP waveforms for deviant stimuli.

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[1] However, because one deviant item may be displayed at the beginning of one sequence and the next deviant may be displayed at the end of the next sequence, the possibility remains that 10 or more standard stimuli could be presented successively without being interrupted by a deviant item.
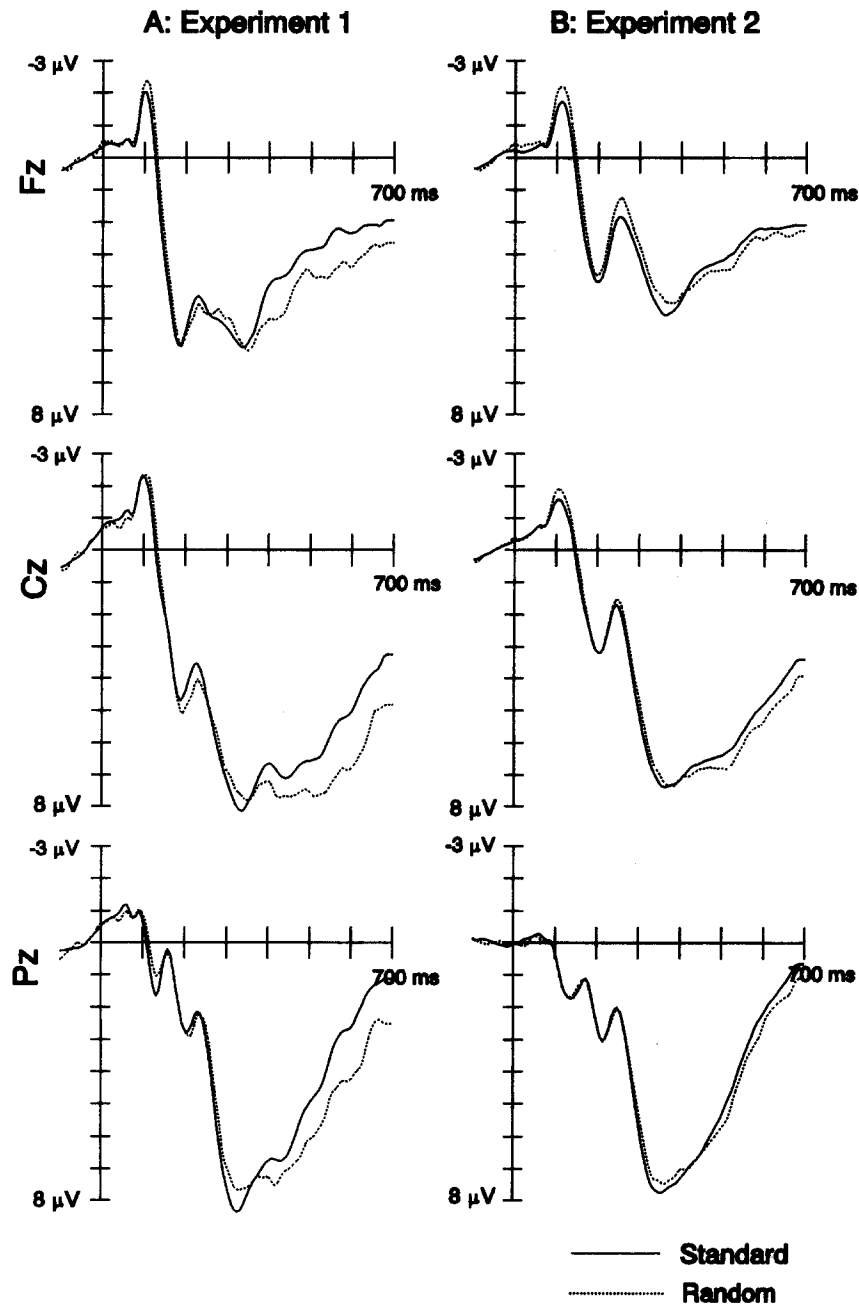
Figure 4. Grand-averaged event-related potential waveforms for Experiments 1 and 2 elicited at frontal (Fz), central (Cz), and parietal (Pz) midline scalp sites by standard stimuli and by stimuli presented in the random blocks.

Method

Participants

Twenty-eight paid volunteers (15 female), aged 21–38 years (mean age: 27.4 years) participated in the experiment. All participants were right-handed and had normal or corrected-to-normal vision. On the basis of the answers regarding the presence of a sequence given by the participants at the end of the first and second half of the experiment, 6 participants were classified as having explicit knowledge (Group E), whereas the remaining 22 participants were classified as having implicit knowledge. Ten of these participants were assigned to Group I−, whereas the remaining 12 participants were assigned to group I+ (see below).

Stimuli and Apparatus

These were identical to those in Experiment 1.

Procedure

Compared with Experiment 1, the number of deviant items was increased. Now each of the 12 stimulus sequences presented during a
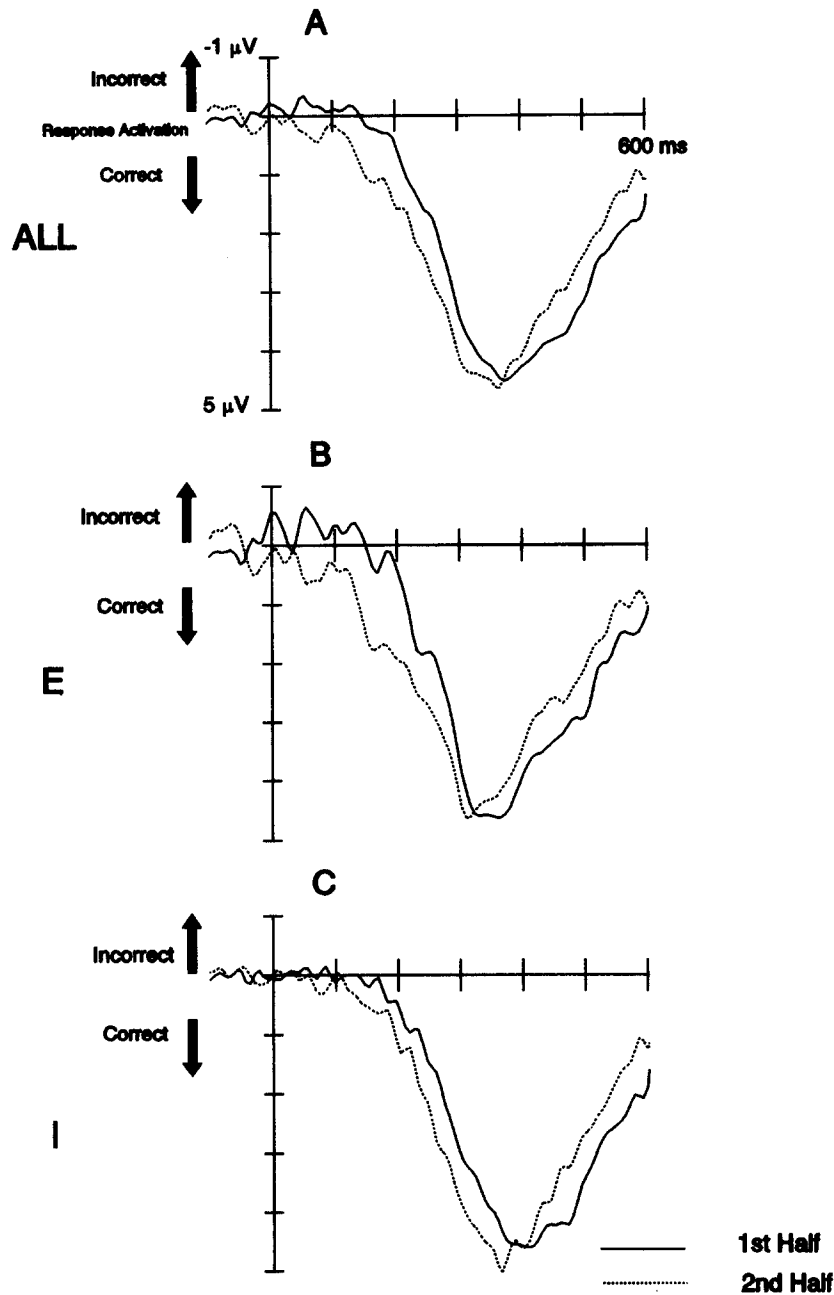
Figure 5. Lateralized readiness potential waveforms elicited in the first and second halves of Experiment 1. Waveforms are displayed for all participants (A) and separately for Participant Group E (B) and Group I (C). Downward-going deflections indicate activation of the correct response.

block included a deviant letter. In all other respects, the experimental procedure was identical to that of Experiment 1.

At the end of the first and second halves of the experiment, participants were tested in the same way as described before. On the basis of their verbal reports, they were again classified into groups. Given the criteria used in Experiment 1, only 6 participants qualified for Group E, whereas the remaining 22 participants were assigned to Group I. Of these, 10 were completely unaware of the presence of a sequence during the entire experiment, whereas the remaining 12 participants at least noticed the presence of a regularity in the second half of the experiment. As there may be important differences between

these participants, Group I was further split into two categories. Those participants who did not notice any regularity were assigned to Group I−, whereas the remaining participants formed Group I+.

EEG Recording and Data Analysis

These were identical to those in Experiment 1 except for the fact that the between-factor participant group now consisted of three levels (E, I+, I−). In addition, LRP waveforms were now also computed for deviant stimuli. To compute the LRP to deviants, only those deviant

stimuli were taken into account that required a response with the hand opposite from the hand used for the stimulus they had replaced in the sequence. In all other respects, the deviant LRP was determined in the same way as was the LRP to standard stimuli.

Results

Behavioral Performance

The overall RT was 475 ms for standard letters, 514 ms for deviant letters, and 496 ms for letters immediately following the deviant (see Figure 6A). The RT difference between standard and deviant stimuli was again reflected in a highly significant effect of stimulus type, $F(1, 25) = 107.20, p < .001$, $MSE = 1259.37$. As before, this difference in response speed was also reflected in the error rates, with 3% of the responses to standard letters but 7% of the reactions to deviant stimuli being erroneous. As can be seen in Figure 6B, the RT costs to deviant letters were different among the three participant groups and were largest for Group E. This was evidenced by an interaction between stimulus type and participant group, $F(2, 25) = 5.00, p < .015, MSE = 1259.37$. Additional one-tailed t tests revealed that the RT costs to deviant letters were significantly larger for Group E than for Group I+ and Group I−, $t(16) = 2.27, p < .016; t(14) = 2.90, p < .006$, respectively. The difference in RT costs between groups I+ and I− only approached significance, $t(20) = 1.42, p < .085$. As in Experiment 1, responses became faster in the course of the experiment: main effect of time, $F(5, 125) = 20.70, p < .001$, GG, epsilon $= .560, MSE = 1048.82$. A two-way interaction between time and stimulus type was obtained, $F(5, 75) = 15.81, p < .001, GG$, epsilon $= .838, MSE = 206.65$. This is presumably due to the fact that the increase of response speed over time was larger for standard stimuli than for deviant stimuli (see Figure 6A).

As before, the RTs measured in the random blocks were delayed as compared with the RTs in the preceding regular blocks and the following block (see Figure 6C). We confirmed this by separate comparisons using paired t tests. The costs of switching from a regular sequence to a random sequence were 35 ms in the first and 41 ms in the second half of the experiment, $t(27) = 7.08, p < .001; t(27) = 8.12, p < .001$, respectively. The RT benefits of switching from the random block back to the regular sequence were 39 ms in the first and 31 ms in the second half of the experiment, $t(27) = 7.06, p < .001; t(27) = 5.94, p < .001$, respectively. As can be seen in Figure 6C, these costs and benefits tended to be larger for Group E than for the other two groups.

Electrophysiological Measures

N2 amplitude. The mean amplitude in the N2 range was again significantly more negative for deviant stimuli than for standard stimuli, $F(1, 25) = 15.58, p < .001, MSE = 3.41$. As reflected by an interaction between stimulus type and electrode location, $F(5, 125) = 9.70, p < .001, GG$, epsilon $= .497$, $MSE = 0.19$, this deviance effect was not equally distributed over all electrodes (see also Figures 7 and 8). Another interaction between stimulus type and the half of the experiment, $F(1, 25) = 6.45, p < .018, MSE = 2.54$, indicated that

this effect was larger in the second half of the experiment. This can also be seen in Figure 8, where the N2 amplitude differences between standard and deviant stimuli at Fz, Cz, Pz, C3', and C4' are displayed for each half of the experiment and for each participant group. Moreover, Figure 8 indicates that this N2 effect differed in size among Participant Groups E, I+, and I−. This was reflected in a significant interaction between stimulus type and participant group, $F(2, 25) = 3.60, p < .042$, $MSE = 3.41$. In addition, a significant three-way interaction was obtained: Stimulus Type × Participant Group × Electrode Location, $F(10, 125) = 2.97, p < .018, GG$, epsilon $= .497, MSE = 0.19$. These effects were further investigated with additional one-tailed paired t tests. These tests were used for single electrode sites to study whether the effect of stimulus deviance on N2 amplitude differed significantly from zero for each participant group. For Group E, these t tests yielded significant results at all electrodes except Fpz (all $p < .05$). For Group I+, a significant effect was obtained at C4', and an almost significant effect was obtained at Pz ($p < .055$). For Group I−, no significant differences could be obtained at all. Additionally, the N2 amplitude for standard letters was compared with the N2 amplitude measures obtained for stimuli presented in the random blocks. As in Experiment 1, no significant difference could be obtained (see Figure 4B).

P3 amplitude. In contrast to Experiment 1, deviant stimuli elicited larger P3 amplitudes than did standard stimuli. Although these amplitude differences were rather small (1.16 μV at Fz, 0.74 μV at Cz, and 0.45 μV at Pz) and are barely to be seen in Figure 7, they were significant at electrodes Fz and Cz, $F(1, 25) = 19.21, p < .001, MSE = 1.74; F(1, 25) = 6.51, p < .017, MSE = 1.97$, and approached significance at Pz, $F(1, 25) = 3.38, p < .078, MSE = 1.23$.

Lateralized Readiness Potential

The LRPs for the first and second halves of the experiment were significantly different within the second and third measurement window, that is, between 100 ms and 300 ms poststimulus, $F(1, 25) = 17.58, p < .001, MSE = 0.10; F(1, 25) = 13.86$, $p < .001, MSE = 0.35$, respectively (see also Figure 9A). Unidirectional t tests revealed that in the second half of the experiment, a significant lateralization to the side contralateral to the response was present within each time window, $t(27) = 2.78, p < .005; t(27) = 6.80, p < .001; t(27) = 7.82, p < .001$, for the three consecutive 100-ms time windows, respectively. In the first half, it was missing only within the first time interval, $t(27) = 3.18, p < .004; t(27) = 7.79, p < .001$, for the second and third 100-ms time windows, respectively. In the second and third time interval, that is, between 100 ms and 300 ms poststimulus, the LRP to deviant stimuli differed significantly from the LRP to standard stimuli, $F(1, 25) = 13.12, p < .001$, $MSE = 0.39$; and $F(1, 25) = 16.56, p < .001, MSE = 0.94$, respectively (see Figure 9B). When these two time windows were collapsed, an almost significant interaction between stimulus type and participant group was obtained, $F(2, 25) = 3.35, p < .051, MSE = 0.52$. As can be seen in Figure 9C, no differences between deviant and standard LRP were present for Group I− between 100 ms and 300 ms poststimulus, whereas considerable differences were present for the other

two participant groups. Additional paired t tests were conducted to compare the LRPs to standard with the LRPs to deviant items within this time interval separately for the three participant groups. For Groups E and I+, highly significant differences were found ($p < .010$), whereas no difference was present for Group I−. Over all participants, the LRP wave-
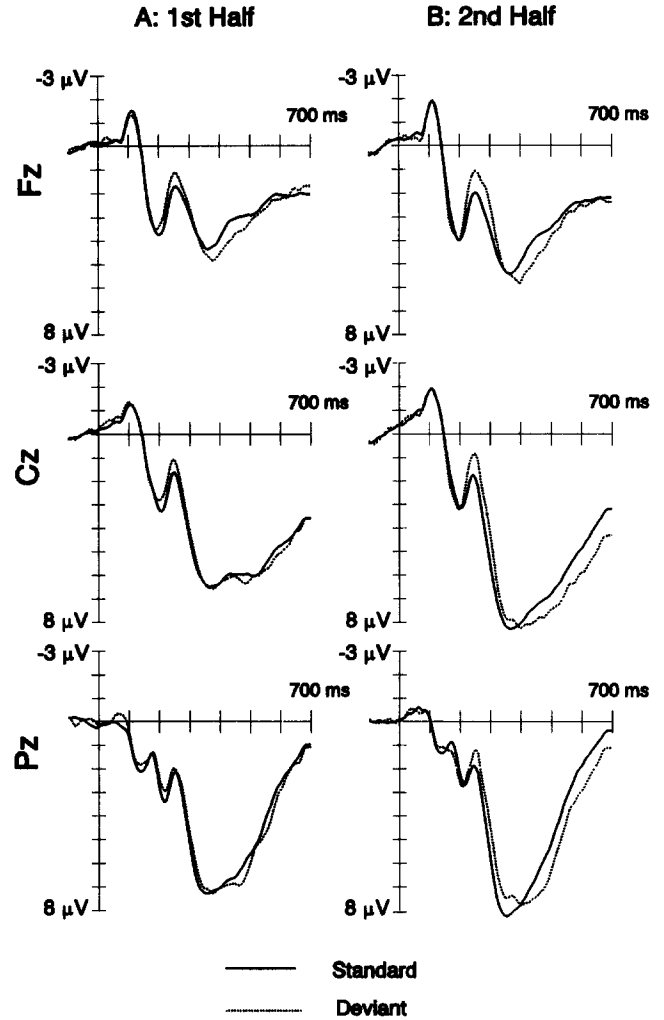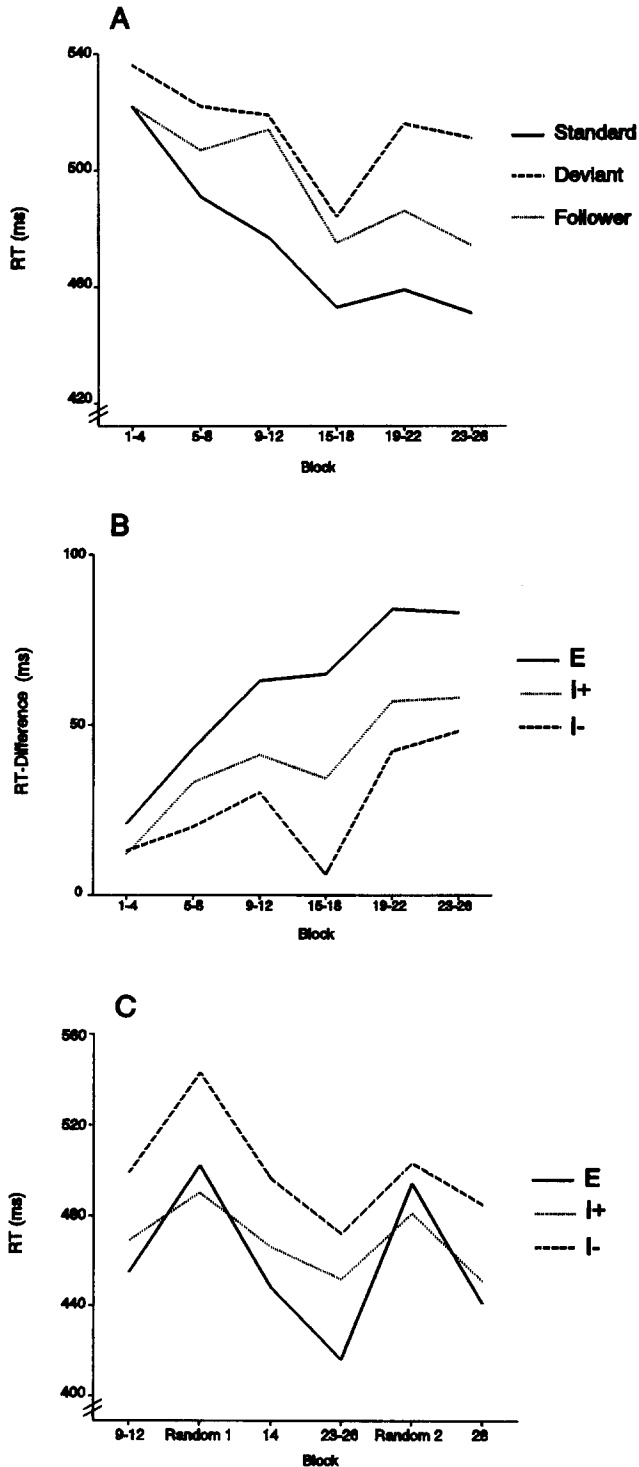

Figure 7. Grand-averaged event-related potential waveforms for Experiment 2 elicited by standard and deviant stimuli at frontal (Fz), central (Cz), and parietal (Pz) midline scalp sites, displayed separately for the first and second halves of the experiment.

forms to deviant stimuli did not differ significantly from zero within the analyzed time intervals. When only the participants from Groups E and I+ were taken into account, however, an unidirectional t test revealed that in the interval between 100 ms and 200 ms poststimulus, the mean amplitude of the LRP waveform elicited by deviant stimuli was significantly below

Figure 6 (left). Reaction time (RT) results of Experiment 2. A: Mean RTs (of four succeeding regular blocks, respectively) as a function of the amount of practice, displayed separately for standard stimuli, deviant stimuli, and stimuli preceded by a deviant stimulus. B: Mean RT differences between standard and deviant stimuli as a function of the amount of practice, displayed separately for Participant Groups E, I+, and I−. C: Changes in mean RT for random blocks as compared with the preceding four regular blocks and the following regular block for the first and second halves of the experiment, displayed separately for Participant Groups E, I+, and I−.
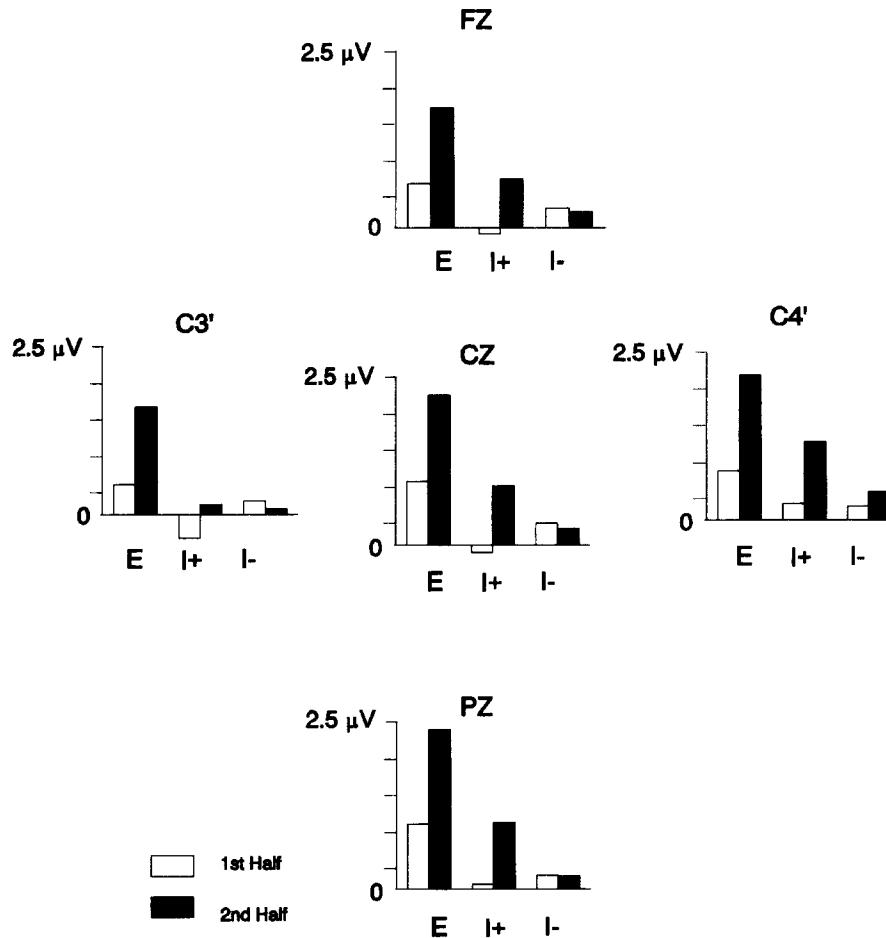
Figure 8. Mean amplitude differences for Experiment 2 between event-related potential waveforms elicited by standard and deviant stimuli in the negative component range. Difference amplitudes at electrodes from frontal (Fz), central (Cz), and parietal (Pz) midline scalp sites and from left and right central scalp sites located 1 cm in front of C3 and C4 are displayed separately for Participant Groups E, I+, and I− and for both halves of the experiment.

zero, thereby indicating an activation of the incorrect response, $t(17) = 2.63, p < .009$.

Discussion

As in Experiment 1, the RT data demonstrated that knowledge regarding the stimulus sequence was acquired by the participants. The RT to deviant letters was 39 ms slower than the RT to standard letters, and both RT costs for random sequences and RT benefits after switching back to the regular sequence were present. However, presumably because of the inclusion of additional deviant stimuli, the RT difference between deviant and standard stimuli was considerably smaller than in Experiment 1. Whereas the RTs for deviant stimuli were nearly identical in both experiments, responses to standard stimuli were about 40 ms slower than in Experiment 1. The presence of more deviant items may have impaired learning of the stimulus sequence or may have led participants to adopt more conservative response criteria. Moreover, on the basis of the verbal reports, only 6 out of 28 participants were

classified as having explicit knowledge, whereas 10 were completely unaware of any sequence. Thus, the delayed RT to standard stimuli in Experiment 2 may be due to the fact that fewer participants had explicit knowledge.

Although it was presumably harder to obtain explicit knowledge of the stimulus sequence in this experiment, both effects of stimulus deviance found in Experiment 1 were present: In addition to the RT effects already mentioned, an enhanced N2 amplitude to deviant stimuli was again obtained, although this effect was smaller than in Experiment 1 (see Figure 7). Moreover, statistically significant interactions between stimulus type and participant group were obtained both for RT and for N2 amplitude in the present experiment. For participants who reported at least some explicit knowledge with respect to the stimulus sequence, these effects were larger than for participants who did not notice any regularity. This is particularly true for the N2 effect (see Figure 8), which is virtually absent for Group I− and is largest for Group E. These findings support the assumption that the deviance-related effects re-
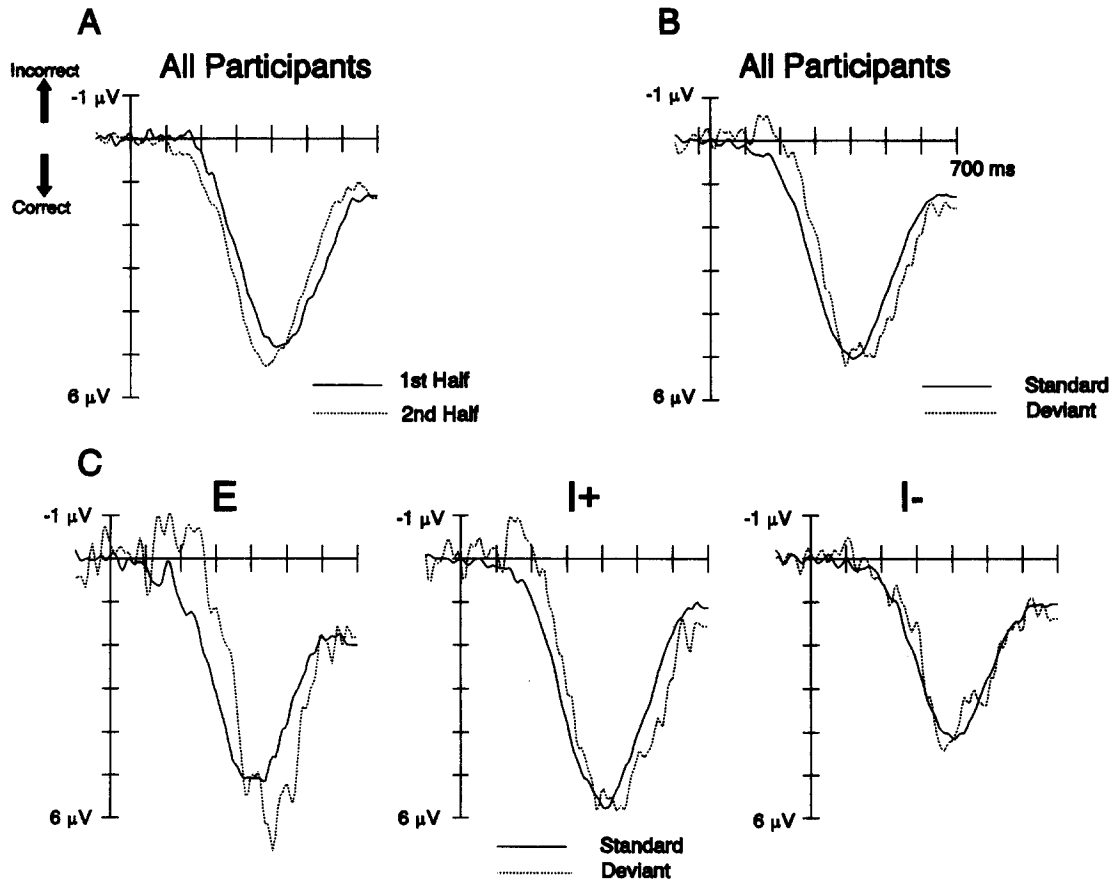
Figure 9. A: Lateralized readiness potential (LRP) waveforms elicited by standard stimuli in the first and second halves of Experiment 2, collapsed over all participants. B: LRP waveforms elicited by standard and deviant stimuli, collapsed over both halves of Experiment 2 and all participants. C: LRP waveforms elicited by standard and deviant stimuli, displayed separately for Participant Groups E, I+, and I−.

ported in this experiment, and most particularly the N2 effect, are a reflection of the amount of explicit knowledge available to the participants.

In contrast to Experiment 1, deviant stimuli elicited an enhanced P3 as compared with standard stimuli. Although this effect was small and almost invisible in the averaged waveforms (see Figure 7), it was significant at Fz and Cz. This was rather unexpected as other measures indicated that it was harder to obtain explicit knowledge in the present experiment as compared with Experiment 1. If this effect is to be interpreted as evidence for the conscious recognition of deviant stimuli, one may expect to find larger P3 modulations for participants having some explicit knowledge. However, no interaction between stimulus deviance and participant group on P3 amplitude could be obtained.

The LRP waveforms obtained in Experiment 2 confirmed the finding of the previous experiment that the selective activation of the correct response starts immediately after the onset of a standard stimulus, thereby demonstrating that selective anticipations may influence the motor system very early. Additionally, it was found that after the presentation of deviant stimuli mapped to a reaction with the unexpected

hand, the incorrect response hand is activated prior to the activation of the correct response. This may be regarded as further evidence that specific anticipations were induced by the presence of the stimulus sequences and that these expectations seem to have an immediate influence on the response-execution stage. Another interesting aspect of the LRP data concerns the finding that not all participants showed signs of incorrect response activation in the case of deviant stimuli. For participants who were unable to recognize any regularity in the course of the experiment (Group I−), no such effect was obtained (see Figure 9C). This finding suggests a close relationship between the conscious availability of specific regularities and the existence of specific motor-preparation processes. This issue will be further elaborated in the General Discussion.

General Discussion

The aim of the present experiments was to obtain behavioral and electrophysiological evidence for the acquisition of knowledge about event sequences. In both Experiments 1 and 2, the behavioral data clearly demonstrated that participants did acquire knowledge about the sequential structure of the

stimuli in the course of the serial RT task. The verbal reports showed that most participants became aware of the presence of a regularity in the stimuli and that at least some participants acquired explicit knowledge about segments of this sequence. This indicates that participants may well become aware of sequential regularities, even if the regular sequence is constantly interrupted by deviant stimuli (cf. Cleeremans & McClelland, 1991; Stadler, 1993).

ERPs and Explicit Knowledge

The degree to which participants became aware of the sequence structure was clearly reflected both in behavioral and in electrophysiological measures. Participants possessing some explicit knowledge developed larger deviance-related RT effects and also produced an enlarged N2 effect as compared with participants lacking explicit knowledge. When comparing the development of the N2 effects between both the halves of the experiments in Experiment 1 and 2 for the different participant groups (see Figures 3 and 8), it becomes obvious that for participants with explicit knowledge, these effects became larger in the course of the experiments, whereas for the other participants the increment of these effects between the halves of the experiments was smaller or even absent.

Given the close relationship between explicit knowledge and the development of the N2 effect, the N2 enhancement elicited by deviant stimuli may be regarded as an indicator of the amount of consciously available explicit knowledge about the stimulus sequence. In contrast to all previously used measures of explicit knowledge in serial RT tasks, this measure can be recorded on-line and is thus not influenced by interference due to memory-retrieval processes or by a change in participants' strategy, which may result from informing participants about the existence of a structure in a direct test. The deviance-related N2 may thus be used to monitor the gradual development of knowledge. Moreover, the N2 effect provides converging evidence validating the backward inference from differences in participants' verbal reports and recognition performance to differences in the processes underlying performance in the preceding serial RT task (Shanks et al., 1994; Shanks & St. John, 1994). The fact that the N2 effect was clearly present for participants showing explicit knowledge about the sequence but was smaller or even absent for participants lacking explicit knowledge indicates that participants in both groups did not simply differ in their ability to remember or verbalize sequential knowledge after the training phase. Rather, the N2 effect provides at least suggestive evidence that the acquisition of sequential knowledge in the serial RT task in explicit and implicit groups was indeed mediated by different underlying brain processes.

In this context, it is noteworthy that these findings suggest a dissociation between electrophysiological and behavioral indicators of sequence learning. Participants who reported that they were unaware of a structured sequence and who showed no reliable N2 effect nevertheless showed considerable RT benefits for standard as compared with deviant stimuli. It is conceivable that these RT effects may be due to implicit-learning processes that are reflected neither in verbal reports nor in electrophysiological measures. Recent positron emis-

sion tomography results indicate that subcortical structures like the basal ganglia are involved in the procedural learning of motor skills (Grafton et al., 1992). Thus, implicit learning in the absence of conscious knowledge may involve activation in subcortical brain structures that is not easily tapped with scalp electrodes. It is a tempting possibility that the dissociation between the N2 effect and the RT benefits may be due to the fact that the N2 in explicit learners reflects the detection of deviance from a sequential structure on the basis of explicit knowledge, whereas the RT benefits in implicit learners are due to the development of new or more efficient motor programs, which may primarily involve subcortical brain areas. However, further experiments are clearly needed to establish this conclusion firmly. At present, we cannot rule out the alternative possibility that behavioral, verbal, and electrophysiological measures tap the same type of knowledge but differ simply in their sensitivity.

It should be noted that the N2 effect obtained in the present experiments appears to be different from ERPs that have been observed in response to deviations from other types of sequential structures. First, the present N2 effect differs from the N400 component that is usually elicited by semantically inappropriate words in a sentence context (e.g., Kutas & Hillyard, 1980, 1983). Likewise, our N2 effect differs from the late positive shift that has recently been reported following syntactic ambiguities or violations in sentences (e.g., Hagoort, Brown, & Groothusen, 1993; Osterhout & Holcomb, 1992). Finally, although an early-latency negative component has been observed in response to deviations in nonlinguistic sequences like melodies (Besson & Macar, 1987; Paller, McCarthy, & Wood, 1992), this effect also appears to be different from the present N2 because it occurred with a much shorter latency of about 100 ms. Probably more relevant for the interpretation of our N2 effect are previous ERP studies with oddball paradigms, in which a simple repetitive stimulation was the context against which deviant stimuli were presented. In these studies, enhanced N2b components were elicited not only by physical deviations but also by semantic deviations (Näätänen & Gaillard, 1983; Ritter, Simson, & Vaughan, 1983). It thus appears reasonable to consider our N2 effect as a variant of the N2b component.

If this interpretation is correct, it is somewhat surprising that no P3 effect was obtained in Experiment 1 and that only a very small P3 effect was found in Experiment 2, because usually a deviance-related N2b is followed by an enhanced P3 component. If participants acquired explicit knowledge of the stimulus sequence, the detection of a deviant stimulus was expected to lead to an enhanced P3. Even if explicit knowledge was confined to a subsection of the stimulus sequence, larger P3s should have been elicited in some deviant trials, thereby presumably leading to a notable P3 amplitude effect in the averaged waveform. Moreover, because learning of the stimulus sequence is likely to proceed in an incremental way, the P3 deviance effect would be expected to have been more pronounced in the second half of each experiment, as this was the case for the RT and N2 effects. On the basis of the present results, it cannot finally be decided why these expectations were not confirmed. One possibility for this may be that in these experiments, both standard as well as deviant letters

served as targets. The P3 is usually largest for task-relevant deviant target stimuli in a series of nontargets. Courchesne, Courchesne, and Hillyard (1978) presented rare deviant stimuli, which were either targets or nontargets (i.e., task irrelevant). Deviant nontargets produced a smaller late positivity than equally deviant targets. The fact that in our experiments participants did not have to detect occasional targets among a series of nontargets, because all stimuli were equally task relevant, may have attenuated the P3.

ERPs and Motor Processes

Another result of the present experiments was that sequential knowledge acquired in the course of the serial RT task influenced motor preparation in a rather direct way. For standard stimuli, significant deflections in the LRP waveforms were obtained during the first 100 ms following stimulus onset, thus indicating the selective preparation of the correct response. In the case of deviant stimuli that were connected to a response with the unexpected hand, the LRP waveforms showed evidence for an early activation of the incorrect response, which was only later replaced by an activation of the correct reaction. This latter effect was present only for participants showing at least some explicit knowledge. One explanation for this fact is that the availability of conscious sequence knowledge was responsible for early motor-activation processes. However, we consider it as an interesting possibility that the reverse functional relationship was operative: Sequential learning may initially be mediated solely by motor anticipation and preparation processes. However, participants may differ in the degree of motor knowledge acquired during the course of the task. When participants acquire motor knowledge faster or more completely, this may in turn result in the development of more detailed explicit knowledge about the underlying sequential regularity (cf. Mathews et al., 1989; Willingham et al., 1993).

Apart from these alternative interpretations, the present findings clearly show that an important process underlying serial learning is the anticipation and preparation of the next motor response and that such preparatory processes may even start prior to the presentation of the next stimulus. This conclusion fits with a recent proposal (Goschke, 1992, 1994; see also Cleeremans & McClelland, 1991; Hoffmann, 1993) according to which sequence learning is based on an anticipation of the next sequence event, which is formed on the basis of a limited number of previous events stored in a temporary context memory and which is then compared with the actual next event. In terms of this model, the LRP effect may indicate the formation of such sequential anticipations, whereas the deviance-related N2 effect reflects the registration of mismatches between anticipated and actual events.

Although the present LRP data provide convincing evidence for anticipatory processes, they do not allow us to decide whether these anticipations are based on the learning of response or stimulus sequences. On the one hand, the LRP effect may reflect the fact that participants acquired procedural knowledge about the sequence of motor responses and that this knowledge allowed earlier preparation of the next response. Learning may even consist of changes in motor-

related systems themselves (e.g., in the formation of a novel motor-sequencing program). This view is consistent with recent positron emission tomography data indicating that procedural learning of a motor skill involves modifications in the same brain areas as those that mediate the execution of the skill (Grafton et al., 1992) and that sequence learning is impaired in patients with degenerative changes in brain structures mediating motor behavior as, for example, in Huntington's disease (Knopman & Nissen, 1991) and Parkinson's disease (Ferraro, Balota, & Connor, 1993).

However, the present LRP data are equally compatible with the alternative interpretation that participants acquired knowledge about the sequence of stimuli and learned to use this knowledge in an anticipatory way to prepare the next motor response. Although at present we cannot decide between these two alternatives, in any case our results convincingly demonstrate a close link between sequential knowledge and response-related processes.

In summary, in the present experiments a first attempt has been made to identify electrophysiological indicators of sequence learning. More specifically, ERP indicators for the incidental acquisition of explicit sequential knowledge and the anticipatory preparation of responses in a serial RT task have been obtained. Although these findings raise a number of open questions, they also demonstrate that the combination of electrophysiological, behavioral, and self-report measures appears to be a promising way to elucidate in finer detail the processes underlying both explicit and implicit modes of learning sequential structures.

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