

Research report

Differences in incidental and intentional learning of sensorimotor sequences as revealed by event-related brain potentials

Jascha Rüsseler^{a,*}, Erwin Hennighausen^b, Thomas F. Münte^a, Frank Rösler^b

^a*Department of Neuropsychology, Institut für Psychologie II, Otto-von-Guericke University, Postfach 4120, 39016 Magdeburg, Germany*

^b*Experimental and Biological Psychology, Philipps-University, Marburg, Germany*

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Abstract

The present study investigated differences in sequential learning between subjects who were or were not informed of the presence of a repeating sequence (intentional or incidental group, respectively). Subjects had to learn a 16-letter-long repeating sequence that was irregularly disrupted by deviating stimuli. Reaction times indicated that both groups learned the sequential regularities. Intentional learners showed a larger learning effect. Event-related brain potentials (ERPs) recorded during performance of the task showed a reliably enhanced amplitude for the N2b- and P3b-components for deviant letters for intentional learners, but not for incidental learners. These results are discussed in the context of models proposing that different neural structures are involved in implicit and explicit serial learning. © 2003 Elsevier Science B.V. All rights reserved.

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1. Introduction

Sequential learning has been studied extensively with the serial reaction time task (SRTT; [31]). For example, subjects are required to press one of four keys corresponding to four horizontally aligned positions on a computer screen. Unknown to subjects, the stimuli (stars or X-marks) are presented in a repeating sequence of positions like 4-2-3-1-3-2-4-3-2-1 (where 1 denotes the leftmost, 4 the rightmost position). Firstly, some of such structured blocks are presented. In a second phase of the experiment the stimuli appear in a random order. The difference in mean reaction time (RT) of the random and the preceding structured block is taken as a measure of structure-specific sequence learning [3,40]. Finally, verbalizable knowledge that subjects acquired about the sequence is assessed with a generation-task (subjects have to predict the position of the upcoming stimulus, [39]) or

recognition tests of either fragments of the sequence or of the complete sequence [34,49].

One of the most intriguing findings obtained with the SRTT is that sequence learning is possible without the development of concurrent explicit, verbalizable knowledge [2,4,5,18,19,29,31,41,45,46]. This type of learning has been termed implicit [13,37,38,47] and is contrasted with explicit learning that leads to the development of accessible and verbalizable knowledge about the task at hand.

Some differences have been found in the SRTT between subjects classified as explicit or implicit learners according to their performance in the generation or recognition tasks. Learning effects are generally larger for explicit learners [29]. Curran and Keele [5] (see also Ref. [4]) suggested that explicit and implicit learning differ in terms of the attentional requirements: explicit learning requires controlled, effortful processing whereas implicit learning is assumed to take place automatically. Furthermore, there seem to be differences in the types of associations that can be acquired. In implicit learning, only simple, pairwise associations can be learned (like 1-4-3-2, each preceding

*Corresponding author. Tel.: +49-391-671-8478; fax: +49-391-671-1947.

E-mail address: jascha.ruesseler@nat.uni-magdeburg.de (J. Rüsseler).

element perfectly predicts the following stimulus) whereas in explicit learning, higher-order associations can also be acquired (like 1-2-3-2-1-3, where elements n and $n - 1$ are necessary to predict the upcoming stimulus).

In the majority of these experiments, the conclusion that learning was implicit is based on backward inference from memory tests (recognition and generation tasks) which, by necessity, are performed some time after the knowledge-acquisition during the SRTT. This makes the evaluation of functional differences between explicit and implicit learning difficult. Perruchet and Amorim [34] argued that the amount of explicit knowledge may be underestimated with this method. One possibility to overcome this problem is to use event-related brain potentials (ERPs) recorded during the learning episode proper as an online-measure for knowledge acquisition, because if ERPs differ for explicit and implicit learners already while the subjects perform the task, this can be taken as strong evidence for learning-related functional differences.

In previous experiments using ERPs to study sequential learning processes, a modified version of the SRTT has been used that contains deviant events in an otherwise regular series of stimuli. Eimer et al. [11] presented four capital letters in a repeating sequence. Occasionally, standard letters were replaced by deviating letters that required a response with the opposite hand compared to the expected standard letter. Subjects were categorized as implicit or explicit learners according to their performance in explicit knowledge tests administered after the SRTT. Both groups learned the underlying sequential regularities. Deviant letters elicited a larger negativity 240–340 ms poststimulus compared to standard letters (N2b-effect) and a slight enhancement of the P3b-component for deviant letters was also found. These effects were only present in the group of explicit learners. The authors concluded that the N2b-component may reflect the amount of consciously available knowledge about stimulus regularities.

In a follow-up study, Schlaghecken et al. [43] used the process-dissociation procedure [22] to identify explicitly learned sequence parts for each participant. N2b- and P3b-components of the ERP were only enhanced for deviants in those parts of the sequence which were explicitly learned, whereas RT-effects were independent of subsequent reproduction performance.

Rüsseler and Rösler [41] used ERPs to disentangle motor-related and stimulus-related learning processes in the SRTT. Stimuli in a regular letter sequence were occasionally replaced by deviant letters that either violated the stimulus sequence but left the response sequence intact (perceptual deviants) or violated the stimulus as well as the response sequence (motor deviants). Again, results of free recall and recognition tests were used to form groups of explicit and implicit learners post hoc. ERPs showed different effects for the two deviant stimulus types and for the two groups. In the group of explicit learners, a larger N2b-component was evoked by deviants violating the

stimulus sequence only (perceptual deviants) and by deviant letters violating the stimulus as well as the response sequence (motor deviants) whereas a P3b-effect was only present for motor deviants. No ERP-effects were obtained in the group of implicit learners. RTs were enhanced for perceptual and for motor deviants compared to standard letters in the explicit group, whereas in the implicit group RT was only enhanced for motor deviants. Thus, implicit learners were not sensitive to a deviation in the stimulus sequence but only to deviations in the response sequence. The authors concluded that different representations are formed during implicit and explicit learning: implicit learners seem to form response–response associations whereas explicit learners seem to develop either stimulus–response associations or stimulus–stimulus as well as response–response associations.

All studies reviewed above rely on backward inference from explicit knowledge tests performed after the SRTT. To overcome this problem, in the present study we compared one group of subjects that was informed about the presence of a sequence prior to performing the SRTT (intentional group) with performance of a group that was not informed about the presence of sequential regularities (incidental group). We hypothesize that ERP-effects for stimuli deviating from the sequence will only be found for intentionally instructed learners (as in the reviewed studies). Such a result would confirm previous claims that ERPs are a valid measure of explicit knowledge [43]. Furthermore, we used deviant events that either violated the response sequence only or the response as well as the stimulus sequence to test whether different representations of sequence knowledge (SR-, SS-, or RR-associations) are affected differently by the learning ‘strategy’.

2. Method

2.1. Subjects

Thirty-two subjects participated in the experiment for course credit or monetary compensation. All were students of the Philipps-University Marburg. Data of four subjects had to be discarded due to excessive eye-movements or movement-related artifacts. Of the remaining 28 subjects, 14 (eight female; age 23–29) participated in the incidental and 14 (six female; age 24–34) in the intentional group. All subjects were right-handed according to self-report and had normal or corrected to normal vision. None of the subjects had participated in experiments concerned with sequence learning before.

2.2. Stimuli and apparatus

Subjects were seated in an electrically shielded, sound attenuated and dimly lit room. Eight capital letters (D, L, N, R, T, V, X, Z) presented in black in the center of a white

square (1.45° visual angle) on a computer display served as stimulus material. From a constant viewing distance of 100 cm letters subtended a visual angle of 0.58° (height) and 0.28° (width). Letters were presented in 46 blocks of 72 stimuli each. The letters remained on the screen until a response was executed. The response-to-stimulus interval (RSI) was held constant at 500 ms. Correctness of the response and response time (to the nearest 5 ms) were recorded.

2.3. Procedure

Subjects placed their left and right middle and index fingers in a circular cavity of a light gate and had to respond to letters appearing on the screen with a short finger lift. For Z or N a response with the left middle finger was required, T and R were mapped to the left index, L and X to the right index and D and V to the right middle finger.

In the structured stimulus blocks (2–22: first half, 24–43: second half) the letters were presented according to the repeating sequence Z N T V L N X T D R D L. In 16.6% of all cases, a regular letter was replaced by one of two types of deviant letters. Perceptual deviants were constructed by replacing the regular letter with the second letter mapped to the same response (e.g. the perceptual deviant for Z is N, for T it is R, etc.). Thus, perceptual deviants violate the stimulus sequence but preserve the response sequence. Motor deviants were constructed by replacing the regular letter by one of the four letters requiring a response with the opposite hand (e.g. the motor deviant for Z can be L, X, D or V). Thus, motor deviants violate both the stimulus and the response sequence. In each replication of the sequence one position was determined randomly in the first six letters and one in letters 7–12. The respective regular letters were then replaced by one of the two deviant types with equal probability. It was excluded that two deviant letters occurred in succession.

In blocks 1, 2, 23, and 44 (random blocks) the letter to be presented was determined pseudorandomly with the constraint that in 12 consecutive letters the stimulus probability of each letter matched that of the sequence and that no immediate letter or response repetitions occurred.

Participants were assigned randomly to one of the two experimental groups. In the intentional group, subjects were told that the letters are presented according to a partly repeating sequence and that learning this sequence should be used to improve performance in the task. No mention of the presence of a sequence was made for participants in the incidental group. All subjects were instructed to respond as accurately and as fast as possible whenever a letter is presented on the screen.

To assess the amount of explicit, verbalizable sequence knowledge, all participants were prompted to write down as many consecutive letters from the sequence as possible

on a sheet of empty paper (free recall task) after finishing the SRTT.

2.4. EEG-recording

EEG was recorded from 61 Ag–AgCl electrodes placed on the subjects' head by means of an elastic cap (Gaggl-system, Graz, Austria). The cap was positioned on the head with reference to the nasion,inion and the preauricular notches. The vertex electrode was positioned according to the 10–20 system [23]. All scalp electrodes were referenced to linked earlobes.

To control for vertical and horizontal eye-movements the electrooculogram (EOG) was recorded from the outer ocular canthi (horizontal EOG) and the sub- and supraorbital ridges (vertical EOG). Impedances of all electrodes were kept below 5 k Ω .

Two sets of 32-channel amplifiers (SYNAMPS) were used for EOG and EEG recording with a digitization rate of 100 Hz. Bandpass filters were set from DC to 50 Hz.

2.5. Data analysis

2.5.1. Behavioral data

Data of the explicit knowledge test for both experimental groups were compared by means of pairwise *t*-tests. The number of correctly recalled consecutive elements was taken as the dependent measure. A recalled letter sequence was scored as correct if at least two consecutive letters matched the letters in the presented sequence. The position of a reported fragment in the sequence was irrelevant for scoring. For example, sequence fragments of length 3 were recalled which are at different positions in the original sequence (correct sequence: Z N T V L N X T D R D L; recalled subject a: Z N T D X; recall subject b: N N V R D L, correct sequence parts underlined). The free recall performance was scored as three in both cases. Thus, the free recall score reflects the longest consecutive correct letter sequence a subject reported. Note that only four participants (one incidental, three intentional) reported more than one correct sequence fragment. In these cases, the longest reported sequence fragment was used for scoring.

2.5.2. RT and errors

Error rates and mean RT were determined separately for standard letters, perceptual deviants, motor deviants and the random letters. This was done separately for the first and second half of the experiment to ensure comparability with the ERPs. Furthermore, mean RTs in the random blocks and mean RTs for standard letters in the preceding structured blocks were computed and compared with *t*-tests.

2.5.3. Event-related potentials

EEG and EOG were divided offline into periods of 1200

ms starting 200 ms prior to letter presentation and ending 1000 ms after stimulus onset. Trials with eye-blinks or horizontal eye-movements (vertical EOG exceeding 120 μ V, horizontal EOG exceeding 100 μ V) or an amplitude range of more than 100 μ V on one of the 63 electrodes in the 1200 ms epoch were excluded. Trials with response errors, responses faster than 100 ms, trials immediately following a deviant and trials which caused a response repetition were also discarded. EEG was averaged separately for each of the three stimulus types (standards, perceptual deviants, motor deviants) in the first and second half of the experiment for each of the two groups. All measures were taken relative to the mean voltage of the 100-ms interval preceding letter onset.

Effects of the experimental variables on the ERP were determined by conducting a series of repeated measures' ANOVAs on ERP mean amplitude values within different poststimulus time windows (N2b: 250–350 ms, P3b: 450–600 ms). For these analyses, only the 19 electrode sites of the standard 10–20-system [23] were used.

To determine whether the experimental manipulations had different effects on ERPs for incidental and intentional learners, an overall repeated measures ANOVA with factors 'group', 'electrode site', 'half' and 'stimulus type' was run for each time window. Furthermore, several subordinate ANOVAs were run to qualify the results. Where appropriate, the degrees of freedom in the ANOVAs were adjusted to control for violations of the sphericity-assumption [20]. Degrees of freedom are reported before, *P*-values after the adjustment.

3. Results

3.1. Test of explicit sequence knowledge

To test whether the instructional manipulation had been successful, performance in the explicit knowledge measure for incidentally and intentionally instructed subject groups was compared. In the free letter recall task, intentional learners performed significantly better than incidental learners (letter sequence recall: 2.07 vs. 6.64 letters, $t(26)=3.305$, $P<0.0028$; see Table 1 for results of individual subjects). Thus, we conclude that the instructional manipulation was successful.

To determine whether the amount of verbalizable knowledge in the free recall test is different from guessing for the incidental group, a simulation of subjects' performance in this test was conducted [42]. Firstly, the mean number of letters reported by incidental learners in the free letter recall task was computed. On average, seven letters were reported. Note that all reported letters are counted, not only those that are part of the sequence. Consequently, in the first simulation, sequences of seven letters length were generated from a pool of 12 letters (N, N, D, D, T, T, L, L, Z, X, V, R) to determine the number of letters which

Table 1

Performance in the free letter recall tasks for each subject. Subjects # 1–16: incidental group, 21–35: intentional group. The number of correctly recalled letters is given (max. 12)

Subject #	Letter recall
1	0
4	0
5	3
6	0
7	7
8	2
9	3
10	2
11	4
12	0
13	2
14	2
15	2
16	2
21	12
22	12
23	11
24	2
25	8
26	12
27	0
28	4
30	10
31	2
32	3
33	0
34	12
35	5

would be correctly reported by guessing (pairs of letters (e.g. NN) were allowed). A pool of 12 letters considers that subjects may have noticed that four of eight letters appeared twice as often as the other four (N, D, T and L). This is not necessarily the case. Therefore, a second simulation with a set of eight letters (N, D, T, L, X, Z, V, R) was conducted, too.

In all simulations, it was first tested whether the generated seven-element sequence was part of the regular stimulus sequence of the experiment. Next, it was tested whether one out of all possible six-letter sequences included in the generated seven-letter sequence was part of the original stimulus sequence, then the five-letter sequences were checked, and so on. The program stopped when the first correct sequence was found. From all simulations, the mean number of correctly generated letters was computed. In the reported simulations 1,000,000 sequences were generated from the relevant stimulus pool. In simulation 1 (1,000,000 replications of a seven letter sequence out of a pool of 12 letters), the mean number of correctly generated letters amounted to 1.91, whereas in simulation 2 (1,000,000 replications of a seven-letter sequence out of a pool of eight letters) it amounted to 1.81 letters. Therefore, it is likely that subjects who recalled sequences of more than two consecutive elements had at least some explicit knowledge about the stimulus reg-

ularities (subjects 5, 7, 9 and 11 of the incidental group). Likewise, four intentional learners (24, 27, 31 and 33) did not recall more than two consecutive sequence elements. Nevertheless, these subjects were not excluded from the samples as the objective of the present experiment was to assess the effect of the instructional manipulation on RT and ERPs without relying on backward inference from tests performed after the SRTT. In addition, however, all reported statistical analyses for ERPs, RT and error data were also computed using only the data of the 10 ‘truly implicit’ and the 10 ‘truly explicit’ subjects. With one exception,¹ the general pattern of results remained the same.

3.2. RT and errors

Both groups learned the sequential structure of the material as reflected in a reliably prolonged RT for random compared to structured blocks. An ANOVA of the differences of RTs to standard letters for random and structured blocks (first half: block 23–22, second half: block 44–43) revealed that subjects of the intentional group learned more (main effect ‘group’, 51 ms vs. 197 ms, $F(1,26)=4.07$, $P<0.0542$) and that learning effects were larger in the second half compared to the first (84 ms vs. 163 ms, $F(1,26)=6.86$, $P<0.0145$). There was no reliable interaction of factors ‘group’ and ‘half’ indicating that both groups benefited from training in the same way.

Responses to standard letters were reliably faster than to perceptual deviants (second half, intentional: 706 vs. 860 ms, $F(1,13)=16.09$, $P<0.0015$, incidental: 718 vs. 777 ms, $F(1,13)=13.5$, $P<0.0028$, see also Footnote 1) or motor deviants (second half, intentional: 706 vs. 1016 ms, $F(1,13)=21.31$, $P<0.0005$, incidental: 718 vs. 844 ms, $F(1,13)=24.7$, $P<0.0002$), respectively. Intentionally instructed subjects learned more than subjects in the incidental group as indicated by a ‘stimulus type’ by ‘group’ interaction ($F(2,52)=5.37$, $P<0.0228$, $\epsilon=0.5857$).

Accuracy data revealed the same pattern of reliable results as RT data and are not reported in detail (see Fig. 1).

3.2.1. ERPs

Letters evoked ERPs with a prominent positive complex peaking over the centro-parietal part of the scalp. This positivity starts about 200 ms after stimulus onset and reaches its maximum at around 550 ms. Latency and scalp topography suggest that it is a P3b-component. The rising flank of this positivity is modulated by the experimental manipulations, especially 250–350 ms after letter presentation (N2b latency range).

ERPs for deviant letters elicited an enhanced negativity

¹Note that the contrast between standard letters and perceptual deviants is no longer reliable if the four subjects who performed better than guessing in the free recall task are excluded.

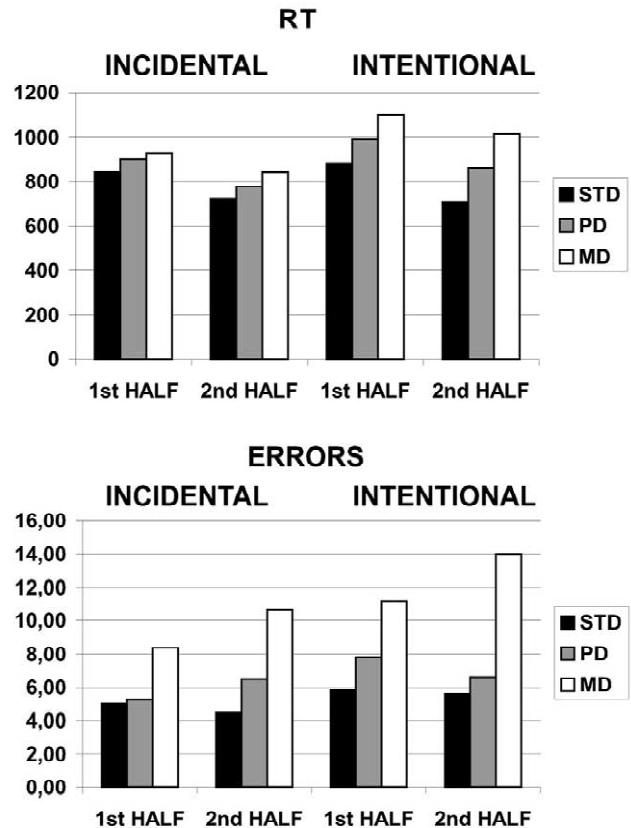


Fig. 1. RT (in ms, top) and errors (in %, bottom) for standard, perceptual and motor deviant letters for explicit and implicit learners in the first and second half of the experiment. Note the shortening of RT from the first to the second half and the differences between standard and both types of deviant letters in the second half of the experiment for both groups.

250–350 ms after stimulus presentation (N2b latency range) for intentional learners which is more pronounced in the second half of the experiment. No effect of stimulus deviance is obtained for incidental learners in the N2b latency range (see Fig. 2). Statistically, this group difference is reflected by a three-way interaction: stimulus type by half by group ($F(2,52)=4.79$, $P<0.0124$, $\epsilon=0.9969$).

The N2b-effect for explicit learners has a broad scalp distribution with a centro-parietal maximum (see Fig. 3). Separate ANOVAs for single electrode sites revealed significant interactions of ‘half’ and ‘stimulus type’ that show that the deviance effect emerges with training (frontal: Fz $F(2,26)=6.38$, $P<0.0081$, $\epsilon=0.8773$; central: Cz $F(2,26)=7.04$, $P<0.0042$, $\epsilon=0.9581$; parietal: Pz $F(2,26)=5.42$, $P<0.0140$, $\epsilon=0.892$; the respective contrasts between perceptual deviants vs. standards and motor deviants vs. standards were also reliable).

ERPs for intentional and incidental learners also differed in the P3b latency range (450–600 ms) as reflected by a ‘stimulus type’ by ‘group’ interaction in the four-way ANOVA ($F(2,52)=3.55$, $P<0.0358$, $\epsilon=1.0604$). Stimulus deviance had no reliable effect on the ERP amplitudes for the incidental group. However, for intentional learners,

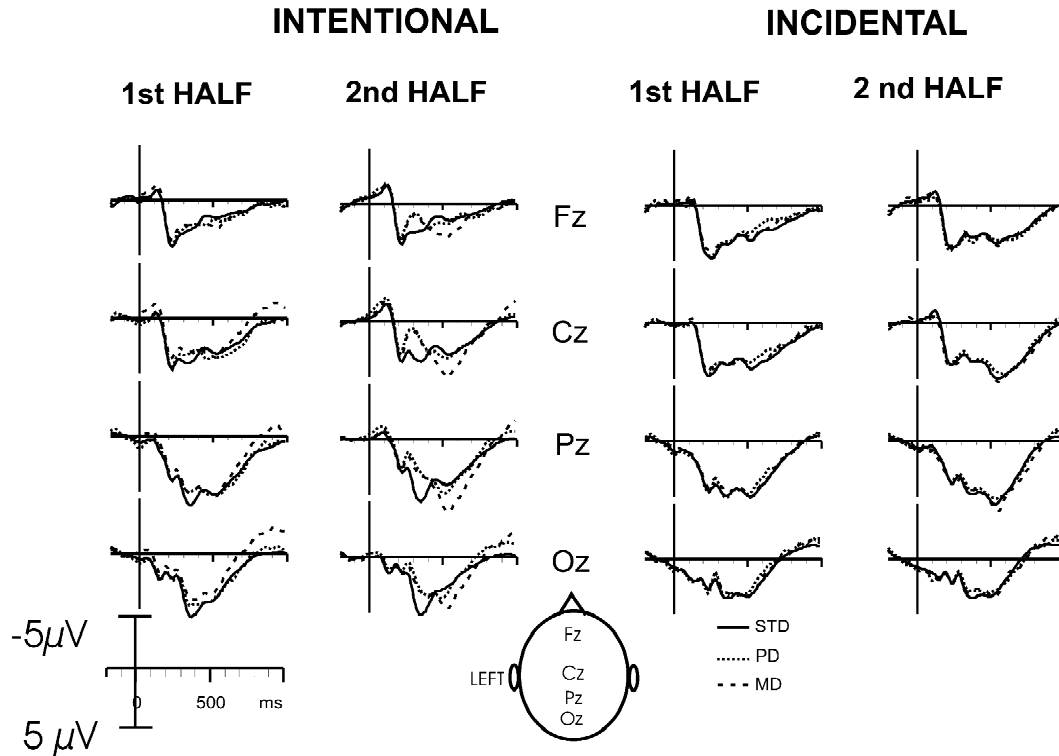


Fig. 2. ERPs at midline electrode sites (Fz, Cz, Pz and Oz) for standard (solid line), perceptually deviant (dotted line) and motor deviant letters (dashed line) separately for both experimental groups (intentional left, incidental right) and first and second half of the experiment. Note the absence of deviance effects for incidental learners.

P3b amplitude was more positive for perceptual as well as motor deviants compared to standard letters in the second half of the experiment. This effect has a broad scalp distribution with a parieto-occipital maximum. Statistically, it is reliable at frontal (Fz: main effect stimulus type, $F(2,26)=4.37, P<0.0232, \epsilon=1$), central (Cz: stimulus type by half interaction, $F(2,26)=5.22, P<0.0124, \epsilon=1$) and parietal electrode sites (Pz: standard letters, second half: $3.9 \mu\text{V}$, perceptual deviants: $4.54 \mu\text{V}$, motor deviants $5.74 \mu\text{V}$, stimulus type by half interaction, $F(2,26)=6.9, P<0.0005, \epsilon=0.8690$). However, only the contrasts between standards and motor deviants turned out to be reliable.

Fig. 3 depicts the scalp distribution of the N2b- and P3b-components for intentional learners in the second half of the experiment. To test whether the neural generators of the N2b- and P3b-effects are different, we standardized the mean amplitude of the difference waves of standards and motor deviants in time-windows 250–350 ms (N2b) and 450–600 ms (P3b) for each subject prior to computing an ANOVA. This is necessary as, because of non-linearity of signal conduction in the brain tissue and in the skull, ANOVA models may confuse differences in the amplitude of an EEG signal (due to differences in source strength) with genuine topographic differences [30]. The ANOVA revealed that the sources for the two components are

indeed different (group by electrode interaction: $F(60,780)=6.6, P<0.0000, \epsilon=0.3029$).

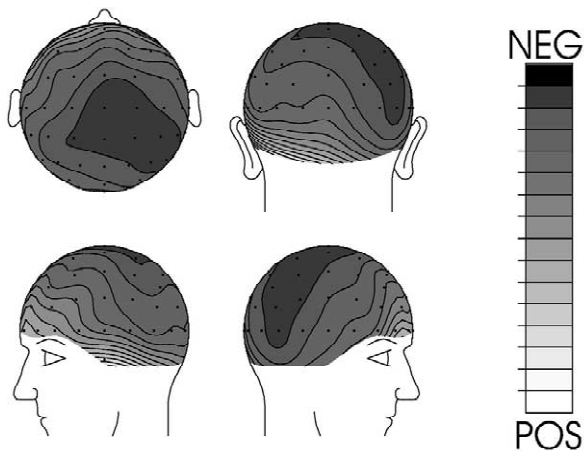
Fig. 4 shows the topography of the N2b-effect in consecutive time-windows. The N2b starts centro-frontally and shifts in topography towards centro-parietal positions with time. Thus, it seems that both a fronto-central and a centro-parietal N2b are influenced by stimulus deviance in this experiment.

To summarize, stimulus deviance had no effect on the ERP-waveforms of incidental learners although they showed better performance in structured parts of the sequence compared to random or deviating stimuli. However, for subjects learning intentionally, ERPs evoked by deviant letters showed a larger negativity for perceptual and motor deviants 250–350 ms after stimulus presentation as well as an enhanced P3b amplitude for motor deviants.

4. Discussion

In the present study, differences between intentional and incidental learning of a perceptuo-motor sequence were analysed by means of ERPs and performance measures. RTs indicated that both groups learned the sequential regularities inherent in the stimulus material: (1) mean RT in random stimulus blocks was prolonged in comparison to

N2b



P3b

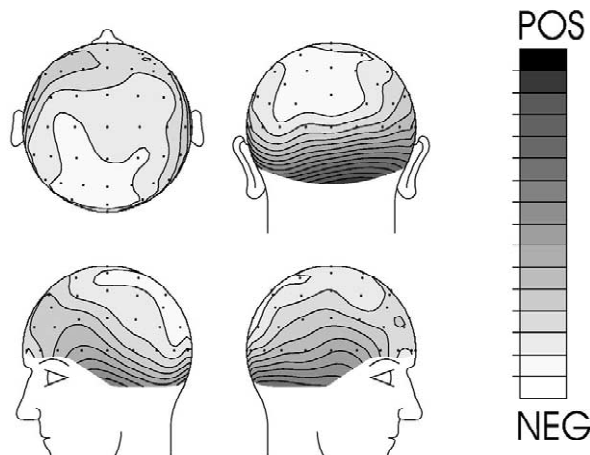


Fig. 3. Scalp distribution of the N2b- and P3b-effects for intentional learners in the second half of the experiment computed as the difference potential between standard letters and motor deviants. Top, N2b. Darker shading indicates larger negativity. Bottom, P3b. Darker shading indicates larger positivity.

non-random letters in the structured blocks; (2) RT for standard letters decreased with practice and (3) responses to standard letters were faster than responses to deviant letters, and this difference was more pronounced in the second half of the experiment, i.e. the magnitude of the effect depended on the amount of training. As in other studies, learning was also evident in performance measures for subjects who did not possess explicit knowledge of the sequence [31]. Intentionally instructed learners showed larger performance effects than subjects who were not told about the presence of a sequence prior to performing the SRTT. Similar results have been obtained by Refs. [5,14]. In our task, learning may have been more difficult because of the inclusion of deviant letters. Furthermore, the aforementioned experiments used spatially arranged response

cues instead of letters. Thus, our results extend previous findings of differences in the amount of intentional and incidental learning to longer and more complex sequences and different response cues.

Deviants that either violated the stimulus sequence or the stimulus and the response sequence evoked a larger N2b-component in intentional learners. Furthermore, deviants violating the response and the stimulus sequence evoked a larger P3b component. For the group of incidental learners ERP-effects of stimulus deviance did not occur at all. Eimer et al. [11] also found ERP-effects of stimulus deviance for subjects only who were able to identify the sequence after performing the SRTT. In contrast, Baldwin and Kutas [1] reported an enhanced positivity for deviant events for implicit learners, too. However, in their experiment subjects experienced about five times as much training as in the present study or in the study of Eimer et al. [11]. Explicit knowledge in the Baldwin and Kutas-study was induced by teaching participants the rules inherent in the stimulus material prior to the serial RT task whereas in the present study learning was intentional, but no teaching of the sequence took place. In Baldwin and Kutas' experiment, subjects had to respond only on trials in which a predefined target movement was presented. In the present study, however, participants had to respond to each letter. Furthermore, most of the subjects performed better than chance in a post-experimental questionnaire that assessed the amount of accessible sequence knowledge acquired during the learning phase. Thus, the ERP-effects found by Baldwin and Kutas [1] could be due to a small amount of verbal knowledge acquired by implicit learners during the task.

In previous research, a comparison of Go- and NoGo-trials in RT-tasks revealed an enhanced amplitude of the N2b-component for NoGo-trials at fronto-central electrode sites [26,32,48] even if Go- and No/Go-trials appeared equally often [10,24,44]. This is similar to the effect observed for deviants in the present experiment (see Fig. 4). Fronto-central N2b-amplitude enhancement was also found for covert cognitive responses [33], indicating that it does not seem to be restricted to the necessity to withhold a motor response but may appear whenever either overt or covert response preparation has to be interrupted.

Gehring et al. [15] found the fronto-central N2b to be sensitive to flanker compatibility in a flanker task. It has been proposed that the sensitivity of the fronto-central N2b to the compatibility of the flanker stimuli is functionally related to an interruption of an incorrect response if a competitive response is primed [27]. The present results are compatible with this view: for motor deviants, the expected and already initiated response has to be inhibited prior to activation and execution of the unexpected, deviating response. In contrast, perceptual deviants do not require a change of the primed response. Nevertheless, RT for perceptual deviants is enhanced. The (conscious) detection of a deviant from an expected stimulus might

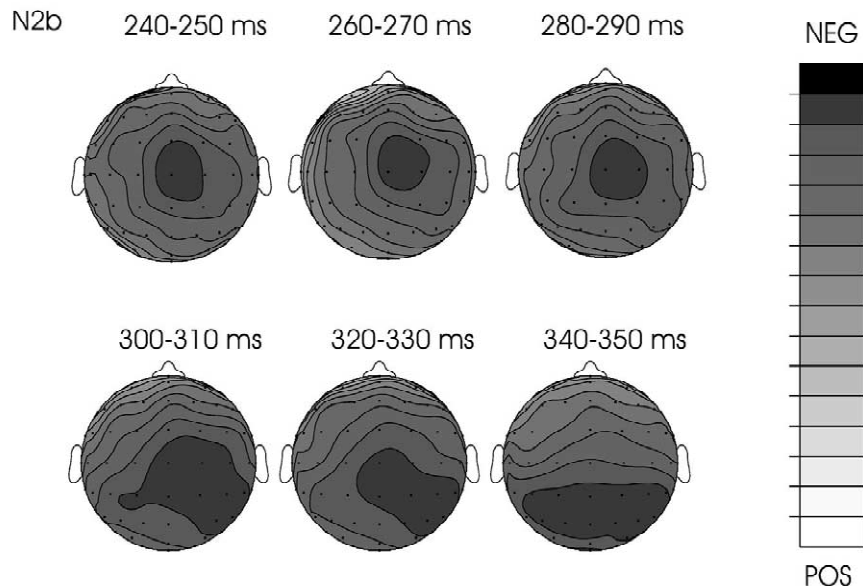


Fig. 4. Scalp distribution of the N2b-component in the second half of the experiment for intentional learners computed as the difference potential between standard letters and motor deviants. N2b is shown in six time-steps each covering 10 ms starting 240–250 ms after letter presentation and ending 340–350 ms. Darker shading indicates larger negativity.

initiate an inhibition of an already prepared response. After an additional check of the correctness of the prepared response, this inhibition will be released and the correct response will be executed. This process might be indicated by the enhanced frontal N2b. This interpretation would also account for the enhancement of RT to perceptual deviants.

Most interestingly, the group of incidental learners does not show an enhanced frontal N2b amplitude for motor deviants despite a prolonged RT for these stimuli. Thus, the fronto-central N2b seems to be no prerequisite for the inhibition of a primed response, but rather seems to be related to a ‘conscious’ detection of a stimulus deviation.

ERPs of intentional learners also showed a reliably larger P3b for motor deviants compared to perceptual deviants or standards. This effect was more pronounced in the second half of the experiment, i.e. it depended on the amount of training. As the P3b was affected by motor deviants only and the centro-parietal N2b was affected by both types of deviants one has to conclude that the generating mechanisms are functionally distinct. Furthermore, a comparison of the standardized topographic maps confirmed that the sources of the N2b- and the P3b-effect are different. Gehring et al. [15] argued that the N2b component could reflect a process which is sensitive to any deviation of an actually perceived stimulus from an internal model that comprises all perceptual features of the next stimulus to be expected. In the present study, both, perceptual and motor deviants, differed perceptually from the next most likely, regular stimulus. Thus, it is not surprising that both bear an effect on the N2b.

In addition to the mismatch with an expected stimulus template, the motor deviant also contains task-relevant

information in the sense that after perceiving it the subject has to change a primed action or motor program. Task relevance in this sense has been found to be an important antecedent condition for the elicitation of a P3b component [7,25]. P3b amplitude is larger in the case of a silent counting response than if a rare stimulus is only passively watched. Thus, encountering a motor deviant does not only enforce an update of the stimulus sequence model but also an update of the currently held action model. It seems likely that this additional updating step is reflected by an increase of P3b amplitude.

In principle, these ERP-effects could reflect (1) the conscious awareness and expectation of particular items in the sequence; (2) the general awareness that a sequence exists; (3) the intention to learn the sequence or (4) some interaction between these factors. To shed some light on this issue, we compared ERPs and RTs for those intentional learners who exhibited good sequence knowledge in the free recall procedure (more than 10 consecutive letters correctly recalled, subjects # 21, 22, 23, 26, 34) with those intentional learners who did not perform better than guessing in the free recall task (two or less consecutive letters correctly recalled, subjects # 24, 27, 31, 33). Both subgroups learned the sequence as reflected in an increase in RT for the random block and for both types of deviant stimuli. As can be clearly seen in Fig. 5, ERP-effects were only present for intentional learners who also exhibited sequence knowledge in the free recall task. Thus, we conclude that the ERP-effects for the intentional group reflect specific expectations of particular items in the sequence (for a similar conclusion, see Ref. [43]).

We found ERP-effects of stimulus deviance only for intentional learners although both, intentional and inciden-

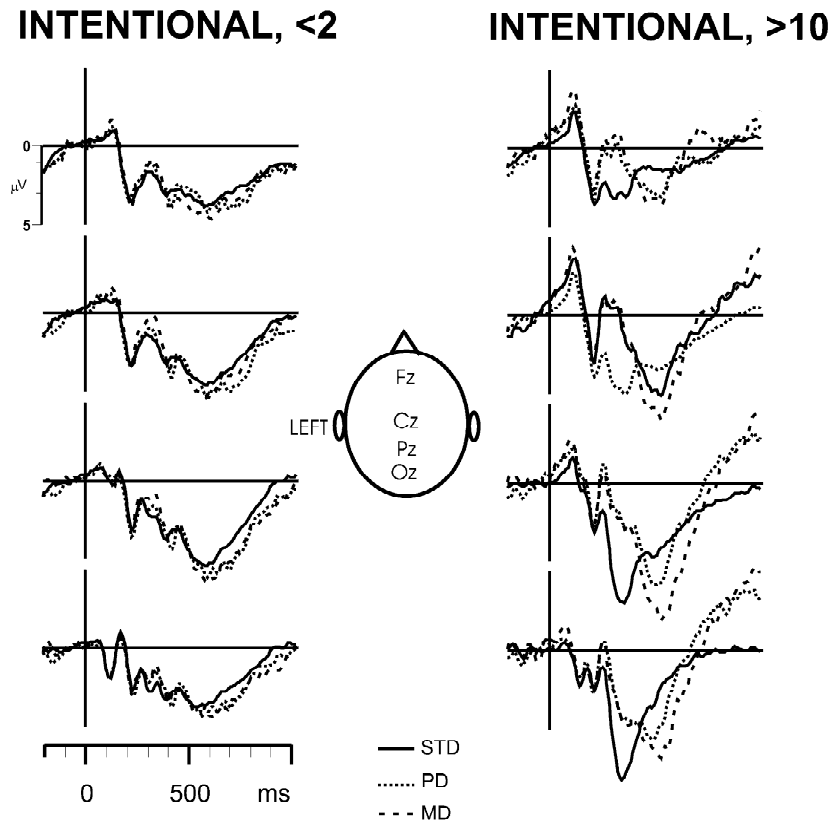


Fig. 5. ERPs at midline electrode sites (Fz, Cz, Pz and Oz) for standard (solid line), perceptually deviant (dotted line) and motor deviant letters (dashed line) in the second half of the experiment for intentional learners with a free recall performance ≤ 2 (left) and > 10 consecutive letters (right). See text for details.

tal learners, showed clear signs of knowledge acquisition. The EEG reflects mostly cortical activity; thus, subcortical structures could be involved in incidental learning. Among others, the basal ganglia, the cerebellum, the thalamus and the corpus callosum have been shown to be involved in serial learning [6,7,9,12,21,28,36,50]. Imaging studies which compared implicit and explicit learning have mostly supported the idea that different neural systems are involved in both forms of learning. In a positron emission tomography (PET)-study of implicit and explicit sequence learning using the SRTT, Rauch et al. [35] found different neural structures to be involved in both forms of learning. Implicit learning was mediated by a distributed system comprising the right ventral premotor cortex, the right ventral striatum, the right thalamus and bilateral visual association cortices. Explicit learning was accompanied by activations of motor-related system components (cerebellum, thalamus, brain stem) and activity in the primary visual cortex, the peri-sylvain cortex, right middle frontal and right middle temporal cortex. Grafton et al. [16,17] used a short (six elements) spatial sequence to compare brain areas involved in implicit and explicit learning with PET. The motor cortex was involved in implicit learning. Sensorimotor cortex, SMA and putamen formed a cortical-subcortical motor loop that seemed to be of prime importance for implicit sequence learning. Parietal and

prefrontal cortical areas were involved in explicit sequence learning. Finally, Doyon et al. [8] found similar brain regions involved in implicit and explicit sequence learning using functional magnetic resonance imaging (fMRI). Increased levels of learning-related activity were found in sensory-motor, premotor and striatal regions as well as in the SMA in both learning conditions.

Taken together, these findings and the results of the present study provide support for the idea that different neural systems are involved during implicit and explicit learning in sequential reaction time tasks.

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