IMPLICIT AND EXPLICIT LEARNING OF EVENT SEQUENCES: AN ANALYSIS WITH EVENT-RELATED BRAIN POTENTIALS

Dissertation
zur Erlangung des Doktorgrades der Naturwissenschaften
(Dr.rer.nat.)

dem
Fachbereich Psychologie
der Philipps-Universität Marburg
vorgelegt

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Marburg/Lahn, 1999

CONTENTS

I. INTRODUCTION

In 1951 Karl Lashley highlighted the fundamental importance of sequential organization for intelligent behavior. Indeed, it is easy to see that acquisition of knowledge about sequential organization of the environment is important for most higher organisms: for example, finding a way in a city requires perception and storage of a sequence of landmarks. Likewise, starting a car, preparing a meal, or doing other manual work needs the initiation and execution of a regular sequence of movements.

The ability to understand and produce language illustrates that not only first order conditional probabilities, but also higher order, sequential dependencies and even more complex logical or grammatical rules determine which element is allowed to follow another in a sequence of events. These examples make clear that the nervous system must be particularly sensitive to regularities which are present in our environment. It recognizes lower and higher order sequential dependencies and is able to abstract more complex rules from the perceptually encountered ‘raw material’. These regularities are permanently stored and can be reproduced intentionally.

The basic ability to acquire and produce sequential dependencies is not exclusive to the human nervous system. Systematic research on animal cognition has shown that other species, e.g. pigeons, rats, cats, dogs and monkeys exhibit sequential behavior and develop sequential representations as well (Compton, 1991; Roitblat, 1987; Roitblat & von Fersen, 1992; Terrace & McGonigle, 1994).

Although there is hardly any doubt about the fact that sequential dependencies are learned by humans and other species it is still an open question how this is accomplished. According to one influential view, the acquisition of motor, perceptual, and cognitive skills can be seen as a process whereby declarative rules, initially communicated in a verbal form, are transformed into procedural knowledge in the course of extended practice (e.g. Anderson, 1983, 1987). In contrast to this idea, everyone has probably experienced that mastery of a skill does not always depend on prior acquisition of explicit, verbalizable knowledge. For example, being able to speak a language does not require explicit knowledge about the underlying grammatical rules. On the other hand, verbalizable knowledge about the dynamics of moving human bodies does not help one to ride a bicycle. Thus, many sequential skills seem to be acquired without encoding of verbal rules and even without the development of conscious knowledge about the underlying structure of the input into our brain. Learning of the latter type has been termed implicit (e.g. Reber, 1967). An increasing amount of research has been conducted in the last decade to reveal how implicit, serial learning is accomplished (Buchner & Wippich, 1998), and the issue is still under investigation.

Another open question concerns the neuronal representation of knowledge acquired in sequence learning situations. Neuropsychology has provided much evidence that declarative learning can be functionally dissociated from procedural learning. The former is tied to an intact temporal lobe system while the latter seems to be linked to an intact cerebellum and basal ganglia.

The distinction between declarative and procedural learning and memory has much in common with the explicit-implicit dichotomy, but it is not completely congruent. Again, the question arises which system is particularly sensitive to sequential order, which system performs the one type of rule learning or the other, and how both systems might interact during acquisition and production of structured event sequences.

Systematic research on these issues needs well-controlled experiments which allow the effects of isolated manipulations of single variables to be studied. The so-called serial-reaction-time (SRT) task is one of several which has been used to study implicit and explicit learning of perceptuo-motor event sequences.

This chapter starts with a definition of implicit learning and a description of the paradigms used to study the phenomenon. Secondly, the SRT-task and some basic findings are reviewed in more detail. Several theoretical accounts of implicit serial learning are discussed. Studies using event-related brain potentials (ERPs) and imaging techniques to reveal the brain structures involved in serial learning are described.

I.1 Implicit learning

I.1.1 Definition of implicit learning

> ***"The language scientists initially adopt to describe phenomena of interest frequently becomes an unsuspected source of difficulty in creative thought and an obstacle on the path to progress."*** (Tulving, 1984)

In implicit learning research, different definitions of the concept of implicit learning have been proposed. A coexistence of multiple meanings for the same concept can be stimulating for research, as long as the differences are small compared to their commonalities. If, however, the differences become larger than the commonalities, different definitions of the very same concept can be counterproductive for scientific progress. The latter seems to be the case in implicit learning research. Therefore, it is necessary to have a look at definitions adopted by researchers in the field and to analyse their commonalities and differences.

Berry & Broadbent (1988) considered learning to be *"implicit, when people are merely told to memorize the specific material presented, but nevertheless learn about the underlying rules."*

Mathews, Buss, Stanley, Blanchard-Fields, Cho, & Druhan (1989) think of implicit learning as *"an alternate mode of learning that is automatic, nonconscious, and more powerful than explicit thinking for discovering nonsalient covariance between task variables."*

Reber's (1993) influential definition characterizes implicit learning as *"a situation neutral induction process whereby complex information about any stimulus environment may be acquired largely independently of the subjects' awareness of either the process of acquisition or the knowledge base ultimately acquired."*

Stadler & Frensch (1994) argue that *"learning is implicit when the learning process is unaffected by intention."*

According to Lewicki, Czyzewska, & Hoffman (1987) implicit learning occurs if *"subjects are able to acquire specific...knowledge...not only without being able to articulate what they had learned, but even without being aware that they learned anything."*

Finally, Baldwin,& Kutas (1997) consider *"task exposure"* which *"facilitates performance without producing corresponding changes in verbalizable knowledge"* as a case of implicit learning.

Frensch (1998) examined these and some other definitions of implicit learning and concluded that they differ in whether they (1) attach the label "implicit" to learning processes alone or to learning and retrieval processes, and, (2) in whether the label "implicit" is synonymous with unconscious/unaware or nonintentional/automatic. He goes on to show that the definitions differ with respect to their uniqueness, i.e. differences between the concept of implicit learning and related concepts like implicit memory or incidental learning, their operationalization, i.e. how a concept can be measured, and their predictive value. From this analysis, Frensch (1998) concludes that a definition of implicit learning that emphasizes the learning process itself and nonintentionality/automaticity is scientifically more useful than other definitions of implicit learning.

To discriminate implicit learning from implicit memory it seems to be useful to stress the learning process proper and, thus, focus on learning processes rather than retrieval.

In empirical studies, nonintentionality is induced by instructional manipulations, i.e. the participants are given no information about the presence of regularities in the stimulus material prior to performing the task. Automaticity can be induced by using the dual-task method, i.e. subjects are exposed to two tasks simultaneously (e.g. a SRT-task and counting of one out of two different tones which are concurrently presented). Therefore, from a perspective concerning the assessment of knowledge, it seems useful to stress nonintentionality (instead of awareness/unawareness) in a definition of implicit learning.

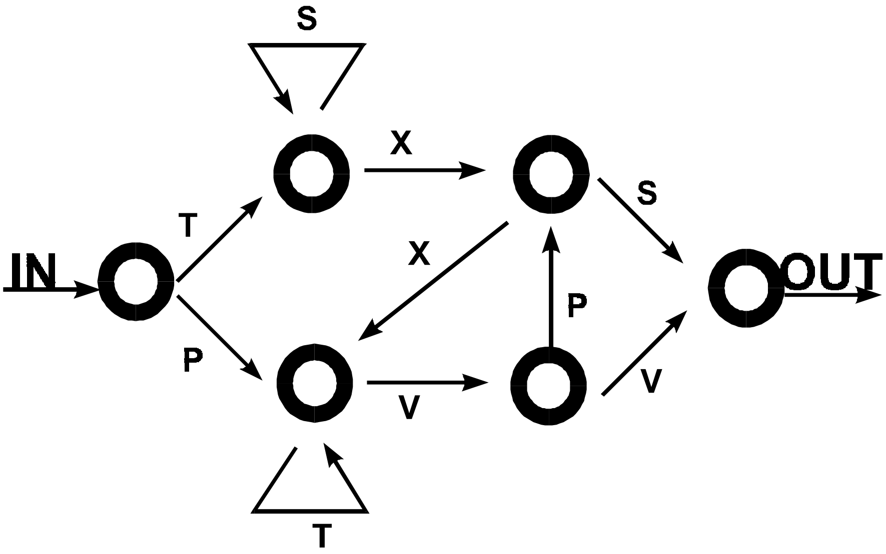
In the following implicit learning is defined as *unintentional learning which leads to performance improvement without verbalizable knowledge about the stimulus regularities which are responsible for performance improvement.*

I.1.2 Experimental paradigms in the study of implicit learning

A variety of experimental tasks have been used to study implicit learning phenomena (for a review, see Seger, 1994).

I.1.2.1 Artificial grammar learning

Implicit learning was first demonstrated by Reber (1967). In artificial grammar learning tasks (AGL), subjects are confronted with trains of letters (typically 3-7 letters long) which are formed according to an artificial grammar (see fig. 1). In a training phase, participants are instructed to memorize the letter trains. In a subsequent test phase subjects are asked to make "wellformedness" judgements on a set of letter trains they have not previously seen and which are either constructed according to the grammar or contain violations of the grammatical structure ("wellformedness" refers to whether the letter string is constructed according to the grammatical rules). Typically, subjects are able to judge 55-85 % of the letter strings correctly without being able to tell the experimenter about the basis of their judgements (e.g. Reber, 1967, 1976; Shanks, Johnstone, & Staggs, 1997; Vokey & Brooks, 1992; for reviews see Reber, 1989, 1993). These results were interpreted (e.g. Reber & Allen, 1978) as support for the hypothesis that rule-based information can be implicitly abstracted given limited experience with highly structured stimulus domains. In a number of studies, however, it could be shown that similarity of test items with the previously presented learning items (Vokey & Brooks, 1992), learning of fragments of the letter train (Perruchet & Pacteau, 1990) and the method of construction of the incorrect letter trains (Shanks, Johnstone, & Staggs, 1997) can account for the observed performance. These results form the basis of an alternative explanation which does not postulate the existence of implicit learning processes in AGL (Perruchet & Pacteau, 1990; Shanks & St.John, 1994) but explains the observed learning effects in terms of chunks consisting of fragments of the letter train which are learned and which are explicitly recallable.



Examples for correct strings:
TXS
TSXS
TSSXXVV

Figure 1: One of the artificial grammars used by Reber (adapted from Reber, 1993). Each transition from one circle to the next along the arrows produces the letter which is next to the arrow.

I.1.2.2 Complex system control

In complex system control tasks, subjects have to learn to control one variable by manipulating another one (e.g. Berry & Broadbent, 1984, 1987, 1988; Broadbent, FitzGerald, & Broadbent, 1986; Stanley, Mathews, Buss, & Kotler-Cope, 1989). Unknown to subjects, the values of the two variables are related by an equation. For example, in Berry & Broadbent's (1984) sugar production task, participants have to control the amount of sugar output of a factory by manipulating the size of the work force. The relation between the two variables is defined as Production = 2 X work force - production on trial n-1 + random factor. Typically, subjects show incongruences between performance improvement and explicit knowledge about the task. Berry (1991) used a number of different types of questions to assess the amount of explicit task knowledge and found a dissociation between task performance and verbalizable knowledge. However, results of a study by Stanley and colleagues (1989) found that this dissociation is not as complete as it initially seemed. More likely, people appear to develop some explicit knowledge as a result performing the task, but it seems that increases in explicit knowledge occur after improvements in task performance and are observable only after preceding interactive experience with the task (Berry, 1991, 1994).

On the basis of the aforementioned data, Berry, & Broadbent (1988) postulated the existence of two distinct learning mechanisms: (1) An implicit or unselective mode (u-mode) in which subjects observe all present variables unselectively and store the contingencies between them, and, (2) an explicit, selective mode (s-mode) in which a few key variables are selected and only contingencies between these key variables are stored. The difference between both modes is viewed as an architectural one, i.e. the s-mode is assumed to involve the use of abstract working memory whereas the u-mode passively aggregates information about the co-occurence of environmental events and features (Hayes & Broadbent, 1988). In light of the results of Stanley, Mathews, Buss, & Kotler-Cope, (1989) and others the sharp dichotomy between these two learning mechanisms has been replaced by thinking in terms of a number of learning mechanisms which differ in the extent to which actions are driven by conscious beliefs (Berry, 1994).

I.1.2.3 Covariation learning

There are some experiments which show learning of covariations between features within visual stimuli or between a feature of a visual stimulus and a verbal label. For example, Musen & Squire (1993) used the Stroop-task (Stroop, 1935) to demonstrate that implicit learning of color-word associations is possible. Subjects were confronted with color words which were printed in incongrous colors and had to name the color in which the word was printed as quickly as possible (e.g. the word "green" printed in red ink, correct answer: red). Each of the color words used was associated with the same incongrous color for six repetitions. After this first phase, the color-word associations were changed without notifying the subjects. A decrease in color-naming time which was specific to learning of the word-color-association could be found (Musen & Squire, 1993, Exp.1). In further experiments, it could be shown that this effect is not dependent on the interference inherent in the Stroop-task (Exp. 2) and that it does not rely on immediate memory (Exp. 4). In all these experiments, subjects could not recognize the color word - word ink - association in a postexperimental questionnaire; thus, it can be concluded that learning in this task was implicit.

Miller (1987) showed that subjects are able to learn associations between task-relevant, centrally presented letters and task-irrelevant flanker letters without being able to verbalize this association. Other studies involved associations between pictures of women and verbal descriptions of their personality (Lewicki, 1986) or tasks which require subjects to learn to classify stimuli into different categories based on (implicitly acquired) covariations (Hill, Lewicki, Czyzewska, & Boss, 1989; Lewicki, Hill, & Sasaki, 1989). Most interestingly, these experiments showed that learning is possible even if covariations to be learned are nonsalient.

I.1.2.4 Complex pattern learning

Lewicki, Hill, & Bizot (1988) measured RT for locating a stimulus (X-mark) in a 2 X 2-matrix. The stimulus position depended on the location of previously presented items. With training, subjects showed a decrease in RT to the critical stimulus without showing any verbalizable knowledge about the underlying regularities (but see Perruchet, Gallego, & Savy, 1990, for contradictory results).

I.1.2.5 Implicit learning in motor tasks

Only a few studies explored implicit motor learning. Pew (1974) demonstrated implicit learning in a pursuit tracking task. Subjects had to keep track of a movement pattern with a pursuit rotor which was random for 66 % of the time and repeated in the remaining 33 % of time. Subjects performed better during the repeated part of the tracking task despite not being able to verbally report that there was a repetition in the movement pattern. Wulf & Schmidt (1997) were able to show that implicitly acquired knowledge about a movement transferred to a condition where the movement pattern of the repeating part remained the same but the amplitude or the timing of the movement were changed. They concluded that participants learned some abstract, fundamental aspects of the spatio-temporal pattern that could be scaled later either in amplitude or in speed.

In an interesting analysis, McLeod & Dienes (1993) found that ball-catching involves learning to run in a way in which a trigonometric function is kept at zero. This strategy used in ball-catching cannot be consciously recalled. Green & Flowers (1991) showed that participants were able to exploit probability relationships between a ball's pathway and the position where the ball was to be caught without being aware of these relationships.

SRT-task. The SRT-task is - together with AGL - the most often-used task in the study of implicit learning processes. As the SRT-task is used in the present experiments, theoretical considerations and experimental results obtained with the paradigm will be reviewed in more detail.

I.2 The SRT- task

Nissen & Bullemer (1987) introduced the SRT-task to study learning of regularities in event sequences by means of performance improvement. In a typical SRT-experiment, visual stimuli (typically the letter ‘X’ or an asterisk) are presented in one of four different positions on a computer screen. Subjects are instructed to press a corresponding key for each position as fast and as accurately as possible. Unknown to subjects, the stimuli appear according to a repeated sequence of positions (e.g. in the sequence known as the Nissen & Bullemer sequence, 4-2-3-1-3-2-4-3-2-1, 1 corresponds to the leftmost, 4 to the rightmost position of the horizontally aligned display (see fig. 2)). Note that after the lOth stimulus the sequence reverts to the beginning.

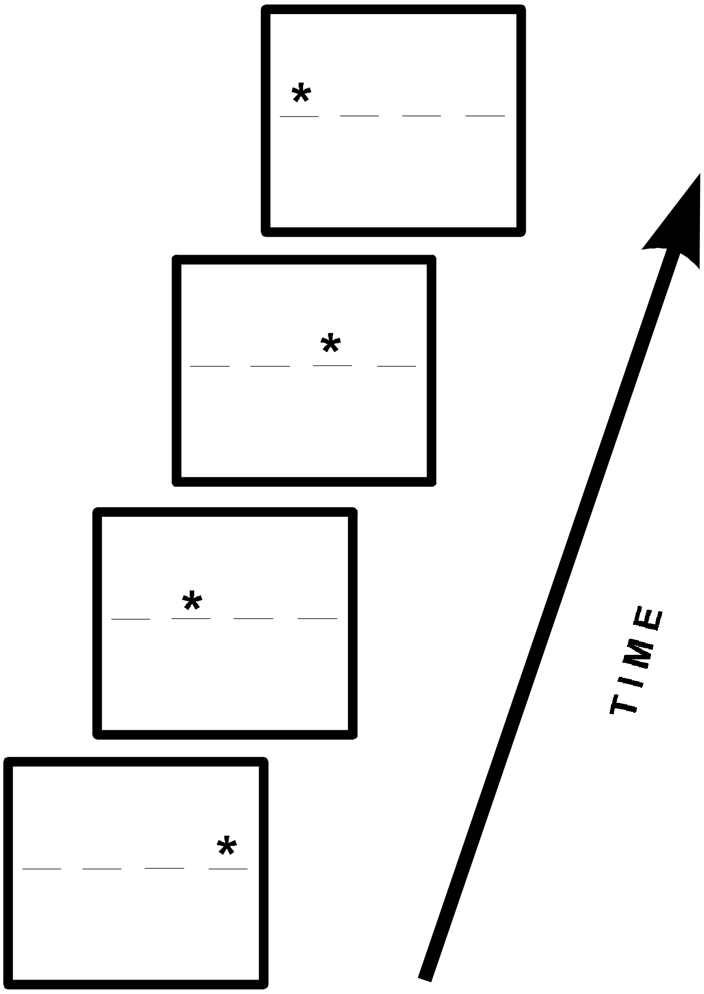


Figure 2: Basic experimental setup in the SRT-task as introduced by Nissen & Bullemer (1987). Whenever a star is presented in one of the four locations, the subject has to press a corresponding key as fast as possible. After the key is pressed the star disappears. 500 ms after the response the next star is presented.

In their initial study with the SRT-paradigm, Nissen & Bullemer (1987) used a between-subjects approach to assess serial learning. They compared performance of a group of subjects who saw the ten-trial Nissen & Bullemer-sequence with a group which received a random sequence throughout the eight training blocks. The initial level of reaction time (RT) was the same for both groups. With increasing practice, an RT-difference between the two groups emerged: RT for the random group remained at the same level throughout the eight blocks whereas RT for the structured group decreased from about 320 ms in the first block to about 170 ms in block 8.

Most subsequent studies of sequence learning used a within-subject approach to assess learning: After some structured training blocks, subjects are transferred to a random sequence of stimuli. Learning of the stimulus sequence is assessed indirectly by comparing mean RT in the random block with RT in the preceding structured (sequential) stimulus block. An increase of RT in the random block is taken as evidence of sequential learning (note that stimuli in the random blocks are matched to those in structured blocks with regard to overall stimulus probability. For brevity, these pseudorandom blocks are termed random.). The prolongation of RT in the random compared to the preceding structured block has been found in a number of experiments (e.g. Cleeremans & McClelland, 1991; Cohen, Ivry, & Keele, 1990; Curran & Keele, 1993; Eimer, Goschke, Schlaghecken, & Stürmer, 1996; Frensch & Miner, 1994; Frensch, Buchner & Lin, 1994; Heuer & Schmidtke, 1996; Howard, Mutter, & Howard, 1992; Stadler, 1992, 1995; Willingham, Nissen, & Bullemer, 1989; Willingham, Greenberg, & Thomas, 1997; for reviews, see Clegg, DiGirolamo, & Keele, 1998; Curran, 1995; Rüsseler & Rösler, 1999).

I.3 Theoretical accounts of (implicit) sequence learning

Several important issues in the implicit learning domain have been investigated with the SRT- paradigm. First, researchers have tried to establish that learning in the SRT-task can occur implicitly, i.e. without concurrent development of verbalizable knowledge. Dissociations between performance (RT-improvement) and explicitly recallable knowledge about the underlying stimulus structure are taken as evidence for implicit learning. In this context, several methodological problems centered around the assessment of explicit knowledge emerged.

Several models of sequential learning have been developed. In general, it is assumed that an associative learning mechanism which links subsequent elements in the structured blocks is responsible for learning. However, models differ with respect to the role of attention and the number of postulated learning mechanisms.

Another line of research concerns the code of the acquired knowledge.

After a review of the relevant literature, event-related potentials (ERPs) are introduced as a promising method for investigating these issues.

I.3.1 Awareness of stimulus-structure in the SRT-task

Nissen & Bullemer (1987) first showed that learning of perceptuo-motor sequences in the SRT-task as reflected in an RT-benefit for sequentially structured compared to unstructured blocks can occur without the development of conscious awareness in amnesic patients. Nissen, Knopman, & Schacter (1987) found that subjects given scopolamine prior to the experiment showed impaired performance in a verbal memory task while sequence learning remained unaffected. Scopolamine is known to have reversible effects comparable to amnesia. The scopolamine subjects failed to exhibit any knowledge of the sequential stimulus structure, indicating that there is a dissociation of brain systems responsible for structured sequence learning and systems responsible for declarative memory.

Other investigators found that healthy subjects also learned sequential dependencies without even noticing that the material contained any structural regularity (e.g. Cherry & Stadler, 1995; Curran & Keele, 1993; Frensch & Miner, 1994; Howard & Howard, 1989, 1992; Mayr, 1996; McDowall, Lustig, & Parkin, 1995; Reed & Johnson, 1994; Stadler, 1993, 1995).

Recently, some authors questioned the notion that learning in the SRT-task occurs without conscious awareness of the sequential regularities. The main criticism concerns the reliability of the explicit knowledge tests.

Several techniques have been developed to assess the subjects' degree of postexperimental sequence knowledge: First, in free-recall tasks subjects are asked to reproduce the previously presented sequence. The percentage of correctly recalled items is taken as an indicator of the amount of explicit knowledge (e.g. Eimer, Goschke, Schlaghecken, & Stürmer, 1996).

Second, in the generate task (e.g. Reed & Johnson, 1994) subjects are confronted with the same stimulus-display as during training but have to predict the next stimulus rather than respond to an imperative stimulus. This procedure is problematic because knowledge of the perceptual event sequence (e.g. the locations on the display) and of the motor sequence (the sequence of subjects' responses) are tagged simultaneously. More importantly, Perruchet & Amorim (1992) criticized the reliability of the generate task. Most of the studies using this procedure provided feedback about the correctness of a given answer (e.g. Willingham, Nissen, & Bullemer, 1989), thus allowing subjects to gain further sequence-related knowledge during the test. As a consequence, only the trials of the first sequence cycle are used as a measure of explicit knowledge. Thus, the procedure hardly can be considered reliable due to the small number of trials (for critical examinations of the generate task, see also Jackson & Jackson, 1995; Jiménez, Méndez, & Cleeremans, 1996b). Therefore, Perruchet & Amorim (1992) developed the recognition task. Subjects are confronted with fragments of the previously seen stimulus sequence (e.g. bigrams, trigrams or quadrupels) and have to indicate whether or not these were part of the previously presented stimulus material (see also Willingham, Greeley, & Bardone, 1993). The percentage of correctly categorized sequence fragments is taken as a measure of explicit sequence knowledge. Perruchet & Amorim (1992) presented data showing that sequence learning can be fully explained on the basis of performance in a recognition task and concluded that learning is explicit (but see Willingham, Greeley, & Bardone (1993) for contradicting results; Perruchet & Pacteau, 1990, for a similar artificial grammar learning study).

In postexperimental questionnaires subjects are typically asked whether they noticed any structure in the presented material. Willingham, Greeley, & Bardone (1993) showed that postexperimental interviews are biased towards reporting the presence of regularities: 24.4 % of subjects exposed to random stimuli mentioned the presence of a repeating pattern.

Recently, Buchner, Steffens, Erdfelder, & Rothkegel (1997) proposed a new method for assessing implicit and explicit knowledge in the SRT-task which is based on the process dissociation procedure used in implicit memory research (Jacoby, 1991). It is assumed that sequence identification is based on recollection, perceptual or motor fluency, systematicity detection and guessing. Subjects perform the generate-task according to two different instructions: In the inclusion condition, they have to produce the sequence in the same way as in the traditional generate task whereas in the exclusion condition, participants are instructed to produce only sequences which were not part of the previously seen material. From this data, several parameters are computed which reflect conscious and nonconscious processes. In a series of experiments, Buchner, Steffens, & Rothkegel (1998) could not find a dissociation between performance and explicit knowledge in the SRT-task.

There is evidence that at least subgroups of subjects show performance improvements without being able to verbally report or reproduce the stimulus sequence irrespective of the method used to assess explicit knowledge. However, in a number of studies the lack of verbalizable knowledge was not complete to the extent that participants were able to recall at least fragments of the sequence. In the light of studies demonstrating a parallel development of verbalizable sequence knowledge and performance improvement (Perruchet, Bigand, & Benoit-Gonin, 1997) the extent to which sequential knowledge can develop without concurrent awareness of the underlying regularities still seems to be unresolved. Consequently, dissociations other than that of consciousness vs. unconsciousness need to be referred to if the uniqueness of the psychological construct implicit learning is to be proved.

Despite the ongoing debate about the issue of awareness in implicit learning, a number of researchers have tried to explore the processes involved in explicit and implicit serial learning.

I.3.2 Attentional vs. non-attentional learning mechanisms

In a model of sequence learning, Cohen, Ivry, & Keele (1990; see also Keele, Davidson, & Hayes, 1996) proposed the existence of two independent learning mechanisms which differ in their attentional demands. In a series of experiments they explored the influence of a distractor task on implicit learning of sequences which differed in their statistical structure. Three different types of sequences were used: Unique sequences which consist of unequivocally paired associations only (e.g. 1-2-3, where 1 is always followed by 2, 2 by 3 and 3 by 1), hybrid sequences which contain unique as well as ambiguous associations (e.g. 1-2-3-2-3-1-2, where

1 is always followed by 2, whereas 3 can be followed by either 2 or 1 depending on the preceding stimulus), and hierarchic sequences which comprise higher order dependencies only (e.g. 1-2-3-2-1-3, where 1 can be followed by 2 or 3, 2 by 3 or 1 and 3 by 2 or 1, depending on the predecessor of the actual stimulus). Without distraction, subjects learned all three sequence types with larger gains in response speed for unique than for hybrid and hierarchical sequences respectively. However, with a concurrently performed tone-counting task, only learning of unique and hybrid sequences was observed (one of two tones differing in pitch was presented after each imperative stimulus, and the subjects had to report the number of high-pitched tones after each block). Cohen, Ivry, & Keele (1990) concluded from these results that unique associations are learned by an automatic mechanism which does not require attention, whereas higher order, hierarchical dependencies are learned by a different, „controlled“ mechanism which can operate only if enough attentional resources are available (see also Curran & Keele, 1993). The model postulates two different implicit learning mechanisms (one attentional, one non-attentional) that operate independently of each other and in parallel.

This model has been challenged from different perspectives. Firstly, it was shown that in contrast to the findings of Curran & Keele (1993) and Cohen, Ivry, & Keele (1990), hierarchic sequences can be learned under dual-task conditions, too (Frensch, Buchner, & Lin, 1994; Heuer & Schmidtke, 1996; McDowall, Lustig, & Parkin, 1995; Seger, 1995). However, these different outcomes of the dual-task studies can also be explained in terms of variations in importance subjects ascribed to the secondary tone-counting task, as the outcome of dual-task situations depends heavily on the attention allocation policy (see Cohen, Wasserman, & Soroker, 1997). If this is not controlled by explicit instructions or pay-off matrices, results can hardly be interpreted at all (Navon & Gopher, 1979).

Secondly, some authors referred to different theoretical constructs to explain dual-task interference. Frensch & Miner (1994; Exp. 2) found sequence learning for short response- stimulus- intervals (RSI, 500 ms), but not for longer ones (l500 ms) in a dual-task situation with hierarchic sequences. In a single-task situation (Frensch & Miner, 1994, Exp. l), a 12-element sequence was not learned with a long RSI (l500 ms) but with a short RSI (500 ms). The lack of learning was explained by assuming that additional short-term memory (STM) capacity is needed for performing the concurrent tone-counting task. Therefore, a smaller number of consecutive elements of the sequence can be held in STM simultaneously and hierarchic associations cannot be formed. However, Willingham, Greenberg, & Thomas (1997; Exps. 3-6) found that whereas the length of the RSI did not affect sequence learning, it did affect performance. One group practiced with a short RSI (500 ms) and was shifted to a long RSI in a subsequent transfer phase (1500 ms; short-long condition) whereas a second group started with the long and was transferred to the short RSI (long-short condition). Subjects in the long-short condition exhibited less sequence learning than short-long subjects in the training phase. However, in the subsequent transfer phase, long-short subjects showed significant transfer indicating that they had learned the sequence. In contrast, for the short-long group, no transfer of sequence knowledge was found. Thus, it seems that prolonging the RSI does not affect learning per se, but does affect performance of the subjects. This could be due to attentional effects: Subjects who started with the long RSI-condition might have found the experiment boring and, as a consequence, were not very attentive, whereas in the transfer phase, they noticed a change in the procedure which caught their attention. Short-long subjects, in contrast, might have found the task much more boring in the transfer phase with the long RSI.

Stadler (1995) observed that learning of sequences with random RSIs between successive elements (i.e. no additional attentional load, but disruption of sequence organization) was as impaired as learning with fixed RSIs and an additional distractor task (i.e. increased attentional load and disruption of sequence organization). He hypothesized that the disruption of sequence organization could be responsible for attenuated learning effects under distraction. However, this seems to be the case only for relatively long RSIs: Using shorter RSIs (50, 450 and 850 ms instead of RSIs up to 1500 ms as in Stadler, 1995) Willingham, Greenberg, & Thomas (1997, Exps. 1 and 2) found no disruption in learning for random compared to fixed RSIs.

Hypotheses which postulate unitary attentional ressources imply that a variety of distractor tasks should affect implicit sequence learning (Heuer, 1996; Heuer & Schmidtke, 1996). To date, apart from tone-counting, two distractor tasks have been used in sequence learning studies. Stadler (1995) found that a letter-string recall task which poses additional load on STM impaired serial learning, whereas Heuer & Schmidtke (1996) found no learning deficit using spatial and verbal versions of the Brooks-task (recall of a visually or verbally described path through a matrix comprising nine squares, see Brooks, 1967). However, learning was impaired if subjects had to perform a variation of the tone-counting task concurrently (pressing a footpedal whenever a higher-pitched tone was presented). Heuer & Schmidtke (1996) explain these results in terms of their task- integration hypothesis: The tone-counting and the key-pressing tasks are treated as one entity by the subjects, thus leading to longer and less structured sequences in the dual- than in the single-task situation (i.e. in the case of an unstructured tone sequence every second stimulus (the imperative stimulus) follows a specified sequence and every other stimulus (the tone) is random).

Schmidtke & Heuer (1997) presented further evidence for a task-integration process using a go/no-go variation of the tone-counting task. They combined a six-element hybrid visual sequence with a six- or five-element sequence of tones. The six-element tone-sequence results in a combined sequence of 12 elements while the five-element tone sequence results in a sequence which repeats no sooner than after 60 elements. In accordance with the task-integration hypothesis, learning was more impaired if the visual stimulus sequence was combined with a five-tone distractor sequence (total sequence lentgh 60) than with the six-tone distraction sequence (total sequence length 12).

Finally, Frensch, Lin, & Buchner (1998; see also Frensch, 1998; Frensch, Wenke, & Rünger, 1999) showed that rather than affecting sequence learning, dual-task interference seems to affect the behavioral expression of what is learned (see also McDowall, Lustig, & Parkin, 1995; Schvanefeldt & Gomez, 1998; Willingham, Greenberg, & Thomas, 1997). They compared learning of hybrid (Exps. 1a and b) and hierarchical sequences (Exp. 2a) for subjects who differed in the amount of training they received under dual- and single-task conditions. Three groups received either 2 dual-task (dt)/5 single-task (st), 4 dt/3st or 6dt/1st in the training phase and were tested under single- (Exp. 1a) or dual-task (Exp. 1b) conditions. The groups did not differ in the amount of implicit leaning. The lack of an influence of the amount of dual-task practice on learning cannot be explained by the model proposed by Curran & Keele (1993). However, there was also a trend for more learning under st than under dt-conditions in the data. The authors concluded that although dual-task interference primarily affects the expression of what is learned, tone-counting also seems to impair learning, albeit to a much lesser degree than previously thought.

Taken together, research on the mechanisms of dual-task interference have yielded results which do not easily fit into a model which assumes an attentional and an independently operating non-attentional learning mechanism.

I.3.3 Influence of various structural components on sequence learning

The goal of the studies reviewed below is to investigate the influence of various structural properties of a sequence on learning (e.g. sequence length, event probability, informational content).

I.3.3.1 Probability information

In the early Nissen & Bullemer (1987) studies, random stimulus blocks served as a control condition for the assessment of sequence learning by computing the RT-difference between a group of subjects confronted with a repeating, structured sequence and a group receiving random stimuli. Nissen & Bullemer (1987) used a 10 element-long sequence (4 2 3 1 3 2 4 3 2 1). Two of the locations (1, 4) were presented twice and two positions three times in one replication of the sequence. Thus, it cannot be ruled out that only simple probability information instead of sequential regularities was learned. In most subsequent sequence learning studies, pseudorandomly constructed, non-structured test-blocks were used which matched the event-probability of the locations in the structured sequence (e.g. Frensch, Lin, & Buchner, 1998). In nearly all studies, sequence learning was found (but see Shanks, Green, & Kolodny, 1994). Thus, it can be concluded that the inherent regularities are really learned.

I.3.3.2 Informational content

As described earlier in more detail, Cohen, Ivry, & Keele (1990) showed that the statistical structure of a sequence (defined here as unique, hybrid or hierarchical) influences the amount of sequence learning, especially under dual-task conditions. However, in the Cohen, Ivry, & Keele (1990)- study, sequence length and structure were confounded: Unique sequences were shorter than both, hybrid and hierarchical sequences. Stadler (1992) used redundancy as an index of statistical structure to disentangle the influence of sequence length and structure on implicit learning. The amount of information a sequence contains depends on the uncertainty about what event will occur in the next trial. The greater the uncertainty, the greater the information which the next event provides when it appears. Stadler (1992) manipulated this by using three sequences which differed in the amount of repeating runs of two, three or four events. The sequence with low statistical structure (2 4 2 3 1 2 1 4 1 3) contained no repetition of a run of two or more locations (hierarchical according to Cohen, Ivry, & Keele, 1990). In the medium structured sequence (2 4 2 3 1 2 3 4 2 3) one run of two trials (2 3) was repeated three times, another two times (4 2) and one run of three trials was repeated two times (4 2 3). The highly structured sequence (2 4 2 3 1 2 4 2 3 4) contained even more of these run repetitions (note that the first six items (underlined) of the sequences are identical). The results indicated that statistical structure has an influence on learning independently of sequence length: Highly structured sequences were learned best, followed by medium and low structured sequences.

In second order conditional (SOC) sequences, each stimulus is equally likely to be followed by any other stimulus. In this case, pieces of information in pairs are inadequate for learning. It is necessary to consider the present and the preceding element to correctly predict the next stimulus. Curran (1997) showed that learning of SOC-sequences (1 2 1 4 2 3 4 1 3 2 4 3) in an SRT-task is possible.

Cleeremans & McClelland (1991) showed that subjects are able to learn even more complex sequences. They used stimuli which were constructed according to an artificial grammar. To complicate things further, in 15 % of all cases ungrammatical stimuli replaced regular, grammatical stimuli. Thus, a probabilistic sequence was constructed. After 60000 practice trials, subjects responded significantly faster to grammatical compared to ungrammatical stimuli, indicating learning of the grammatical structure of the stimulus material. In a second experiment, they showed that subjects became increasingly sensitive to the context set by previous elements of the sequence, and could benefit from dependencies in runs of up to three elements (see also Jiménez, Méndez, & Cleeremans, 1996; Jiménez & Méndez, 1999).

I.3.3.3 Relational structures

In a telephone number like 123345 not only statistical factors but also the relation between subsequent elements can be used to describe the structure of the sequence: elements one, two and three (123) and elements four, five and six (345) each are ascending series of digits. Several researchers have explored the influence of such structural properties of sequences on serial learning.

A systematic analysis of the influence of relational structures on explicit sequence learning has been presented by Restle and coworkers (Restle, 1970, 1973, 1976; Restle & Brown, 1970; Restle & Burnside, 1972). In their experiments, subjects were confronted with a horizontal row of six lights (1, 2, ...6) which were illuminated according to a fixed sequence. Subjects had to predict the next light to be illuminated. Several relations between concurrent lights were introduced: Repetition of the very same light (R), transposition (T, a move to the left or right (2 1 or 2 3)) or the mirror element (M, 6 1 or 1 6). In his tree traversal model of serial pattern learning, Restle (1970) proposed that these relations operate not only on single elements, but also on sequence parts. For example, a sequence like (1 2 1 2 2 3 2 3 6 5 6 5 5 4 5 4) contains relations which can be described as follows (see table 1): The first element of the sequence (1) is transposed (1 2), and repeated (1 2 1 2). This quadruple is transposed again leading to the first half of the complete sequence (1 2 1 2 2 3 2 3). Finally, on the highest hierarchical level, the first part of the sequence is mirrored to complete the sequence.

Table 1: Hierarchical coding of a sequence or a corresponding motor program as proposed by Restle (1970). M: mirror operation, T: transposition, R: repetition. See text for details.

M															
T								T							
R				R				R				R			
T		T		T		T		T		T		T		T	
1	2	1	2	2	3	2	3	6	5	6	5	5	4	5	4

The tree traversal model postulates that reaction time for a stimulus increases as a function of the number of transitions between levels in the hierarchy, i.e. the number of nodes which have to be crossed. For example, Rosenbaum, Kenny & Derr (1983) found increasing response latencies for starting elements of subsequences. Thus, in explicit sequence learning, relational structures are relevant for the subject to build up an internal, hierarchical representation of a sequence or of the corresponding motor program.

Hoffmann & Sebald (1996) tested whether relational structures contribute to learning in the SRT-task. Subjects had to respond to six centrally presented letters (KLMNOP) by pressing one of six horizontally aligned response keys. Thus, it was possible to vary relational structure in the stimulus and response sequence orthogonally by varying the key-letter mapping. Results indicated that a high degree of relational structure in the response as well as in the stimulus sequence facilitated learning.

In sum, these studies showed that a variety of structural properties facilitate sequential learing. In particular, it is obvious that both, the statistical structure of the response- as well as of the stimulus- sequence, influence performance.

I.3.4 The role of short-term memory in implicit sequence learning: The Frensch & Miner-model

Frensch & Miner (1994) proposed a general framework for understanding implicit and explicit learning processes which is heavily based on a more general idea about the function of memory (Cowan, 1988, 1993). They assumed

- two functionally separable memory stores, namely short-term- (stm) and long- term memory (ltm);
- a central executive that controls voluntary processing and directs attention;
- stm represents an activated subset of ltm, and only a subset of the activated ltm content may be in the focus of attention at a given time;
- the degree of activation of information in stm declines with time (Frensch & Miner, 1994).

Learning is assumed to occur in stm. Explicit learning presumedly occurs only in the subset of stm-information which is in the focus of attention and involves active processes like hypothesis testing that are controlled by the central executive. Implicit learning, in contrast, presumedly involves activated information (stm) inside and outside of the focus of attention. It is *"achieved through a passive, associative process that is capable of detecting and storing covariational environmental information"* and is independent of the central executive (Frensch & Miner, 1994, p. 97).

Several testable predictions can be derived from this framework: First, if implicit learning takes place in stm, its capacity should be highly correlated with the amount of implicit learning and, second, a prolongation of the time between presentation of consecutive stimuli should lead to a greater decline in the activated information in stm and, therefore, to impaired implicit learning. Frensch & Miner (1994) compared implicit serial learning and stm-capacity assessed by a digit-span and a location-span task for two groups of subjects which differed in the RSI (short: 500 ms, long: 1500 ms). The predictions derived from their theoretical framework were mostly confirmed: The long-RSI group showed impaired learning compared to the short-RSI group, and digit span correlated with learning for the short RSI-condition, albeit only under dual-task conditions.

In another series of studies, Frensch & Miner (1995) were able to show that sequence learning can occur in two separate subsystems of stm, namely the phonological loop which holds phonological information in the short-term store, and the visual-spatial sketch pad which is responsible for visual information (see

Baddeley, 1992). Phonological or visual sequences were learned better than combined (visual and phonological) sequences, indicating that the two subsystems operate independently of the central executive. Furthermore, implicit learning of visual sequences depended on the familiarity of the items and the availability of a verbal label.

To summarize, these studies relate sequence learning to memory processes. Empirical research is compatible with the notion that stm plays a critical role in sequence learning, but the processes have not been addressed in much detail.

I.3.5 Connectionist models of sequence learning

Two connectionist models have been developed which simulate human performance in the SRT-task (Cleeremans & McClelland, 1991; Cleeremans, 1994, 1997; Keele & Jennings, 1992). Both models assume that sequences are learned by means of high-level associations between combinations of the actual and previous stimuli and/or responses. It has been shown that a learning mechanism which only encompasses paired associations of stimuli is not sufficient, because sequences that do not contain first order but only higher order dependencies can be learned by human subjects (e.g. Reed & Johnson, 1994). Therefore, computational networks that model human SRT-task performance have to be able to learn higher order associations. For example, in a sequence like 1-2-3-2-1-3, the network has to learn that 1-2 is followed by 3, whereas 3-2 is followed by 1. In a model proposed by Cleeremans & McClelland (1991) this is carried out by introducing a Simple Recurrent Network (SRN) consisting of an input unit, context units, one hidden layer and the output unit. The hidden unit feeds back on the context unit which thus provides information about the preceding stimuli. This model closely fits with data obtained in experiments with human subjects (Cleeremans & McClelland, 1991).

The results of simulation studies give support to the idea that the underlying learning mechanism is of an associative nature. An inductive mechanism which represents sequence knowledge in a more abstract rule-based format does not seem to be a prerequisite for this type of systematic behavior.

I.3.6 Direct comparisons of implicit and explicit sequence learning

Unlike research on implicit memory (for reviews, see Roediger & McDermott, 1993; Schacter, 1987; Schacter, Chiu, & Ochsner, 1993) which is motivated by the hypothesis of a functional dissociation between implicit and explicit memory, investigators using the SRT-task have not concentrated on directly comparing both forms of learning. Only two studies included explicit conditions: Curran & Keele (1993, Exp. l) compared SRT-performance for incidentally and intentionally instructed subjects with and without a distractor task (counting one of two tones of different pitch). Without distraction, the intentionally learning subjects acquired significantly more knowledge about underlying structural regularities than incidentally learning subjects, but this advantage disappeared when both groups were transferred to the distraction condition. It seems that whatever may be responsible for the advantage of intentional learning, it depends on the full availability of attentional resources, but further studies are clearly needed to clarify this issue. (For example, the sequence used by Curran & Keele (1993) was shorter than in most experiments; apart from tone counting no other distractor tasks have been used so far and the possible dependency of the advantage of intentional learning on the statistical structure of the sequence has not been studied yet).

Frensch & Miner (1994, Exp. 1) compared incidental and intentional learning for different RSIs. They found implicit learning if the RSI was short (500ms), but not if it was long (l500ms). In contrast, intentionally instructed subjects showed learning for both RSIs, but nevertheless learning was inversely related to RSI in this condition, too. The authors conclude that implicit sequence learning depends on short-term memory resources, i.e. subsequent stimuli have to be coactivated to form associations between adjacent sequence elements (see above).

I.3.7 The role of stimulus-based and response-based processes in sequence learning

Many studies of sequence learning addressed the question of to what extent enhanced SRT performance is a consequence of learning stimulus (S)-, response (R) -, or stimulus-response-sequences.

I.3.7.1 Evidence for learning of stimulus-response associations

Willingham, Nissen, & Bullemer (1989) conducted a study which showed that both perceptual and motor processes may contribute to the acquisition of perceptuo-motor sequences. X-marks appearing at four different locations in four different colors were used as stimuli and participants were instructed to respond to the colors. With this set-up, subjects failed to show an RT-advantage for structured compared to random blocks if the task-relevant colors changed randomly with the stimulus locations forming a predictable sequence - i.e. when the response sequence was random but the perceptual sequence structured. In contrast, for a structured sequence of colored stimuli (response sequence present) the well-known RT-benefit was found, indicating response rather than stimulus learning. However, when subjects were instructed to respond to the location of uncolored stimuli in a subsequent transfer phase no RT-benefit was found, although the locations followed the same regularities as during training, i.e. the response sequence was the same as before. The authors concluded that stimulus structures are learned only if they are relevant for subsequent behavior and if they can be mapped directly onto responses. Thus, it seems that S-R- associations are learned.

I.3.7.2 Evidence for learning of stimulus-stimulus associations

On the basis of cognitive, patient and neuroimaging data (Posner & Petersen, 1990; Posner & Rothbart, 1992), Posner postulated the existence of three different attentional networks: The vigilance network involves right frontal brain areas and is activated in tasks including those which require maintenance of a state of alertness, as is the case in the foreperiod of RT-tasks. The anterior attention network involves areas of the midprefrontal cortex and parts of the supplementary motor area and is activated, for example, in tasks involving target detection (e.g. Corbetta, Meizen, Dobmeier, Shulman, & Petersen, 1990). The posterior attention network consists of parts of the parietal cortex, associated thalamic areas of the pulvinar and reticular nuclei and parts of the midbrain's superior colliculus. It is involved in orienting to locations in space and, therefore, seems to be the primary candidate for involvement in implicit spatial sequence learning. In this context, implicit spatial sequence learning could be viewed as a programmed series of successive orientations of the posterior attention network.

To date, there is some evidence from SRT-experiments with respect to this theorizing. Mayr (1996) used objects which could appear at four different locations which formed an imaginary square. The objects as well as the location of a stimulus followed repeating sequences. Mayr (1996) used sequences of different length to obtain two sequences which are totally independent of each other. Subjects had to respond to the objects by pressing the appropriate key. In different test blocks, either the objects or the locations were chosen randomly. Thus, it was possible to assess response-based and location-based learning separately. Mayr (1996) found independent and simultaneous learning of both sequence types. Most importantly, he could show that implicit learning of a spatial sequence is possible even if the location is not associated with the required response. In such a situation, learning which button to press next cannot explain the learning effect. However, it is possible that motor learning occurred in the sense that a sequence of eye movements, rather than a sequence of covert attention shifts, was learned.

Stadler (1989) studied sequence learning in a speeded visual search task. The location of the actual target depended on the sequence of locations of previous targets. He also found positive transfer despite changes in the motor characteristics of the task. Howard, Mutter, & Howard (1992) compared learning in subjects who simply observed structured event sequences with subjects who responded with key-presses. They failed to show any differences in learning. Note that in the ‘observation only group' subjects had to press a key for the first ten trials of each block. This could have given subjects a hint about the length of the sequence. Additionally, it cannot be ruled out that they continued with covert responding for the rest of the observation trials. Nevertheless, these results provide some support for the view that S-S associations are of prime importance for serial learning.

I.3.7.3 Evidence for learning of response-response associations

In contrast, the results of several studies which used variants of the SRT-task give support to the idea of motor learning. Nattkemper & Prinz (1997) used eight different letters as stimuli and mapped two letters each onto one response finger. In an otherwise repeating event sequence two types of deviant letters replaced standards: letters which required a response with the same finger as a regular letter (violation of the stimulus-, but preservation of the response sequence) and letters requiring a response with a different finger (violation of both, the stimulus and response sequences). If sequential structure is learned and represented perceptually, RT to deviants requiring a same-finger response should increase compared to RT for regular letters, whereas motor learning should result in RT-enhancement only for letters that additionally violate the response sequence. Nattkemper & Prinz (1997) found increasing RTs for deviant letters which violated the response sequence, but not for deviants that only violated the stimulus sequence. This indicates that sequential regularities are stored in the form of motor programs.

Similar findings are reported by Hoffmann & Koch (1997) who found that changing the stimulus aspects in a sequence learning task while leaving the response aspects unchanged did not affect implicit serial learning.

In transfer experiments, subjects are first exposed to sequentially structured material and then transferred to stimuli which are constructed according to a new set of rules. Alternatively, the effectors to be used for response execution can be changed. Cohen, Ivry, & Keele (1990) found that exposure to differently structured material in an SRT-task resulted in negative transfer, whereas shifting subjects to different effector systems (i.e. the use of different fingers during training and test) led to an almost perfect transfer of the acquired knowledge. In an extension of these studies, Keele, Jennings, Jones, Caulton, & Cohen (1995) replicated transfer across effectors when the response modality remained the same. However, transfer was less complete if the response modality was switched from key-pressing to verbal answers. The authors concluded that learning may have a response- but not an effector-specific component, i.e. sequence knowledge is represented as a motor program which is not effector-specific. The phenomenon of (incomplete) manual to verbal transfer shows that a purely response-based mechanism of sequence learning is unlikely.

Taken together, these studies provide converging evidence that motor responses play an important role in sequential learning. However, this does not imply that specific sequences of low-level motor responses are learned in the SRT-task, nor do these studies show that only response sequences can be learned.

I.3.7.4 Evidence for response-effect learning

Ziessler (1994) claimed that the acquisition of sequence knowledge can be viewed as response-stimulus (R-S) learning. He used a visual search task and manipulated the number of different responses related to one target stimulus. The relation of target identity and the position of the following target was learned better by subjects who responded to each target with one specified response than by subjects who had to choose between two response alternatives. Ziessler (1994, 1998b) hypothesized that learning of the underlying rules occurred only if the position changes appeared to the subjects as effects of their previous responses (response-effect learning).

Recent studies give support to the idea that response-effect learning may play a role in the SRT-task as well (Ziessler, 1997, 1998a; Nattkemper & Ziessler, 1998). For example, Hoffmann & Sebald (1997; see also Hoffmann, Sebald, & Stöcker, 1998) introduced redundant effects to the presentation of the imparative stimulus which could be either contingent or noncontingent on the required responses. To introduce contingent response-effect relations, pressing keys in a classic Nissen-Bullemer-task was combined with the presentation of tones. Pressing of key A produced tone c, pressing of key B produced tone e, pressing of key C produced tone g and pressing of key D produced tone c'. Consequently, pressing keys according to the required response-sequence led to a regular sequence of tones. Noncontingent response-effect relations were introduced by mapping the tones to the imperative stimuli, i.e. the X-marks appearing at one of the four different locations. Thus, each press of the key produced two or three different tones (dependent on the following X-mark) rather than one as in the contingent tones condition. Note that, in contrast to the dual-task experiments discussed above, subjects were not required to do anything with the tones. Results demonstrate the relevance of response-effect-relations for sequence learning: Subjects who received noncontigent tones together with the press of the key did not show more sequence learning than a control group which did not hear any tones at all. In contrast, the contingent tone group showed a significantly larger learning effect. Thus, sequential learning can be reliably improved simply by introducing redundant but contingent action effects. Interestingly, it has been found that contingent action-effect relations led to improved learning only if the contingent stimulus was presented concurrently with the press of a key, but not if there was a time-delay of 75 ms between the response and the contingent tone (Stöcker & Hoffmann, personal communication).

Taken together, the reviewed studies show that several elements are responsible for sequence learning. The accumulated evidence indicates that stimulus-response-, stimulus-stimulus-, response-response- as well as response-effect- associations contribute to sequence learning. However, the evidence for contribution of each of these processes to learning has been obtained in different experimental settings, e.g. transfer experiments (Cohen, Ivry, & Keele, 1990) or simultaneous learning of two independent sequences (Mayr, 1996), and with different stimuli which served as response cues (e.g. letters in Nattkemper & Prinz, 1997; spatial positions in Hoffmann & Sebald, 1997). It is most likely that subjects act differently in these situations as the environment, i.e. the presented stimuli, gives different cues which can be used for learning. To date, the conditions under which these mechanisms contribute to sequence learning and when they do not have not been specified. Nevertheless, a general theory of sequential learning, whether explicit or implicit, has to be able to explain the reviewed experimental findings.

I.3.7.5 ERPs as a tool in cognitive brain research

Event-related brain potentials (ERPs) seem to be particularly useful in studying the role of stimulus- and response- based processes in sequence learning because different components of the ERP are selectively sensitive to stimulus evaluation and response preparation processes. Furthermore, ERPs derived from the human EEG reflect immediate brain activity changes which accompany the processing of single stimuli in an event sequence.

When an electrode is placed on the human scalp and the resulting signals are amplified and displayed on an oscilloscope, it is possible to observe voltage fluctuations that change as a function of global brain states such as vigilance or activity level. These fluctuations are commonly referred to as the electroencephalogram (EEG). The EEG reflects the sum of activity of a large number of active neuronal systems. Thus, the neuronal activity which underlies one specific cognitive process only makes a small contribution to the ongoing EEG. However, it is possible to isolate this specific activity from the overall EEG by means of averaging: ERPs are computed by averaging EEG-segments which are time-locked to specific events, e.g. stimulus presentation or subjects' responses. With more and more repetitions of event presentations the ratio of activity related to stimulus processing (ERP) vs. other spontaneously ongoing activity (noise) increases because activity not related to stimulus processing is assumed to fluctuate randomly and is thus "averaged out". In contrast, activity related to stimulus processing is time-locked to the eliciting event and is assumed to remain constant across repetitions of stimulus presentation (see, for example, Lutzenberger, Elbert, Rockstroh, & Birbaumer, 1985).

The waveform resulting from this averaging process consists of a series of positive and negative voltage deflections which are referred to as peaks or components. ERP-components are labelled according to their polarity (N: negative, P: positive) and their latency, e.g. N200 denotes a negativity 200 ms after stimulus onset. Alternatively, components can be labelled according to their functional significance (e.g. LRP, the lateralized readiness potential). A problem arises if a component is compared across different experimental paradigms: A component may be sensitive to the same experimental manipulation, have the same scalp topography but differs in onset latency. For example, the onset of the P300 component is delayed if stimulus identification gets more difficult. Nevertheless, the functional significance is the same regardless of the difficulty of stimulus identification (P300 amplitude is sensitive to stimulus probability and task relevance in both cases). Therefore, it seems to be useful to take the same label for the component in both experiments, i.e. P300. As a consequence, it is common practice to use labels for some components according to their functional significance regardless of their latency (e.g. for the components P100, N100, N200, P300).

Another distinction refers to the properties which influence amplitude (and latency) of ERP-components. Exogenous components (latency: 10-100 ms) are mainly influenced by physical stimulus properties such as intensitiy or size and reflect the function of peripheral sensory organs and subcortical transmission. Endogenous components (latency: 100-500 ms) are independent of physical stimulus characteristics but depend on psychological variables such as allocation of attention to a stimulus, stimulus relevance or stimulus probability.

I.3.7.5.1 ERP-correlates of stimulus evaluation processes

Irregular deviant stimuli of low probability which are presented in an otherwise regular event-sequence elicit an enhanced negativity with a peak latency of about 200 ms (N200-component). If such stimulus changes are task relevant, the N200 will be followed by an enhanced positivity with an onset latency of about 350 ms (P300-component; e.g. Courchesne, Courchesne, & Hillyard, 1978; Duncan-Johnson & Donchin, 1982; Gehring, Gratton, Coles, & Donchin, 1992; Squires, Donchin, Herning, & McCarthy, 1977).

The N200-component seems to reflect stimulus evaluation processes which are sensitive to the probability of the eliciting events (for reviews, see Pritchard, Shappell, & Brandt, 1991; Ritter, Ford, Gaillard, Harter, Kutas, Näätänen, Polich, Renault, & Rohrbaugh, 1984). For the visual modality, it has been shown that an enhanced N200 at central and parietal electrode leads is accompanied by conscious detection of the stimulus deviation (the so-called N2c, see Pritchard, Shappell, & Brandt, 1991).

P300 is an electrically positive deflection of the ERP characterized by a scalp distribution with a parietal maximum. It was found in many studies that the amplitude of the P300 is sensitive to the subjective stimulus probability and to the task-relevance of the presented material (Matt, Leuthold, & Sommer, 1992; Sommer, Matt, & Leuthold, 1990; Squires, Donchin, Hernig, & McCarthy, 1977; for reviews see Donchin & Coles, 1988; Johnson, 1988).

Despite the fact that N200 and P300 components are often elicited by similar experimental manipulations, their timing (N200 precedes P300) and their sensitivity to experimental variations suggest that both manifest different kinds of stimulus evaluation processes. For example, Gehring, Gratton, Coles, & Donchin (1992) showed that in a warned choice RT paradigm the N200-component for unpredictable stimuli was enhanced regardless of their location in the visual field, whereas the P300 amplitude was enhanced only if unexpected stimuli appeared at task-relevant locations. In light of this evidence the authors concluded that the N200 reflects the evaluation of basic attributes of unexpected stimuli (i.e. their physical features), whereas P300 reflects the evaluation of more abstract stimulus features (e.g. their task relevance or probability). Thus, it seems that both components are sensitive to deviations of the perceptual input from expectancies but that they reflect mechanisms which evaluate functionally distinct aspects of stimulus properties.

I.3.7.5.2 ERP-correlates of response preparation

The lateralized readiness potential (LRP) is regarded as an index of hand-specific response preparation (for overviews, see Coles, 1989; Leuthold, 1994). It is derived from the readiness potential (RP), a slow negativity that emerges up to one second before voluntary movement onset and which rises gradually to its maximum over central scalp sites just before movement execution (Kornhuber & Deecke, 1965). The RP preceding voluntary finger and hand movements is greater contralateral to the executing hand, i.e. if a left-hand response is prepared, it is greater over the right than over the left side of the scalp and for right hand response preparation it is greater over the left hemisphere. The asymmetry of the RP seems to start after the selection of the responding hand (Kutas & Donchin, 1988).

De Jong, Wierda, Mulder, & Mulder (1988) and Gratton, Coles, Sirevaag, Eriksen, & Donchin (1988) independently proposed a method to exclude asymmetries which are not related to the movement. This is achieved by first averaging the RP separately for left and right hand movements. Second, the waveforms of contra- and ipsilateral electrodes are subtracted for left- and right-hand movements, and the two resulting difference waves are finally averaged. The resulting measure is known as LRP (see fig. 3).

One important property of the LRP which follows from its computation is that the LRP-amplitude is related to the correctness of a response. Selection of the correct response results in a negative, selection of the incorrect response in a positive deflection of the LRP.

Several findings qualify the LRP as a specific index of response preparation. First, part of the LRP seems to be generated in the precentral motor cortex contralateral to the activated muscle group (see Sommer, Leuthold, & Ulrich, 1994). Second, numerous studies demonstrated a systematic relationship between the LRP and response-selection (e.g. Gratton, Bosco, Kramer, Coles, Wickens, & Donchin 1990; Gehring, Gratton, Coles, & Donchin, 1992; Hackley & Miller, 1995; Miller & Hackley, 1992; Osman, Bashore, Coles, Donchin, & Meyer, 1992; Osman, Moore, & Ulrich, 1995; Osman & Moore, 1993).

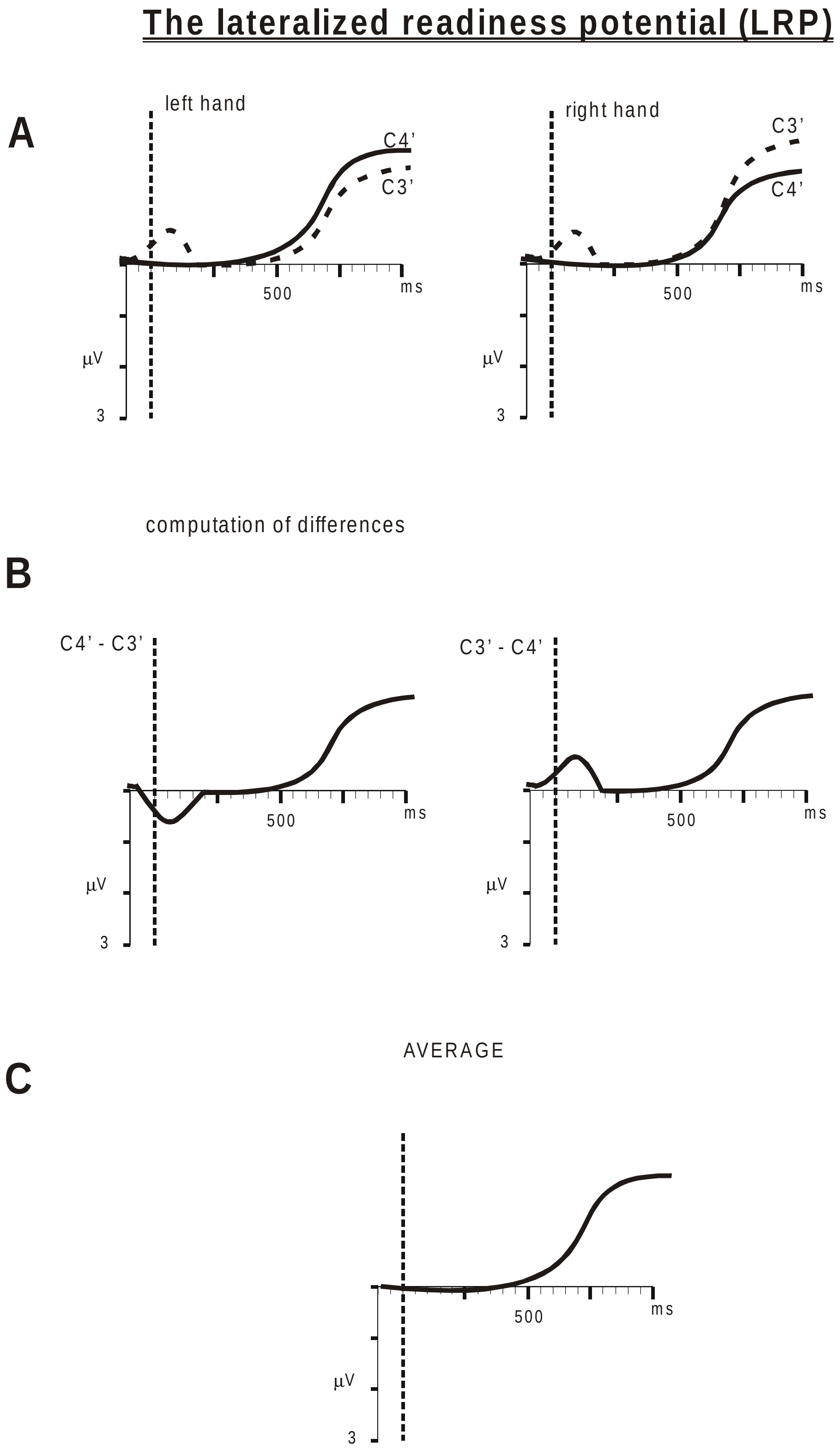


Figure 3: Computation of the lateralized readiness potential (adapted from Coles, 1989). (A) Idealized ERP-waveforms for left- and right- hand responses at electrode sites C3' and C4' (one cm above C3 and C4). At time 0, a warning stimulus is presented which informs the subject about the required response hand in the trial. At time 1000 ms, the imperative stimulus is presented. Note the unlateralized negativity at C3' for both hands. (B) Difference potentials for left hand responses (C4'-C3') and right-hand responses (C3'-C4'), respectively. (C) Average of the two waveforms depicted in (B): The lateralized readiness potential. See text for details.

For example, a validation of the LRP as an index of response preparation was presented by Gratton, Coles, Sirevaag, Eriksen, & Donchin (1988). In a choice-RT-task adapted from Eriksen & Eriksen (1974), subjects had to respond to the central letter of a five-letter display with either a left- (e.g. for the letter H) or a right- hand button press (e.g. for the letter S). To the left and right side of the imperative letter, compatible or incompatible "noise" letters were presented (HHHHH = compatible, left hand response; SSSSS = compatible, right hand response; SSHSS = incompatible, left hand response; HHSHH = incompatible, right hand response).

First, all reactions were classified according to the respective electromyogram (EMG)-onset- latency. Fast responses (EMG-onset latency: 150-199 ms) had an accuracy-level of around 50 %, indicating that subjects were guessing. Most importantly, there was a difference in LRP-polaritiy for correct and incorrect responses for fast reactions: Correct reactions had a negative polarity just 500 ms after the presentation of a warning-tone (that is 500 ms prior to presentation of the imperative stimulus) whereas incorrect responses lead to a positive LRP-amplitude in the same time-frame. No such difference was obtained for slow reactions (EMG-onset 300-349 ms after presentation of the imperative stimulus). Thus, it was shown that there is a strong relation between the polarity of the LRP and the selected response.

If the trials were sorted according to the compatibility of the stimulus array, another interesting result was found: In the LRP-waveforms for incompatible trials with a response latency between 300-349 ms, an activation of the incorrect response was found (positive-going LRP) prior to activation of the correct response (negative LRP-amplitude). No such effect was present for the compatible stimulus arrays. Thus, the measure 'LRP' suggests that processing of the "noise" letters can result in preliminary incorrect response activation, even though the correct response is given. This influence is evident only for long-latency responses where no or only marginal prestimulus response activation was found (Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988).

Several investigators have used the onset-latency of the stimulus-locked LRP as an index of the time when response selection has begun (e.g. Osman, Bashore, Coles, Donchin, & Meyer, 1992; Osman & Moore, 1993; Osman, Moore, & Ulrich, 1995; Smid, Mulder, Mulder, & Brands, 1992; for a critical review of methods of LRP-onset-latency computation, see Smulders, Kenemans, & Kok, 1996). Miller & Ulrich (1998) demonstrated the use of onset-latencies of the stimulus-locked and the response-locked LRP to gain insight into the locus of an effect present in the subjects' mean RTs. In their experiments, the effects of the number of alternative responses were examined (e.g. Brainard, Irby, Fitts, & Alluisi, 1962). In experiment 1, participants had to respond to six different letters with two or six response fingers (two-choice condition: A, B, C: left index finger, D, E, F: right index finger; six-choice condition: A: left ring finger, B: left middle finger, C: left index finger, D: right index finger, E: right middle finger, F: right ring finger). The question was whether the number of alternatives would influence processes between stimulus onset and LRP-onset, processes between LRP-onset and the keypress-response, or both. Stimulus-locked LRPs are computed using time-points defined in relation to the time (in ms) from stimulus-onset. Thus, an effect of the number of alternatives on the duration of processes between stimulus-onset and LRP-onset should affect the onset latency of the stimulus-locked LRP. In contrast, response-locked LRPs are defined in terms of the number of milliseconds preceding the overt response. Therefore, an effect of the number of alternatives on the duration of processes between LRP-onset and the overt response should affect the onset latency of the response-locked LRP. In the Miller & Ulrich (1998)- study, the number of alternatives had an effect on both variables: Onset-latency of the stimulus-locked LRP was earlier for the two-choice condition compared to the six-choice condition, whereas for response-locked LRPs, onset for the two-choice condition was delayed relative to the six-choice condition. Thus, increasing the number of alternatives in a choice-RT-task influences the duration of processes prior to and after the onset of hand-specific response preparation.

There is ample additional evidence that the time of the onset of the stimulus-locked LRP indicates the beginning of specific motor activation of the selected response-hand: (1) the LRP is - at least partly - generated by the primary motor cortex; (2) it is influenced by movement-precues (Osman, Bashore, Coles, Donchin, & Meyer, 1992); (3) the LRP is better time-locked to response- than to stimulus-onset (Hackley & Miller, 1995). Furthermore, the LRP proved to be independent of postselection parameters (e.g. direction, force or velocity of the movement, see Becker, Iwase, Jürgens, & Kornhuber, 1976; Kristeva, Cheyne, Lang, Lindinger, & Deecke, 1990; Sommer, Leuthold, & Ulrich, 1994).

I.3.7.5.3 ERP-studies of sequence learning

To date, there are two experiments in which implicit and explicit sequence learning was studied by means of ERPs. Eimer, Goschke, Schlaghecken, & Stürmer (1996) recorded ERPs while subjects performed a variant of the SRT-task. Four capital letters (A,B,C,D) were presented in a repeated 10-element sequence on a computer monitor and subjects had to press a corresponding key for each stimulus. Standard letters were occasionally replaced by deviating letters which required a response with the opposite hand. Subjects were categorized as implicit or explicit learners according to their performance in postexperimental free recall and recognition tests. Both subject groups learned the underlying regularities as reflected by the well-known RT-advantage for structured vs. random blocks and a difference in RT for standard and deviant letters which evolved in the course of the experiment. In two studies which differed only in the number of interspersed deviant stimuli, it could be shown that deviating letters elicited a larger negativity 240-340 ms poststimulus compared to regular letters (N200-effect). This effect was significantly larger in the second experimental half and only present for subjects possessing some explicit sequence knowledge. Furthermore, a slight enhancement of the P300-amplitude for deviant compared to regular stimuli was found in all subjects.

The authors concluded that the N200-component may reflect the amount of consciously available knowledge about stimulus regularities. This conclusion relies on how well verbalizable sequence knowledge was assessed. In this study, subjects were asked whether they had noted any structural regularities or not after the first half of the experiment. Therefore, it cannot be ruled out that participants overtly searched for such regularities in the second half.

The LRP to standard stimuli revealed a significant activation of the correct response 200 ms after stimulus onset in the first experimental half, whereas in the second half a significant LRP-onset was present as soon as 0-100 ms after letter onset. Additionally, in the second half of the experiment a significant activation of the incorrect response was found for deviants preceding the correct reaction. This LRP-onset effect suggests that sequence knowledge is encoded in the form of motor representations.

Baldwin & Kutas (1997) compared implicit and explicit sequence learning more directly. In two experiments, they first analysed which components of the ERP are sensitive to sequence learning and, second, compared ERPs between a group of subjects who knew about the presence of a sequence (explicit group) and subjects who did not know about sequential regularities (implicit group). In these experiments, subjects had to respond to a specified movement of a flashing square in a 3*3 grid of locations. The position of the square was determined according to an artificial grammar. Occasionally, a grammatically incorrect location replaced a grammatically correct one. The detection of the violation of grammatical structure was reflected in a larger positivity 200-500 ms after stimulus presentation for grammatically correct compared to grammatically incorrect movements for target stimuli (P300 effect). Thus, it could be shown that ERPs are sensitive to violations of implicitly acquired expectations. In a second experiment, Baldwin & Kutas (1997) compared ERPs for two groups of subjects who differed with respect to the instructions they received prior to performing the SRT-task. Explicit learners were informed about the presence of a stimulus regularity and the repeated stimulus sequence was explicitly pointed out to them whereas implicit learners were not informed about the presence of a sequence. Again, a larger positivity 200-500 ms poststimulus was found for grammatical compared to ungrammatical target movements. However, no difference between explicit and implicit learners in the P300 effect emerged. Furthermore, explicit learners exhibited a larger frontal negativity than implicit learners starting about 500 ms prior to execution of the correct response in the response-locked ERPs which was interpreted as reflecting the intentional aspect of response preparation (Baldwin & Kutas, 1997). This difference between implicit and explicit learners was taken as support for the view that explicit and implicit learning are - at least in part - subserved by different brain systems.

Neuroimaging studies and experiments with neurologically impaired patients also provided interesting results with respect to the neuronal basis of sequence learning.

I.4 Neuronal basis of sequence learning

Three groups of studies have been conducted to examine which brain structures are involved in sequence learning: (1) Investigations of sequence learning in subjects with explicit memory deficits (Korsakoff-syndrome, Alzheimer's disease (AD)) or (2) striatal dysfunction (Parkinson's-disease (PD), Huntington's-disease (HD)), and (3) neuroimaging studies.

I.4.1 Sequence learning in subjects with explicit memory deficits

Research on sequence learning in patients with explicit memory deficits (Korsakoff-syndrome, AD) is of interest because spared SRT-learning in these subjects suggests that performance is not dependent on brain regions crucial for explicit learning (see Curran, 1995, 1998). Amnesic patients typically show a damage of medial temporal lobe regions (Parkin & Leng, 1993) including the hippocampus, or of the diencephalon, whereas AD-patients suffer from more widespread damage of neural tissue (neurofibrillary tangles and neuritic plaques in limbic, temporal and posterior association cortex, damage to frontal regions; see Arnold, Hyman, Flory, Damasio, & Van Hoesen, 1991).

Nissen & Bullemer (1987, Exp. 4) found no difference in RT-improvement for structured compared to random blocks between six Korsakoff-syndrome patients and a healthy control group. This suggests that amnesics do learn sequential regularities in the SRT-task.

To date, there are four studies which examined SRT-learning in AD-patients. Knopman & Nissen (1987) and Grafman, Weingartner, Newhouse, Thompson, Lalonde, Litvan, Molchan, & Sunderland (1990) found little but significant learning for a sample of AD-patients. However, Knopman, & Nissen (1987) additionally showed that nine of their AD-subjects did not learn the sequential structure at all. In a later study, Knopman (1991) tested the retention of sequence knowledge in AD-patients 1-2 weeks after the learning session and found no difference between AD-patients and healthy controls. Both groups had also shown the well-known RT benefit for structured blocks in the first session. Ferraro, Balota, & Connor (1993) compared performance of very mildly and mildly demented AD-patients with that of non-demented PD-patients and healthy controls, respectively, and found only the mildly demented AD-patients to be impaired in their amount of sequence learning.

Conclusions from these results are limited because the above-mentioned studies display several methodological shortcomings. First, overall-RT for patients is in general longer than that of healthy controls, thus making it difficult to compare the amount of learning in both groups. The size of the RT-difference between structured and random blocks may depend on the overall RT level (Chapman, Chapman, Curran, & Miller, 1994). Second, the interpretation of group differences is difficult as most of the patients receive medication. It cannot be ruled out that performance differences depend on medication, especially in cases where the drugs are known to affect motor functions (e.g. L-dopa for PD-patients). Third, in all of these studies only the 10-element ‘Nissen & Bullemer (1987) sequence’ was used. Therefore, it is difficult to generalize about the results (note that this sequence contains the very salient part ...4-3-2-1 at the end of the ten trial sequence, see above). Finally, the studies have not explicitly tested the role of attentional, memory or motor processes on sequence learning (for example by using dual tasks, varying the statistical structure of the sequence, or introducing deviant events).

To summarize, SRT-studies with Korsakoff- and AD-patients have provided evidence that learning of sequential regularities seems not to depend on brain structures which are needed for explicit learning and memory. However, in patients with more severe damage (like mildly demented AD), performance impairments are observed. The causes which lead to these deficits are not clear yet, but they may be due to attentional or short-term memory insufficiencies.

I.4.2 Sequence learning in patients with striatal dysfunction

Studies of SRT-learning with PD- or HD-patients are especially interesting because they provide the possibility of testing the proposal that skill learning depends on the integrity of the striatum (e.g. Squire, 1992). Furthermore, in PD-patients the impact of defects in motor control functions on perceptuo-motor sequence learning can be studied.

Knopman & Nissen (1991) and Willingham & Koroshetz (1993) found that HD-patients learned the sequential structure in an SRT-task, but to a lesser degree than healthy control subjects. For PD-patients, Ferraro, Balota, & Connor (1993) found learning impairments for non-demented patients compared to age-matched controls using the Nissen-Bullemer sequence. Pascual-Leone, Grafman, Clark, Stewart, Massaquoi, Lou, & Hallett (1993) compared sequence learning in PD-patients on and off medication. The state of medication had one effect only, namely that overall RT was slower without medication. Sequence learning for PD-patients was observed, but it was less pronounced than in healthy controls. In a second experiment, Pascual-Leone et al. (1993) used sequences of 8, 10 and 12 elements to examine the effect of sequence length on learning. For controls as well as PD-patients, learning was inversely related to sequence length, but PD-patients were impaired with each of the three sequences. In a third experiment, performance of subjects who were explicitly taught the 10-element Nissen-Bullemer sequence was examined. In this explicit learning task, again a difference between PD-patients and healthy controls emerged. This shows that PD-patients are less efficient in utilizing sequential knowledge to improve SRT-performance even if sequential dependencies are explicitly pointed out to them. This finding makes the interpretation of the aforementioned studies somewhat difficult, as it cannot be decided whether implicit or explicit learning deficits (or both) are responsible for the SRT-learning impairment in PD-patients.

In a more recent study, Jackson, Jackson, Harrison, Henderson, & Kennard (1995) found no sequence learning at all for 11 PD-patients without medication.

In sum, these results suggest that motor functions mediated by the striatum seem to be crucial for procedural learning as induced by the SRT-task.

I.4.3 Neuroimaging studies of sequence learning

Neuroimaging studies can be used to examine more directly which brain structures are involved in sequence learning in the SRT-task. Positron Emission Tomography (PET), for example, can be used to detect metabolic effects with a longer latency which accompany particular learning states. In brief, radioactive-labelled oxygen is injected while subjects perform a task, and variations in regional cerebral blood flow (rCBF) are measured by detecting the emissions of the oxygen tracer (e.g. Mazziotta, Huang, Phelps, Carson, MacDonald, & Mahoney, 1985). Across different scanning sessions, the contributions of different neural structures to particular mental operations are assessed by looking at task-related changes in the emission of the tracer.

Grafton, Hazeltine, & Ivry (1995) compared rCBF in a PET-study in single- vs. dual-task SRT-conditions. Subjects started with three random followed by three structured stimulus blocks and had to perform a tone-counting task simultaneously (dual task condition; 6 element sequence, ambiguous structure according to Cohen, Ivry, & Keele, 1990). As none of the participants became aware of the sequential regularities of the stimulus material, the authors considered learning in the dual-task phase to be implicit. Finally, three blocks of the same sequence were presented without the distractor task (single-task condition). 7 of 12 subjects became aware of the sequence, thus learning in the single task condition was considered to be explicit. RT-analysis confirmed that learning took place in both phases of the experiment although subjects learned more in the single task ‘explicit’ condition.

In the ‘implicit’ dual task-condition, learning-related enhanced activity was found in contralateral motor effector areas (incl. motor cortex, SMA, putamen), in the rostral prefrontal cortex and in the parietal cortex (comparison of rCBF in block 1 (random), and during the following blocks of the dual-task phase). During (explicit) single-task performance, activity was enhanced in the right dorsolateral prefrontal cortex, right premotor cortex, right ventral putamen, and biparietal-occipital cortex (comparison of rCBF in block 1 of single-task performance and during the following single-task blocks). The authors conclude that the major difference between explicit and implicit learning is an enhanced activity in right prefrontal cortex during explicit learning which may be related to episodic memory functions. Moreover, it was concluded that motor learning involves a number of different cerebral areas (Grafton, Hazeltine, & Ivry, 1995; see table 2).

There are some methodological problems with this study. First, subjects responded with their dominant right hand only, thus making the interpretation of laterality effects difficult. Second, Grafton, Hazeltine, & Ivry (1995) used an unusually short sequence and did not assess explicit knowledge in an appropriate way. Therefore, it cannot be ruled out that learning in the dual-task phase was explicit, too, at least to a certain degree.

Rauch, Savage, Brown, Curran, Alpert, Kendrick, Fischman, & Kosslyn (1995) used a more complex sequence (12 elements, hierarchical structure according to Cohen, Ivry, & Keele, 1990) and controlled the amount of explicit knowledge more thoroughly. Subjects started with three random stimulus blocks followed by three structured and three random blocks. A series of explicit memory tests revealed that none of the subjects had developed explicit sequence knowledge up to this point. Next, the experimenter informed the participants about the repeating sequence in the stimulus material. Three structured blocks and an assessment of explicit sequence knowledge concluded the experiment. RT analysis revealed a learning effect for both the implicit and the explicit learning episodes. Again, subjects learned significantly more in the explicit than in the implicit condition. During implicit learning, PET-data revealed significant activity in the right ventral premotor cortex, the right ventral caudate/nucleus accumbens, the right thalamus, and bilateral visual association cortices (area 19; implicit - random condition). During explicit learning, activation foci were found bilaterally in the cerebellar vermis, the left fusiform cortex, the left inferior frontal cortex, the right thalamus, the right middle frontal cortex, and the right brain stem (explicit - random condition). A direct comparison of implicit and explicit learning (implicit - explicit condition) showed activity in the right ventral premotor cortex. This suggests that the right ventral premotor cortex might be of principal importance for a distinction between explicit and implicit learning. Note that due to a limited axial field of view some areas that may be important for sequence learning could not be studied (SMA, DLPFC (dorsolateral prefrontal cortex)).

Table 2: PET-studies of implicit and explicit sequence learning using variants of the SRT-task. See text for details.

study	**task/comparison**	**results** (learning-related increase in rCBF; Brodman area in parenthesis)[1]
Rauch et al. (1995)	12 element hybrid sequence; spatial; index and middle fingers of both hands as effectors Implicit:single task; random vs. structured blocks Explicit: subjects were informed about the presence of a sequence in half 2; random vs. structured blocks	Implicit learning: right ventral premotor cortex (6) right ventral caudate/nucleus accubens (6) right thalamus bilateral visual association cortex (19) Explicit learning: primary visual cortex peri-sylvain cortex cerebellar vermis, bilaterally left fusiform cortex (19) left inferior frontal cortex (45) right thalamus right middle frontal cortex right middle temporal cortex (39) right brain stem Direct comparison explicit vs. implicit: Bilateral visual cortex (17) Left inferior parietal cortex (39/40) Hypothesis: Different neuronal structures are involved in explicit and implicit sequence learning. Implicit learning is mediated by a distributed system (right ventral premotor cortex, right ventral striatum, right thalamus, bilateral visual association cortex). Explicit learning is mediated by a subsystem relevant for motor learning (cerebellum, thalamus,

		brain stem) and subsystems which may reflect the implementation of conscious strategies (visual imagery, language mediation).
Grafton et al. (1995)	6 element hierarchical sequence; spatial; right hand response only Implicit: dual task (tone counting as distractor task); comparison of rCBF during three structured blocks (three scans during learning); effects are compared with effects in random blocks Explicit: single task; comparison of rCBF during three structured blocks (three scans during learning)	Implicit learning: left anterior frontal cortex (10) left sensorimotor cortex right putamen left parietal cortex (40/7) left putamen suppplementary motor area (6) left lingual gyrus (18) Explicit learning: bilateral parietal/occipital cortex (19/39) right dorsolateral frontal cortex (46) right middle temporal cortex (21) right premotor cortex (6) right superior frontal cortex (6/8) right n.accumbens/putamen right middle frontal cortex (10) Hypothesis: Different neuronal structures are involved in explicit and implicit sequence learning. Motor cortex is involved in implicit, procedural learning of a movement sequence like the one in the SRT-task. Sensorimotor cortex, SMA and putamen are principal components of a cortical-subcortical motor loop which seems to be of prime importance for implicit sequence learning. Parietal/prefrontal cortical areas which constitute an attentional/cognitive network are involved in explicit sequence learning. Spatial stm is also involved in learning. Bilateral inferior parietal cortex is hypothesized to play a role in the conscious representation of sequence patterns.
Doyon et al. (1996)	10 element hierarchical sequence; spatial; right index finger response on touch screen Implicit: Not studied. Explicit: Highly learned sequence vs. random control	Explicit learning: bilateral anterior cingulate cortex ventral striatum cerebellum medial posterior parietal cortex medial prestriate cortex medial posterior parietal cortex

	condition	
Hazeltine, Grafton, Ivry (1997)	6 element hybrid sequence; colors; right hand response. implicit: dual task (tone counting as distractor task); comparison of rCBF during three structured blocks (three scans during learning); effects are compared with effects in random blocks explicit: single task; comparison of rCBF during three structured blocks (three scans during learning) comparison of spatial and non-spatial (colors) implicit sequence learning: dual task color condition vs. dual task spatial condition, comparison of scan during the second structured block	Implicit learning: precentral gyrus (4/6) SMA (6) left sensorimotor area (4) bilateral area 40 left thalamus/putamen Explicit learning: right premotor cortex (6) bilateral anterior cingulate (24/32) right inferior frontal cortex (45) right thalamus right inferior occipital cortex (19/39) right inferior temporal cortex (20) Spatial vs. color learning: Larger activation in "color task": bilateral anterior cingulate (24) left inferior temporal gyrus (37) left frontal insula left caudate left middle frontal gyrus (10) left precentral gyrus (6) left inferior parietal lobule (40) right pulvinar thalamus right superior frontal gyrus (9) Larger activation in "spatial task": left hippocampus bilateral middle occipital gyrus (19/39) left superior occipital gyrus (19) right occipital cortex (17) right inferior parietal lobule (40) right inferior frontal gyrus (44/6) right superior occipital gyrus (19) Hypotheses: Dissociable neural systems are involved in explicit and implicit skill acquisition. Implicit learning mostly in motor areas. Changes observed with implicit sequence acquisition were independent of stimulus features, suggesting that the respective areas encode representations of particular movements.

[1] Note that decreases of rCBF are not listed in the table. A decrease in rCBF in the experimental condition relative to the control condition means that the respective brain area is less active in the experimental condition. However, the functional interpretation of such a decrease is not yet clear.

Most importantly, all four PET-studies found differences with regard to the neuronal systems involved in explicit and implicit sequence learning (see table 2).

Striatal involvement in implicit sequence learning has been found in all four PET-studies as well as in a recent study using functional magnetic resonance imaging (fMRI; Rauch, Whalen, Savage, Curran, Kendrick, Brown, Bush, Breiter, & Rosen, 1997). In the latter study, individual subjects showed considerable intersubject variability with respect to the precise territories involved, but all seven subjects who showed robust learning effects exhibited significant learning-related activation within the putamen. Taken together, these results suggest that the striatum plays a critical role in implicit sequence learning (note that neither of the three PET-studies found the right inferior striatum to be involved in explicit sequence learning).

However, different ideas have been put forward with respect to the structures involved in explicit and implicit sequence learning. Rauch et al. (1995) concluded from their PET-data that implicit sequence learning might be mediated by a distributed system (right ventral premotor cortex, right ventral striatum, right thalamus and bilateral visual association cortex). In contrast, explicit sequence learning may be mediated by a subsystem relevant for motor learning (cerebellum, thalamus, brain stem) and subsystems which may reflect the implementation of conscious strategies (visual imagery, language mediation). In contrast, Grafton, Hazeltine, & Ivry (1995, see also Hazeltine, Grafton, & Ivry, 1997) have put forward the idea that the motor system is primarily responsible for implicit learning whereas parietal/prefrontal areas are involved in explicit learning.

Two recent studies explored the relevance of motor processes for explicit and implicit sequence learning in more detail. In both studies, a centrally presented digit (1,2,3 or 4) served as imperative stimulus. Digits were presented in a repeating sequence of either 12 or 10 elements. Explicit knowledge was assessed after every training block. Pascual-Leone, Grafman, & Hallett (1994) mapped the motor cortex with transcranial magnetic stimulation (TMS) to study changes in the cortical output maps of the relevant muscles. Cortical output maps of the task-relevant muscles became increasingly larger during implicit learning. When full explicit knowledge of the sequence was achieved the cortical output maps regressed to their baseline topography. The authors concluded that rapid functional plasticity of cortical outputs is of prime importance for the transfer of knowledge from an implicit to an explicit state and that explicit knowledge emerges from earlier implicit knowledge (see above for a discussion of this point).

Zhuang, Toro, Grafman, Manganotti, Leocanti, & Hallett (1997) showed that event-related desynchronization (ERD), computed from the human EEG, reaches a maximum level during explicit learning, and declines after full explicit knowledge of the sequence is obtained. ERD is most prominent over motor areas. Localized ERD is interpreted as reflecting an increase in activity of relatively small and independent cell assemblies. Taken together, the results of these two studies suggest that the transition from implicit to explicit knowledge in the SRT-task goes together with a change in cortical motor activation. These changes could imply the generation of a motor plan which represents the whole motor sequence in higher cortical modules (Zhuang, Dang, Warzeri, Gerloff, Cohen, & Hallett, 1998).

As is evident from the above-mentioned studies, no coherent picture of the neuronal basis of implicit sequence learning has emerged to date (see also Curran, 1995, 1998). However, several brain regions have been identified as being relevant for sequence learning (cerebellum, basal ganglia, DLPFC, SMA, premotor cortex, visual association areas, right frontal cortex). It is not yet clear which of these regions are causally linked to the acquisition and storage of sequence knowledge and which are of secondary importance, in that they are merely reflecting attentional or other unspecific task effects.

I.5 Summary and overview of the experiments

Research with the SRT-paradigm has yielded a large body of evidence that human subjects are able to learn the structure of event sequences. For subpopulations or for certain experimental conditions (dual task), sequence learning seems to be possible without concurrent awareness of the acquired rules. The paradigm has also been used to explore the neuronal structures involved in explicit and implicit learning. It has been established that both forms of learning are supported by different neuronal systems (e.g. Hazeltine, Grafton, & Ivry, 1997). However, different hypotheses with regard to the contribution of cortical regions to explicit and implicit learning have been put forward (see I.4.3). In the present experiments, ERPs are used to study differences in the neuronal systems involved in explicit and implicit learning. In contrast to PET, ERPs have a better temporal resolution, i.e. changes in cortical activity can be studied on a millisecond time-scale. This can provide new insights into the time-course of cortical activation in explicit and implicit sequence learning.

Many studies tried to characterize the underlying learning processes in more detail. For example, experiments employing the dual-task methodology provided evidence that performance in sequence learning tasks depends on a unitary learning mechanism. However, the effectiveness of this mechanism is modulated by attentional allocation strategies. Studies of implicit serial learning in clinical populations with functional deficits of the brain stress the importance of response-response associations: Amnesic patients show no learning deficit (e.g. Nissen & Bullemer, 1987), whereas patients with deficits in motor control functions (Parkinson's disease) are clearly impaired in serial learning (e.g. Ferraro, Balota, & Connor, 1993). Transfer experiments with healthy subjects (Keele, Jennings, Jones, Caulton, & Cohen, 1995), experiments which involve a change of stimulus aspects while leaving response aspects of the task unchanged (Hoffmann & Koch, 1997) and studies which introduce deviants in an otherwise regular sequence of letters (Nattkemper & Prinz, 1997) all show that motor processes are important for implicit learning.

Other investigators have shown that implicit sequence learning is also possible for non-motoric sequences (e.g. Mayr, 1996). This shows that non-motoric systems also contribute to the observed learning-effects in the SRT-task.

In the present experiments, the processes involved in sequence learning are analysed by means of ERPs. In all experiments, a version of the SRT-task introduced by Nattkemper & Prinz (1997) is used. In an otherwise repeating sequence deviant events occasionally replace regular events. Two different types of deviants are used: Perceptual deviants change only the stimulus but not the response sequence, whereas motor deviants change stimulus as well as response sequences. In experiments 1 and 2, sequences of letters are used whereas in experiment 3 a spatial sequence is presented.

In experiment 1, the sensitivity of ERPs to perceptual and motor deviance of events is explored. Furthermore, differences between implicit and explicit learners are analysed. Experiment 2 is an attempt to replicate the results of experiment 1 with a more complex event sequence. Furthermore, the explicit group is informed about the presence of sequential regularities whereas the implicit group is not.

In experiment 3, a spatial sequence which also contains deviant stimuli is used to examine whether differences between implicit and explicit learning can be found in the spatial domain. Moreover, the hypothesis that several independent, domain-specific brain systems exist which are capable of sequence learning is investigated.

II. EXPERIMENT 1: EVIDENCE FOR DISTINCT CODING OF PERCEPTUAL AND MOTOR REPRESENTATIONS IN EXPLICIT AND IMPLICIT SEQUENCE LEARNING

II.1 Introduction

The goal of this study is to provide evidence that implicit and explicit learning of event-sequences involve different processing systems. To objectify this claim, ERPs are recorded while subjects perform a variant of the SRT- task. Furthermore, the ERP-components sensitive to sequence learning are explored.

In several studies it was found that learning of perceptuo-motor sequences as reflected in an RT-benefit for structured vs. unstructured blocks emerged without the development of conscious awareness for the sequential structure of the stimulus material (e.g. Cherry & Stadler, 1995; Curran & Keele, 1993; Eimer, Goschke, Schlaghecken, & Stürmer, 1996; Frensch & Miner, 1994; Howard & Howard, 1989, 1992; Mayr, 1996; Nissen & Bullemer, 1987; Reed & Johnson, 1994; Stadler, 1992, 1993, 1995; Willingham, Nissen, & Bullemer, 1989). Although the large number of positive findings leaves little doubt that sequential structures can be learned implicitly, it is still an open question which types of representations are formed during implicit sequence learning (for reviews, see Clegg, DiGirolamo, & Keele, 1998; Curran, 1998; Goschke, 1998; Hoffmann & Koch, 1998; Rüsseler & Rösler, 1999). To date, the available evidence is contradictory, indicating either learning of response-response (R-R), stimulus-stimulus (S-S) or stimulus-response (S-R) associations.

In the present study, ERPs are used to explore whether functionally different processes contribute to explicit and implicit learning of event sequences. In particular, the claim emerging from the reviewed PET-findings that motor processes are of primary importance for implicit sequence learning whereas motor as well as stimulus-based processes are relevant for explicit sequence acquisition will be investigated. ERPs seem to be especially suited for this purpose: (1) they provide an online-index of information processing and, (2) different ERP-components are known to reflect either perceptual and stimulus-evaluation processes (e.g. N200, P300) or response preparation processes (LRP). Moreover, ERPs reflect a completely different type of signal than PET. ERPs are evoked by electrical rather than blood flow changes and are coupled much more directly to the processing of single events, because they can be measured during the short epoch which extends between stimulus presentation and response execution.

The present study.

To disentangle the contribution of stimulus- and response- based processes to sequence learning, a modified version of the SRT-paradigm was employed. Instead of one character which changes its location on a display, a set of eight different letters that always appeared at the same location was used. Subjects had to respond to a particular letter by lifting one of four fingers (left and right hand index and middle fingers; see also Eimer, Goschke, Schlaghecken, & Stürmer, 1996). Two different letters were always related to one response finger (Nattkemper & Prinz, 1997). This arrangement allowed the introduction of two types of deviant stimuli in the otherwise regular sequence of events: Perceptual deviants were created by switching between the two stimuli which were related to the same response. Thus, the sequence of perceptual events was changed but the sequence of responses was preserved. Motor deviants were created by exchanging a regular stimulus with one which required a response with the opposite hand. Motor deviants were, of course, also perceptual deviants.

If the system encodes and stores the perceived stimulus sequence, then any deviation from the regular stimulus sequence should become apparent in the ERP. Most likely, the amplitude of ERP-components which are known to be sensitive to stimulus evaluation processes like N200 or P300 should be influenced. If the system encodes the sequence of motor acts, then the LRP should be affected as well. For motor deviants, an activation of the expected but incorrect response could be present prior to the activation and execution of the correct response. This preactivation could result in a positive-going 'dip' in the LRP which precedes the negative-going deflection indicating the activation of the correct response.

With respect to the three hypotheses - S-S-learning, S-R-learning or R-R-learning - the following outcomes can be predicted: For pure S-S-learning, an amplitude change in the N200 and P300 components but no activation of incorrect responses for motor deviants in the LRP (positive going 'dip') should be found. For pure R-R-learning, the opposite outcome is expected: No amplitude changes for N200 and P300, but an activation of the incorrect but expected response-hand for motor deviants. Finally, if both processes contribute to sequence learning (S-S as well as R-R associations) both effects, amplitude changes of the N200 and P300 and an LRP 'dip' for motor deviants, are expected.

Recent neuroimaging research with PET suggests that implicit and explicit learners process sequence knowledge differently (e.g. Grafton, Hazeltine, & Ivry, 1995). In particular, the motor system seems to be of prime importance for implicit learning while perceptual systems seem to contribute to explicit learning. These processing differences should become manifest in the ERP effects, too. It is expected that implicit learners, who may acquire "motor knowledge" only, show an LRP-effect but no amplitude changes of the perceptual components N200 and P300. In contrast, explicit learners who may acquire knowledge of the stimulus sequence, should show N200 and P300 amplitude changes and an LRP dip.

With respect to the behavioral data the following predictions can be derived: If learning of S-S-associations is an important component of sequence learning, then RTs for perceptual as well as for motor deviants should increase relatively to RT to standard letters. In contrast, if only R-R-associations are learned, an increased RT for motor but not for perceptual deviants should emerge. If both processes contribute to learning, an increase of RT for perceptual and an additional RT-prolongation for motor deviants should be found.

II. 2 Method

Subjects. In total, 21 subjects participated in the present study. Data of two subjects had to be discarded because of extensive occular artifacts. The final sample comprised 12 female and 7 male subjects between 20 and 36 years of age. According to self-report, two subjects were left-handed. All participants had normal or corrected-to-normal vision. All but two were students of the Philipps-University Marburg. Participants either received course credit or were paid on an hourly basis plus an additional bonus. No subject had participated in other sequence-learning experiments before.

Stimuli and Apparatus. Subjects were seated in an electrically shielded, sound-attenuated and dimly lit room. Eight capital letters (K,L,M,R,S,T,V and X) served as stimuli. The letters were presented at the center of a computer display (Atari SM 124, refresh rate 72 Hz) located in front of the subject. The letters appeared in black on a white square subtending a visual angle of 1.45^{O}. Letters subtended visual angles of $0.58\,^{O}$ (height) and $0.28\,^{O}$ (width) at a constant viewing distance of 100 cm. Each letter remained on the screen until a response had been given by the subject. RTs were measured from stimulus-onset to the subjects' response in steps of 5 ms. The RSI was held constant at 500 ms. If there was no response within 5 s the stimulus disappeared and the trial was counted as an error.

The letters were related to the response keys as follows (see fig. 4): For M and T, subjects had to respond with their left middle, for V and R with their left index, for X and K with their right index and for L and S with their right middle finger. Subjects placed their left and right middle and index fingers in four circular cavities, each equipped with a light gate. To respond to a stimulus, the respective finger had to be briefly lifted from the cavity.

The experiment comprised regular and pseudorandom stimulus blocks of 96 letters each. An eight element stimulus sequence was used: V L K T X S M R (unique statistical structure according to Cohen, Ivry, & Keele, 1990). The corresponding finger lift sequence is I m i M i m M I (M and I denote middle and index fingers of the left hand, m and i middle and index fingers of the right hand). Thus, the response sequence is more complex than the stimulus sequence in the sense that two preceding responses must be remembered to correctly anticipate the next response alternative (hierarchical structure according to Cohen, Ivry, & Keele, 1990) whereas only one letter is needed to correctly predict the next stimulus. Regular blocks were constructed as follows: First, a random starting letter of the sequence was chosen. Second, the following letters were determined according to the rules of the sequence, thus leading to 12 replications of the sequence for each block of 96 trials. Finally, in each replication of the sequence one regular letter was replaced by one of two different types of deviant letters: Perceptual deviants changed the perceptual event sequence but left the response sequence unchanged. To achieve this a regular letter was replaced by the second letter related to the same response (e.g. the letter M was replaced by T, both requiring a response with the left middle finger). Motor deviants changed both the perceptual and the response sequence. In this case a regular letter was replaced by any of the four letters which required an opposite hand response (e.g. the letter M was replaced by K; see fig. 4). The position of the deviant letter was determined randomly. In pseudorandom blocks stimuli were determined randomly under the condition that in a series of eight subsequent stimuli each letter occurred once. Thus, the probability of each letter was the same in regular and pseudorandom blocks.

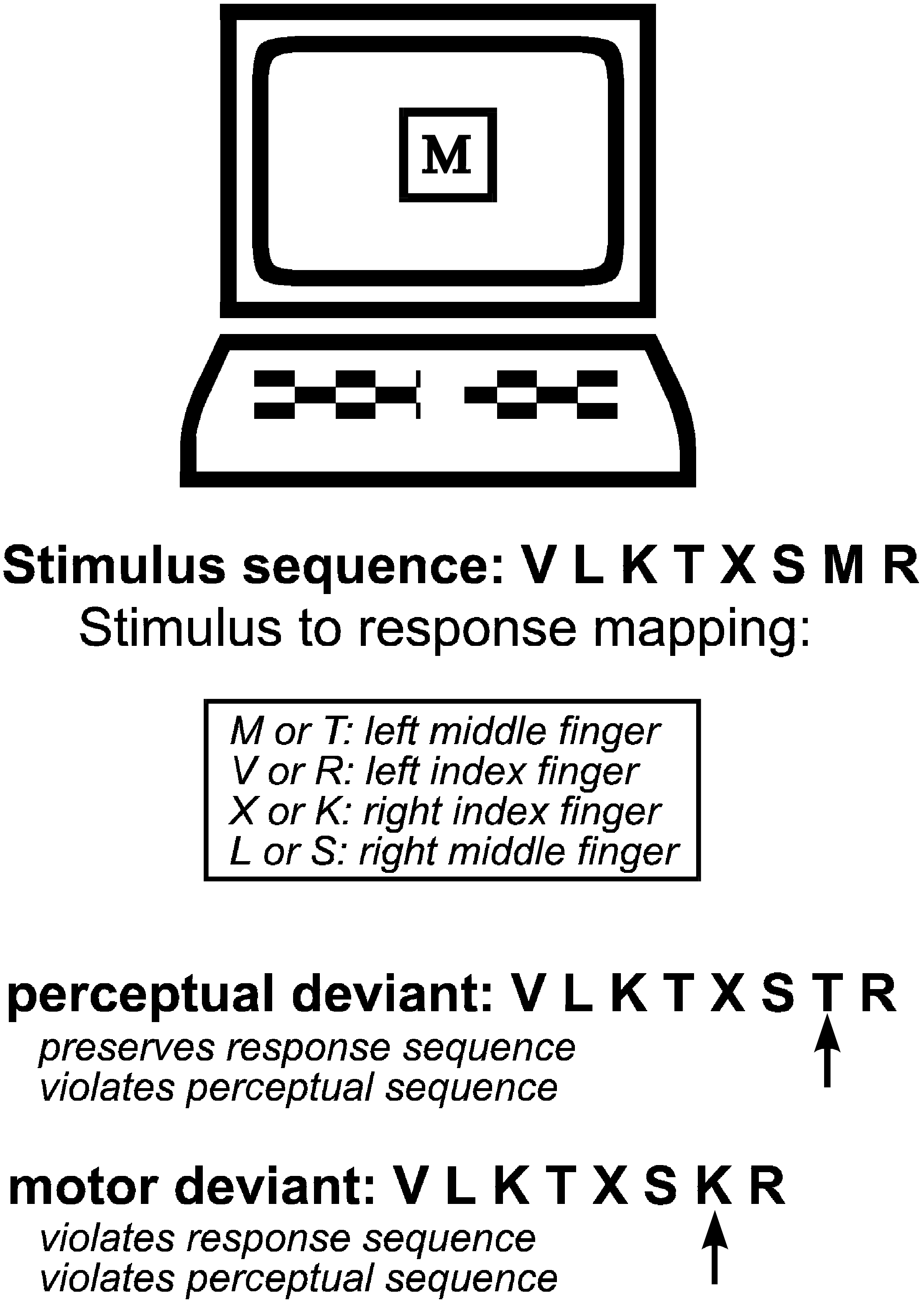


Figure 4: Mapping of letters to responses in experiment 1. Arrows indicate deviant stimuli.

For the recognition procedure (see below) bigrams, trigrams and quadruples of letters were constructed. One half of these letter trains was identical to original sequence fragments, the other half was identical in all but one element. 10 bigrams, trigrams and quadruples each were used. Five of these fragments of a given length were not part of the original eight letter sequence (see appendix A).

Procedure. After electrode montage subjects started to learn the relation between stimuli and responses with practice blocks until they completed at least one block of 96 trials with less than six errors. Letters were presented randomly in these blocks. Before the start of the EEG-recording participants were advised to avoid muscular and eye movements and to minimize eye blinks during the experiment proper. Subjects first performed four pseudorandom blocks. Blocks 5 to 19 were regular, block 20 pseudorandom, blocks 21 to 35 regular, block 36 pseudorandom and blocks 37 as well as 38 were regular again. After each block subjects received feedback about the number of erroneous responses and mean RT. Accuracy and speed were both stressed in the instruction. Subjects started the next block by placing their fingers in the circular cavities.

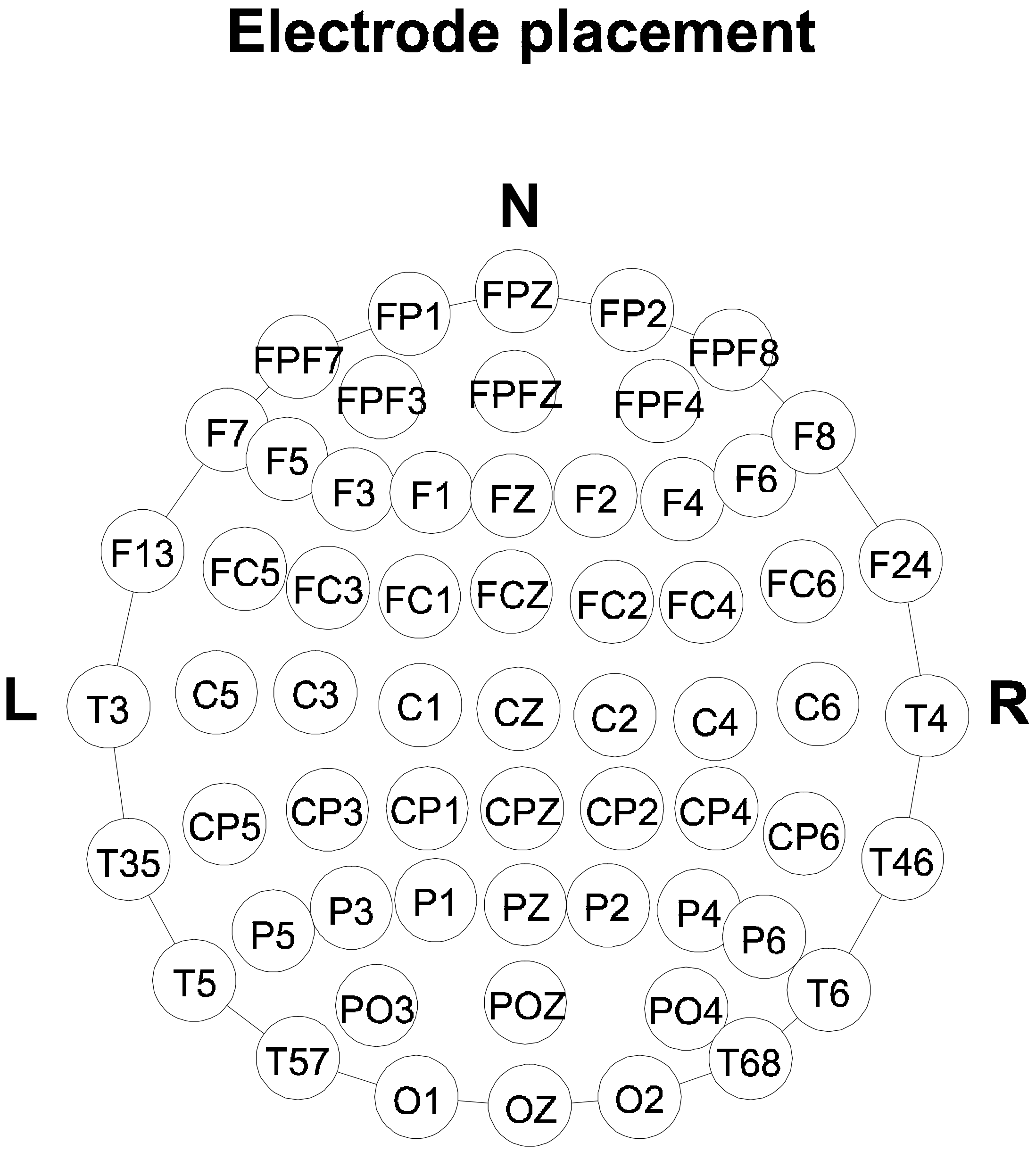
Upon completion of the 38 experimental blocks, subjects had to answer a postexperimental questionnaire comprising four questions and three rating scales. In question 1, subjects had to state whether they had noted any structural regularity in the stimulus material (yes/no-response). Question 2 asked if the letters had appeared in a random or in a predictable order. At this point, subjects were informed that the stimulus sequence had a predictable structure and were asked to report everything they had noticed about the regularities of the letter sequence. In question 4, participants were asked to freely reproduce the letter-sequence (free recall procedure). Questions 5 to 7 formed the recognition test. Subjects were given 10 bigrams (question 5), 10 trigrams (question 6) and 10 quadruples (question 7) of letters. For each of these letter sequences they had to indicate on a five point rating scale whether it had been part of the stimulus sequence in the foregoing experiment.

After completing the questionnaire subjects were fully debriefed about the purpose of the study and the electrodes were removed.

EEG-recording, artifact rejection and signal extraction.

EEG was recorded from 61 Ag-AgCl electrodes placed on the subjects’ head by means of an elastic cap (Gaggl-system, Graz, Austria). The positions of the 61 scalp electrodes are depicted in figure 5. Electrodes are labelled according to a modified version of the 10-20-system of electrode placement (Jasper, 1958). 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. Prior to electrode fixing individual scalp-sites were cleaned and abraded through holes in the cap designed to fix the electrodes. Electrodes were fixed on the cap after injection of a conduction gel (SYNAPSE® by MED TEK CORPORATION). All scalp electrodes were referenced to linked earlobes.

To control for vertical and horizontal eye-movements the electroocculogram (EOG) was recorded from the outer occular canthi (horizontal EOG) and the sub- and supraorbital ridges (vertical EOG) respectively. Impedances of all electrodes were kept below 5 kΩ.



Electrode placement

Figure 5: Schematic outline of the 61 electrode positions used for EEG-recording. Labeling of electrodes in accordance with an extrapolated 10-20 system.

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.

An ATARI MEGA ST2®-computer controlled stimulus presentation as well as behavioral and electrophysiological data collection. The EEG-signals were stored by an IBM-compatible Intel-Pentium PC® running MS-DOS® and NEUROSCAN® ACQUIRE software. Prior to the beginning of each experimental block a DC-reset was initiated automatically.

EEG was averaged off-line for epochs of 1500 ms, starting 500 ms before and ending 1000 ms after stimulus-onset. An individual prestimulus baseline (-200 - 0 ms) was used. Epochs were averaged separately for each experimental half (1st half: block 5-19, 2nd half: block 21-35, 37,38) and stimulus type (standards, perceptual deviants, motor deviants; the pseudorandom blocks were excluded). Prior to averaging, trials with overt response errors, occular or muscular artifacts were rigorously rejected (maximum voltage > 50 µV at electrodes vEOG, hEOG or Cz).

Separate LRPs were computed for each stimulus type, experimental half and subject. For computation of stimulus-locked LRPs epochs beginning 500 ms prior to and ending 1000 ms after stimulus onset were used. First, separate averages for correct left- and right-hand movements were computed. Second, the difference of potentials at contra- and ipsilateral electrodes was calculated (for left-hand movements: C4-C3, for right-hand movements: C3-C4). Finally, these two waveforms were averaged. To summarize, the LRP was computed according to the following formula: $\text{LRP} = [\text{Mean}(C4 - C3)_{\text{left-hand-movement}} + \text{Mean}(C3\text{-}C4)_{\text{right hand movement}}] /2$ (see Coles, 1989). Negative deflections in the resulting LRP waveform indicate activation of the correct whereas positive deflections indicate activation of the incorrect response hand, respectively.

Dependent variables and statistical analysis. Groups were formed on the basis of postexperimental questionnaire results. The percentage of correctly generated elements in the free-recall procedure and a recognition score for bigram, trigram and quadruple ratings were computed. Answers on the five-point rating scale in the recognition task were scored as follows: For items which had actually been presented in the sequence 2 and 1 points, respectively, were assigned to the ratings "totally confident" and "fairly confident that the letters had been part of the sequence", 0 points for the rating "don’t know", and -1 and -2 points, respectively, to the ratings "fairly confident" and "totally confident that the letters had not been part of the sequence". For items which had not been part of the stimulus sequence scoring was reversed. This results in a score varying between - 20 and 20 points for bigrams, trigrams and quadruples, respectively. Increasing positive values indicate increasing explicit knowledge of the sequence as assessed by a recognition test. 0 or negative values indicate no explicit knowledge. The three scores were added to one overall "recognition score".

Error rates and mean RTs were determined separately for standard, pseudorandom, perceptual and motor deviant letters for each block and both halves of the experiment.

Mean amplitudes of the ERP were calculated for each of the 18 standard electrodes of the 10-20-system (Jasper,1958) for six consecutive time-windows of 100 ms length beginning 250 ms poststimulus. For topographical analyses, all 61 electrodes were used (see below).

LRP-onset latency was computed separately for each stimulus-type and for both halves of the experiment. For each subject, the maximum of the LRP-amplitude 500 ms pre- to 1000 ms poststimulus was determined. The point where 50 % of this maximum is reached for the first time was taken as the LRP-onset latency for this subject (Smulders, Kenemans, & Kok, 1996).

The ANOVA approach was used to analyze the repeated measure design. Separate analyses were run for errors, RTs, ERPs and LRPs. For the analysis of ERPs, first, a global ANOVA was run to determine the effects of the experimental manipulations. Subsequent analyses were run according to significant interactions (see results section for details). In all ANOVAs the degrees of freedom were adjusted to control for violations of the sphericity-assumption where appropriate (Huynh & Feldt, 1980). Degrees of freedom are reported before, p-values after the adjustment.

II. 3 Results

Behavioral data.

Postexperimental questionnaire. To test whether acquisition of sequential regularities differ between explicit and implicit learners RT and ERP-data for two postexperimentally formed groups of subjects were compared. These postexperimental groups were formed according to the following criteria: Subjects with a recognition score ≤ 7 or a free-recall rate below 38 % were categorized as implicit (see Eimer, Goschke, Schlaghecken, & Stürmer, 1996 and Frensch, Lin, & Buchner, 1998, who used similar criteria). These subjects have no or only a small amount of explicit sequence knowledge as assessed by the free recall and recognition procedures. 10 subjects were categorized as implicit, the remaining 9 as explicit learners. Table 3 shows the recognition and free-recall scores for all subjects. The two scores correlate with r =.85 (p < .0001) and thus seem to tap on the same explicit knowledge base. Therefore, it seems to be justified to use a combination of the two measures for categorization.

17 of the 19 subjects stated that they had noticed sequential regularities (question 1). However, the answer to this question was not used as a categorization criterion as it is known to be subject to a response bias. Willingham, Greeley, & Bardone (1993) found that 24.4 % of a group of subjects confronted with unstructured material reported to have noticed sequential regularities. Data of questions 2 and 3 were not analyzed due to problems with categorizing the heterogenous answers of the subjects.

Subjects of the two postexperimental groups did not differ in respect to the amount of training they had received prior to the experimental blocks (E: 4 blocks, I: 3.8 blocks on average, respectively, t = 1.53, p >.145).

Table 3: Recognition score (R-score), percent of correct items in free recall and group categorization (group: E = explicit, I = implicit) for each subject in experiment 1. Recognition scores were computed as the sum of the scores for recognition of bigrams, trigrams and quadruples and could vary between +-60. Negative scores or zero indicate that the subject did not possess any explicit sequence knowledge, positive scores indicate different degrees of explicit sequence knowledge. Free recall is defined by the percentage of correctly recalled consecutive letters. See text for further details.

Subject#	*R-score*	*Free recall*	*Group*
11	-2	0	I
7	0	25	I
13	0	0	I
18	0	0	I
12	0	25	I
2	2	0	I
17	3	0	I
5	4	37.5	I
19	7	25	I
14	13	25	I
15	12	100	E
4	13	37.5	E
1	15	50	E
16	17	37.5	E
6	20	75	E
9	22	100	E
3	29	100	E
10	42	100	E
8	44	100	E

Accuracy. Overall error-rate was small (5.08 %) and did not differ between explicit and implicit groups. Error-data were analyzed by means of a three-way repeated measures ANOVA with GROUP (explicit (E) vs. implicit(I)) as between and HALF (1 vs. 2) and STIMULUS TYPE (standard (std) vs. pseudorandom vs. perceptual deviants (pd) vs. motor deviants(md)) as within subject factors. A HALF by STIMULUS TYPE interaction revealed that the error rate for motor deviants was higher than for the other stimulus types but only in the second half of the experiment ($F(3,51) = 3.67$, $p < .018$, $\varepsilon = 1.0987$; see figure 6).

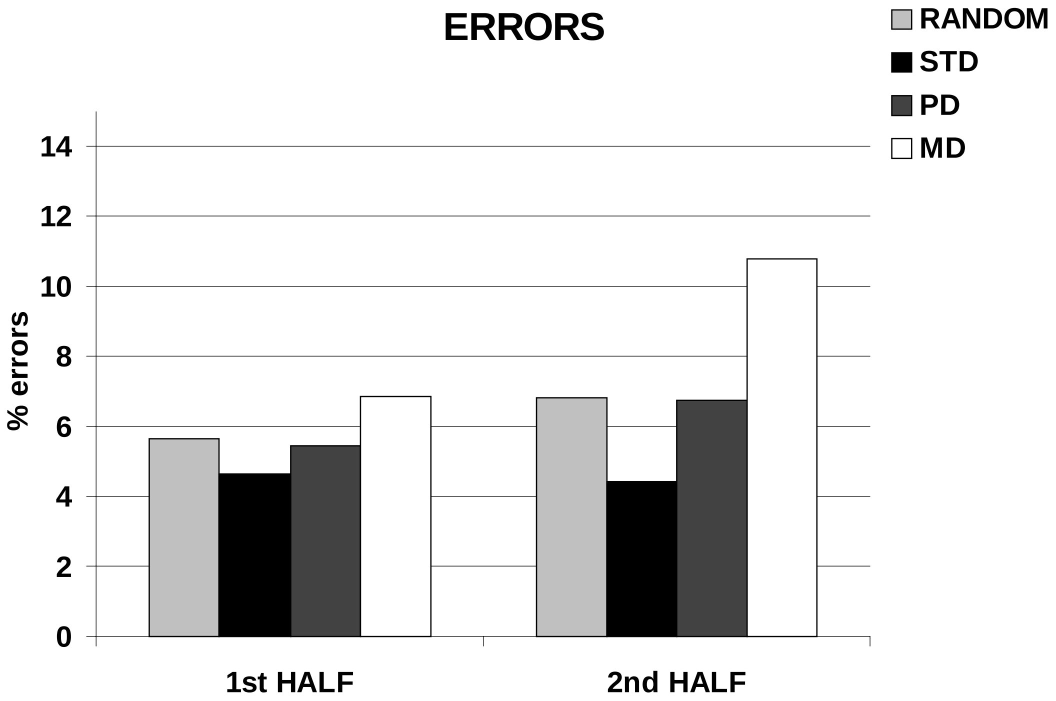


Figure 6: Errors of experiment 1 for the whole sample (n=19) as a function of stimulus type and half. PD = perceptual deviant, MD = motor deviant.

Reaction time. To assess learning of the sequential structure of the stimulus material, RT of the pseudorandom blocks (20, 36) was compared with RT in the preceding and following regular blocks (19,21,35 and 37). Mean RT of standard and pseudorandom stimuli for these blocks were submitted to a two-way repeated measures ANOVA with BLOCK (6) as repeated measures and GROUP (E vs. I) as between subjects' factor. Mean RT in pseudorandom blocks was prolonged as compared to the preceding and the following regular blocks (main effect BLOCK, $F(5,85) = 10.44$, $p < .0001$, $\varepsilon = 0.5075$; see figure 7). Moreover, explicit subjects were disturbed more than implicit subjects in the pseudorandom blocks as revealed by a significant BLOCK by GROUP interaction ($F(5,85) = 3.12$, $p <.0432$, $\varepsilon = 0.5075$). Separate paired t-tests for explicit and implicit subjects showed significant learning effects for both groups (see table 4).

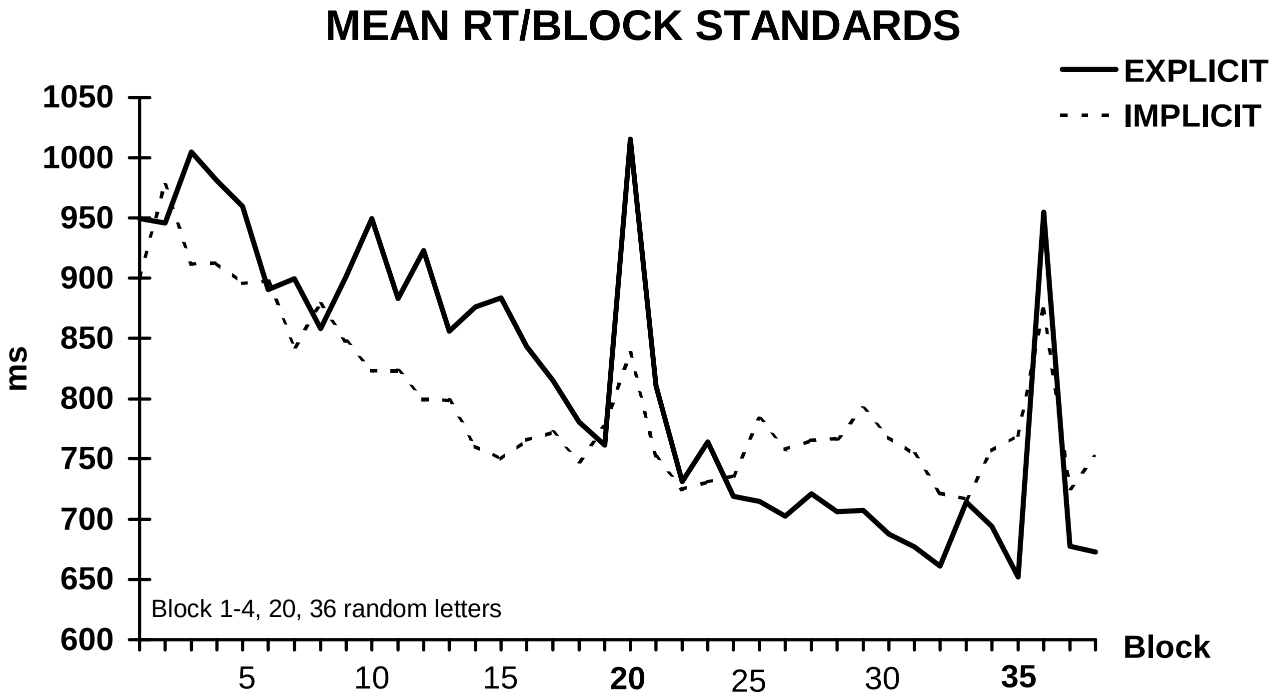


Figure 7: RT (in ms) for standard and pseudorandom letters for experiment 1 separately for the explicit (solid line) and implicit (dashed line) groups. Note that in block 20 and 36 the letters are presented pseudorandomly. Sequence learning is indicated by an increase in RT in the random compared to the preceding structured block.

Visual inspection of fig. 7 suggests that implicit learners responded faster to standard letters in the first half of the experiment whereas explicit learners were faster in the second half. This is confirmed by a GROUP by HALF- interaction in a two-way ANOVA for standard letters (F(1,17) = 4.72, p <.0443).

Table 4: Pairwise comparisons of mean RTs derived from pseudorandom blocks (20,36) and the preceding and following regular blocks (19,21 and 35,37).

Comparison (block)	*Group*			
	Explicit		Implicit	
	Δt [ms]	t	Δt [ms]	t
20 vs. 19	254	3.45**	62	1.25
20 vs. 21	143	3.51**	87	2.9*
36 vs. 35	303	2.61*	104	3.63**
36 vs. 37	277	2.45*	148	3.51**

* p < .05, ** p < .01

Note: df = 8 for explicit, df = 9 for implicit group

To test the contributions of stimulus and response anticipation to sequence learning, mean RT for standard letters, perceptual and motor deviants was compared. In order to obtain a more detailed picture of learning, the experiment was partitioned into 7 subsequent learning epochs (blocks 5-9, 10-14, 15-19, 21-25, 26-30, 31-35 and 37-38). Separate ANOVAs for explicit and implicit subjects with STIMULUS TYPE (std vs. pd vs. md) and LEARNING EPOCH (7) as within subjects factors were conducted. For explicit as well as implicit subjects RTs to standards, perceptual and motor deviants differed significantly (main effect STIMULUS TYPE, for explicit group: $F(2,16) = 8.13$, $p < .0158$, $\varepsilon = 0.5854$; implicit group: $F(2,18) = 28.73$, $p < .0001$, $\varepsilon = 1.1894$). For explicit subjects, this difference changed during the course of the experiment (LEARNING EPOCH by STIMULUS TYPE interaction, $F(12,96) = 2.92$, $p < .0479$, $\varepsilon = 0.2757$; see figure 8).

Planned contrasts for learning epoch 6 showed for explicit learners that RT to perceptual deviants was longer compared to standards ($F(1,8) = 13.36$, $p < .0065$) and RT to motor deviants was longer compared to perceptual deviants ($F(1,8) = 11.91$, $p < .0087$). In learning epoch 1 no reliable difference was found between the three stimulus types.

In contrast, for implicit learners only the contrasts between standards vs. motor deviants ($F(1,9) = 16.7$, $p <.0027$) and perceptual vs. motor deviants ($F(1,9) = 8.46$, $p < .0173$) reached significance in learning epoch 6. Implicit subjects failed to show a reliable RT-difference between standards and perceptual deviants ($F(1,9) = 0.86$, $p < .3785$). Again, no difference between the three stimulus types was found in the first learning epoch. The same pattern of results was found for an analysis of RTs including data of the complete second experimental half (as in the ERP-data).

Taken together, these results suggest differences in the contribution of response- and stimulus- related processes to sequence learning between explicit and implicit learners.

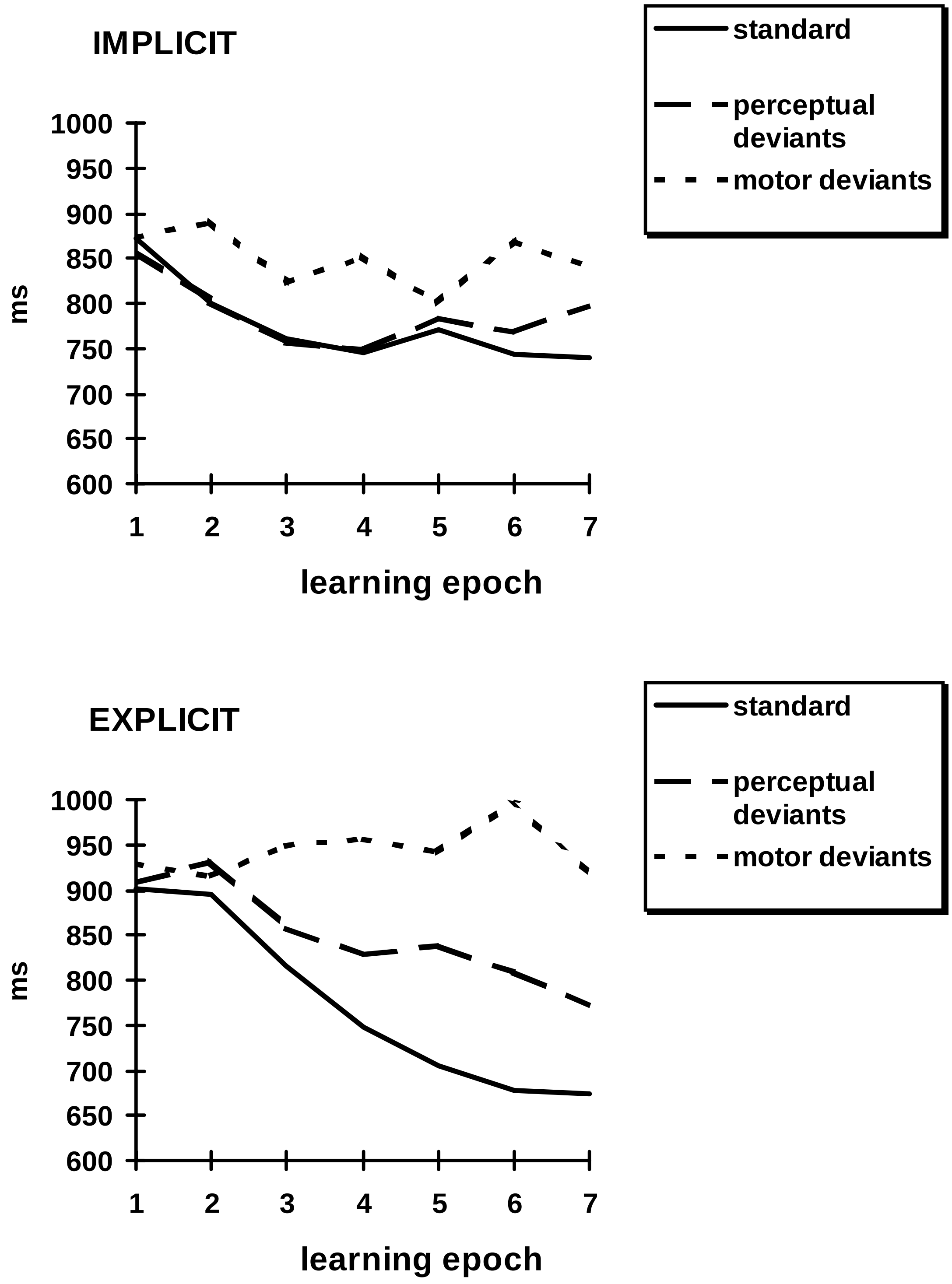


Figure 8: RT for implicit (top) and explicit (bottom) subjects for standards (solid lines), perceptual (long dashed lines) and motor deviants (short dashed lines), respectively, in experiment 1 for 7 learning epochs.

Event-related potentials. Separate analyses were conducted for ERP-components reflecting stimulus-evaluation and response selection processes, respectively.

Stimulus-locked ERPs.

Overview. The most prominent feature of the stimulus-locked ERPs is a positive complex peaking over the parieto-occipital part of the scalp. This positivity starts to rise at about 200 ms after stimulus onset. It reaches its maximum between 300 and 600 ms and resolves completely at about 800 to 900 ms. Topography and latency of this positivity suggest that it is a member of the P300 family. The rising flank and the maximum of the positivity is interrupted by subpeaks which are modulated by the experimental manipulations. A superordinate ANOVA with factors GROUP (E vs. I) as between subjects factor and ELECTRODE (18), STIMULUS TYPE (std vs. pd vs. md), HALF (1 vs. 2) and TIME (250 - 850 ms in 6 steps of 100 ms) as repeated measures factors was run to test whether the ERPs of both groups reflected the experimental variations. Significant four-way interactions with factor GROUP (HALF by ELECTRODE by TIME by GROUP ($F(85,1445) = 5.25$, $p < .0042$, $\varepsilon = 0.0325$) and STIMULUS TYPE by ELECTRODE by TIME by GROUP ($F(170,2890) = 7.29$, $p < .0032$, $\varepsilon = 0.0108$) show that the ERPs of explicit and implicit subjects responded differently to the experimental manipulations, and therefore data of the two groups must be analysed separately.

Explicit group. A sequence of hierarchical ANOVAs was run to decide whether it is feasible to test specific effects of the experimental manipulations at particular electrodes and within particular time-windows. The four-way ANOVA with factors HALF (1 vs. 2), ELECTRODE (18) , STIMULUS TYPE (std vs. pd vs. md) and TIME (6) revealed significant three-way interactions HALF by ELECTRODE by TIME ($F(85,680) = 5.15$, $p < .0195$, $\varepsilon = 0.0231$) and STIMULUS TYPE by ELECTRODE by TIME ($F(170,1360) = 12.99$, $p < .0042$, $\varepsilon = 0.0069$). Separate ANOVAs for distinct time-windows delineated the following pattern of significant effects (see fig. 9). First, a larger negativity for motor and perceptual deviants compared to standards was found between 250 and 350 ms poststimulus (i.e. the rising flank of the positivity is delayed for these stimuli). This effect starts to develop in the first half of the experiment but does not become significant until the second half. It is most prominent at electrode Cz (see fig. 10). According to its latency and polarity it is assumed that this effect is due to a modulation of the N200 component.

Second, a larger positivity between 350 and 650 ms for motor deviants compared to standard and perceptual deviants in the second experimental half was found. This effect reaches its maximum at electrode Pz (see fig.10). Statistically, this is reflected by significant two-way interactions of factors HALF by ELECTRODE and STIMULUS TYPE by ELECTRODE in the respective time-windows in the subordinate three-way ANOVAs with factors HALF, ELECTRODE and STIMULUS TYPE (see table 5).

To get a more detailed picture of the spatial distribution of the effects of stimulus deviance, separate analyses for each of the 18 electrodes (local ANOVAs with factors STIMULUS TYPE and HALF) for time-windows with a significant STIMULUS TYPE by ELECTRODE interaction in the superordinate three-way ANOVA were run. These showed significant effects of STIMULUS TYPE at all electrodes except Fpz for the N200 latency window (250-350 ms; for example at Pz: standard: 4.8 µV, perceptual deviants: 3 µV, motor deviants 2.4 µV). For the P300 latency window (350-650 ms poststimulus), significant main effects of STIMULUS TYPE at occipital, parietal, temporal and central electrode sites were obtained which reflect the larger positivity for motor deviants compared to perceptual deviants and standard letters.

Table 5: Explicit group: Interactions of separate three-way ANOVAs with factors HALF, ELECTRODE and STIMULUS TYPE for six consecutive time-windows.

Effect	*N200*	*P300 latency range*	
	250-350 ms	350-450 ms	450-550 ms
Half * Elec	F(17,136) = 3.17 p <.0151 ε = 0.3062	F(17,136)=6.01 p <.0007 ε = 0.2516	F(17,136)=5.88 p <.0053 ε = 0.1583
Type * Elec	F(34,272)=3.51 p <.0016 ε = 0.2486	F(34,272)=8.18 p <.0001 ε = 0.1741	F(34,272)=6.02 p <.0001 ε = 0.3258

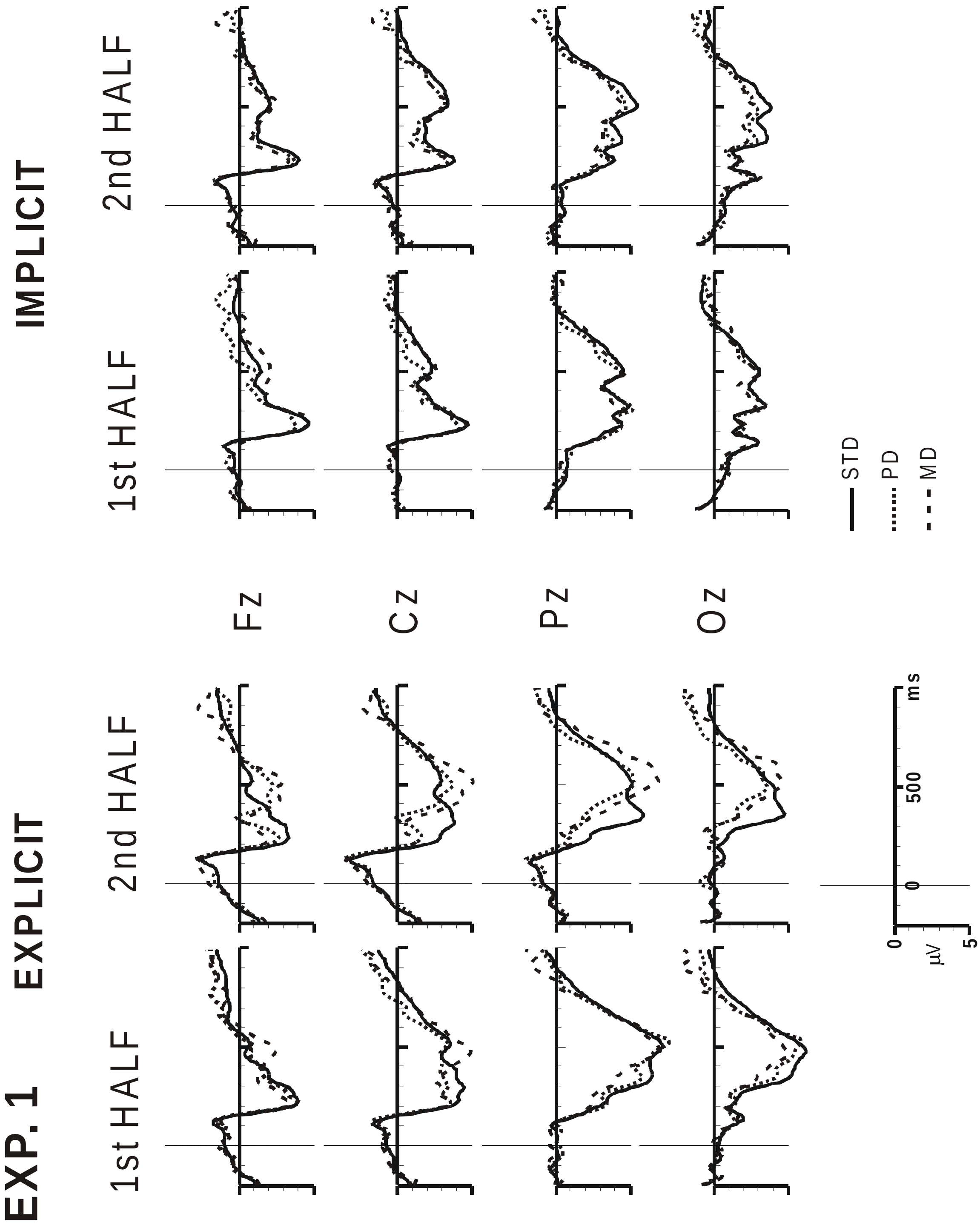


Figure 9: ERPs of experiment 1 during learning of sequential regularities. ERPs to standards, perceptual and motor deviants at midline electrodes Fz, Cz, Pz and Oz are depicted separately for postexperimental group and experimental half. Time-window extends from 200 ms pre- to 1000 ms poststimulus. Note the enhanced negativity for deviant letters between 250 - 350 ms poststimulus (N200-effect) and the enhanced P300 amplitude for motor deviants in the second half for the explicit group.

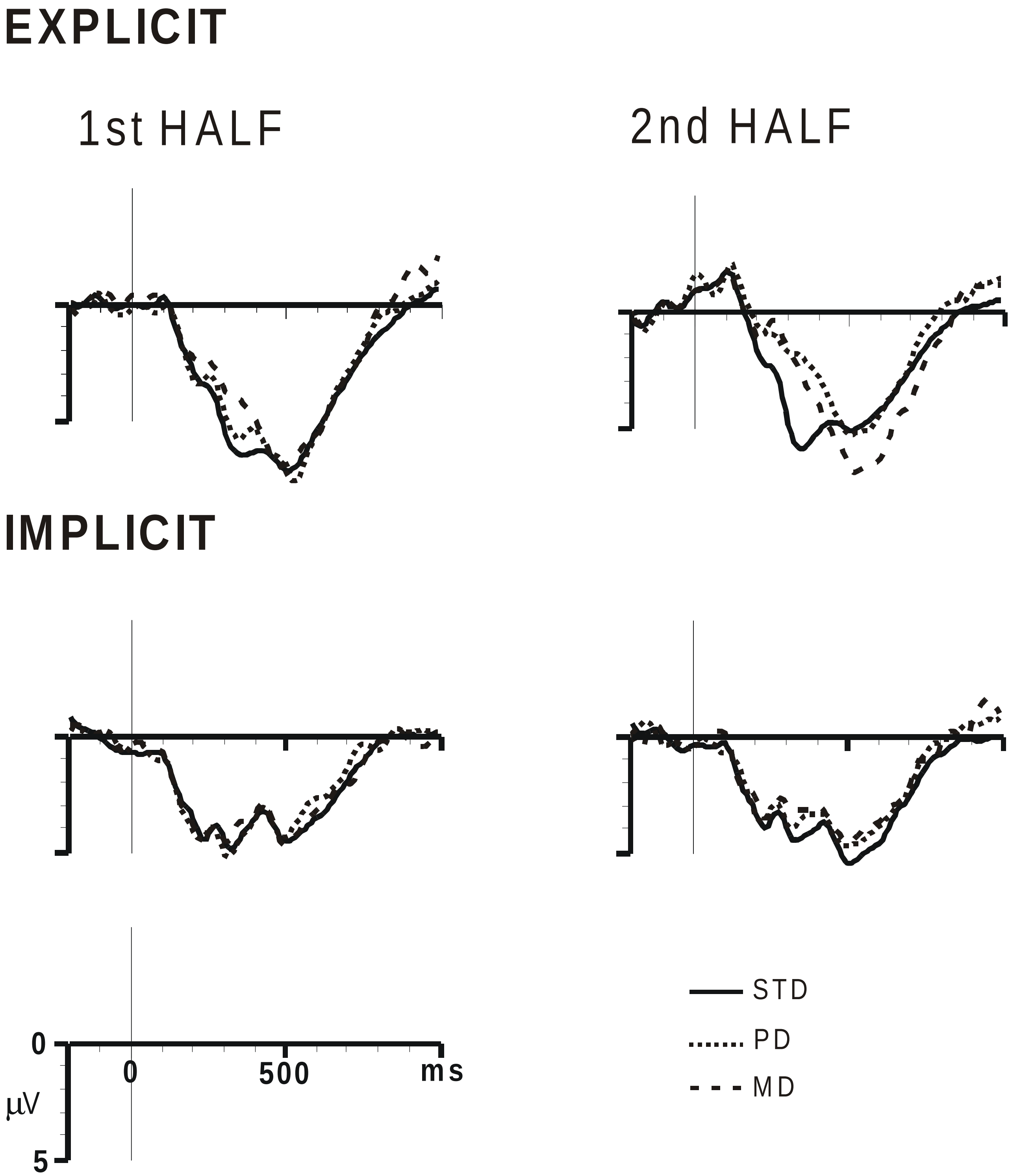


Figure 10: ERPs of experiment 1 during learning of sequential regularities. ERPs to standards, perceptual and motor deviants at electrodes Pz are depicted separately for postexperimental group in each half og the experiment (enlarged from fig. 9). Time-window extends from 200 ms pre- to 1000 ms poststimulus. Note the enhanced negativity for deviant letters between 250 - 350 ms poststimulus (N200-effect) and the enhanced P300 amplitude for motor deviants in the second half for the explicit group.

As an interim summary it can be said for “explicit” subjects: (1) compared to standards, perceptual and motor deviants evoked a more pronounced N200; (2)

compared to standards and perceptual deviants, motor deviants evoked a more pronounced P300.

To test whether the N200 and P300 effects emerged from different neuronal generators, the difference potential ‘motor deviants - standards’ in the N200 (250-300 ms) and P300 (450-550 ms) latency ranges for explicit subjects was computed using a point by point subtraction. Because of non-linearity of signal conduction in the brain tissue and the skull, ANOVA models may confuse differences in the amplitude of an EEG signal (due to differences in source strength) with genuine topographic differences (due to differences in source configuration; see McCarthy & Wood, 1985). Therefore, the amplitudes of the difference potentials were standardized over the 61 electrode locations, separately for each subject and the two latency ranges (with M = 100, S.D. = 15). By using this method, amplitude and variance differences between subjects and conditions are eliminated. The normalized values reflect the standardized deviation of the amplitude from the grand mean across electrodes. Additionally, the sign of the negative amplitudes of the N200 effect was inversed prior to standardization. These standardized values were submitted to a two-way repeated measures ANOVA (ELECTRODE (61) by LATENCY RANGE (2)). The topographical difference between the N200 and P300 effects is reflected by a significant interaction ELECTRODE by LATENCY RANGE ($F(60,480) = 3.08$, $p < 0.0035$, $\varepsilon = 0.1498$)(see fig. 11), i.e. the two effects are most likely caused by different cell assemblies.

Implicit group. As for the explicit group, a hierachical series of ANOVAs was run to decide if it is feasible to test specific effects at particular electrodes and within particular time-windows. The superordinate ANOVA with factors STIMULUS TYPE, HALF, ELECTRODE, and TIME provided a marginally significant three-way interaction STIMULUS TYPE x ELECTRODE x TIME ($F(170,1530) = 4.05$, $p < .0506$, $\varepsilon = 0.0089$). Subordinate ANOVAs for distinct time windows revealed no significant effect at all for the N200-latency range, i.e. the time-window 250 - 350 ms postimulus. For three time windows in the P300 latency range (350-650 ms) the

Figure 11: (a) Standardized topographic maps of the normalized difference amplitude 'ERP standards - ERP motor deviants' for time epoch 250-300 ms poststimulus (N200-effect). Increasing relative negativity is indicated by larger values, i.e. by lighter shading (mean = 100, s.d. = 15). (b) Standardized topographic maps of the normalized difference amplitude 'ERP standards - ERP motor deviants' for time epoch 450-550 ms poststimulus (P300-effect). Increasing relative positivity is indicated by larger values, i.e. by lighter shading (mean = 100, s.d. = 15). For both maps, the mapping algorithm of Junghöfer, Elbert, Leiderer, Berg, & Rockstroh (1997) was used (parameter F = 0.2).

interaction STIMULUS TYPE x ELECTRODE was found to be marginally reliable. However, local ANOVAs revealed that this effect was due to unsystematic amplitude changes: Standards and perceptual deviants were slightly more positive than motor deviants at posterior electrodes and slighly less positive at frontal electrodes. Thus, as can also be seen in fig. 9, the difference between motor deviants and standards is opposite to the one observed for the explicit group and far less systematic in both topography and strength.

To summarize, explicit subjects showed an enhanced negativity for perceptual and motor deviants compared to standard stimuli in the N200-latency range and an enhanced positivity for motor deviants 350 - 550 ms poststimulus (P300-latency range). Both effects become numerically larger in the second half of the experiment. Implicit subjects failed to show any effects of stimulus type in the N200-latency range and only unsystematic effects in the P300-latency range. Thus, ERP components which are sensitive to stimulus evaluation processes were significantly affected by the factor stimulus deviance. However, this effect became manifest only in subjects who possess significant verbalizable knowledge about the sequence structure.

Stimulus-locked LRPs. Stimulus-locked LRPs were analyzed to test whether sequence learning had an effect on response preparation processes. Stimulus-locked LRPs did not differ for explicit and implicit subjects (see fig. 12). This was confirmed by a four-way repeated measures ANOVA with GROUP (E vs. I) as between and HALF (1 vs. 2), STIMULUS TYPE (std vs. pd vs. md) and TIME (mean LRP-amplitude in 20 consecutive time-windows starting with stimulus-onset) as within subjects' factors. None of the interactions with factor GROUP reached significance (smallest $p > .22$), nor was the main effect GROUP ($F(1,17) < 1$) reliable. Therefore, LRP-data of implicit and explicit groups were pooled for further analysis.

Figure 12 also reveals that the initial LRP (70-80 ms poststimulus) is slightly positive in case of motor deviants in the second experimental half. This suggests that the incorrect response is partially activated before the correct response is fully initiated (0.47 µV, $t(1,18) = 2.11$, $p < .0482$).

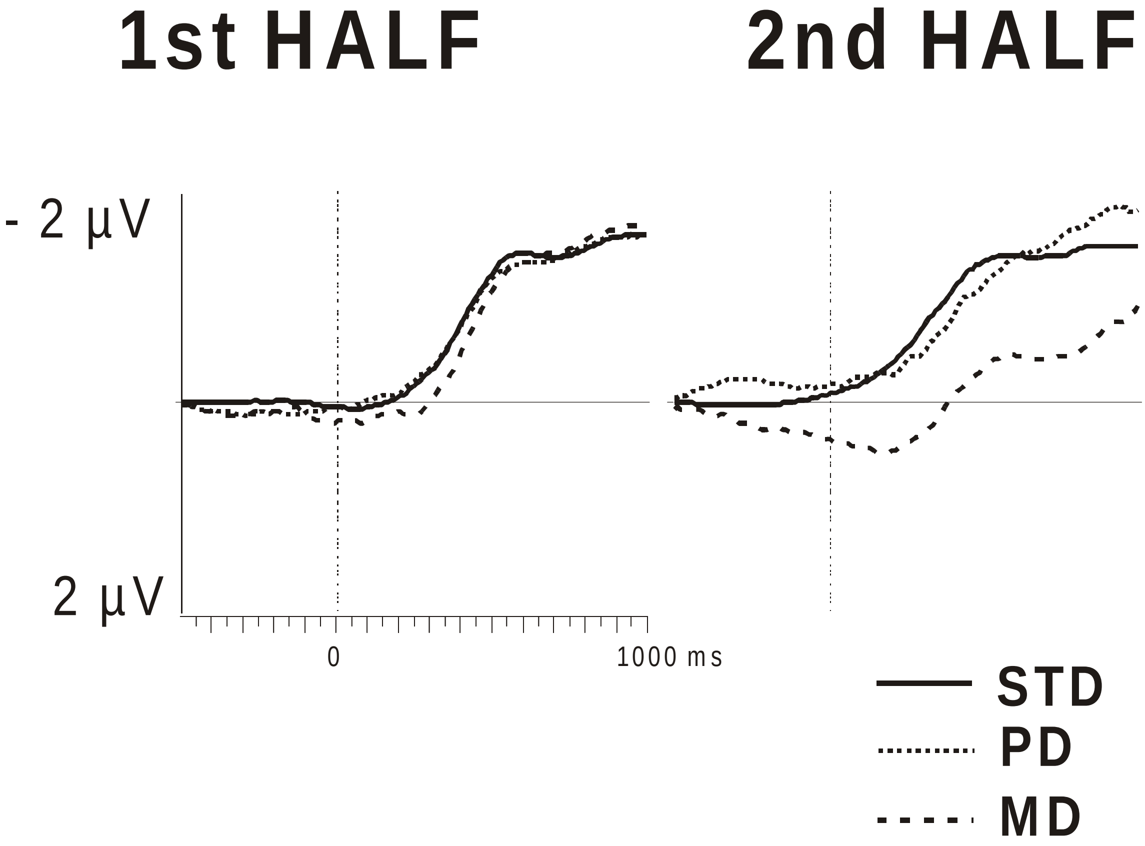


Figure 12: Stimulus-locked lateralized readiness potentials for experiment 1 for both groups (n=19 subjects). Stimulus-locked LRP is shown separately for standards (STD), perceptual (PD) and motor deviants (MD) as well as first vs. second experimental half starting 500 ms pre- and ending 1000 ms poststimulus. Negative amplitudes indicate activation of the correct, positive amplitudes indicate activation of the incorrect response.

Onset latencies of the stimulus-locked LRP are summarized in table 6. For standard stimuli, a shortening of onset-latency in the second compared to the first half of the experiment emerged (t(1,18) = 3.11, p < .006). Onset-latencies for perceptual and motor deviants did not differ between first and second half, but there was a trend of later LRP-onset for motor deviants in the second half.

Table 6: Onset-latencies (and standard deviations) of stimulus-locked LRPs in ms from stimulus-onset for each of the three stimulus-types and both halves of the experiment. std = standard letters, pd = perceptual deviants, md = motor deviants.

	std	*pd*	*md*
First half	441 (98)	487 (139)	567 (196)
Second half	367 (156)	477 (221)	649 (257)

To summarize, analyses of the stimulus-locked LRP show that for all subjects learning of sequential regularities of the stimulus material is reflected in electrophysiological measures sensitive to response preparation. For motor deviants, an activation of the incorrect response was found in the second half before the correct response was fully activated. This positive "dip" of the LRP in the case of motor deviants reveals that the expected response is initiated without a full analysis of the currently presented stimulus. Moreover, for standard stimuli, onset latency of the LRP was shorter in the second than in the first half of the experiment. The shortening of the correct LRP onset reveals that the system improves in its ability to anticipate reliably the next most likely motor response.

Additional analyses. Due to the experimental design, the probability of immediate response repetition is 12.5 % for standards and perceptual deviants, whereas with a motor deviant response repetition probability amounts to 25 %. Thus, response repetition probability and motor deviance are partially confounded and the ERP- and RT-differences observed between the different stimulus types could also be due, at least in part, to these probability differences.

To test for this possible factor, all statistical analyses for RT, ERP and LRP-onset latency measures were recomputed for all trials excluding response repetition trials. The effects reported for the N200 and P300 for explicit subjects and the effects for the LRP-data were again obtained in this additional analysis as is the case for RT-effects. Thus, the confounding of response repetition probability and stimulus deviance did not contribute to the ERP-effects described above.

II. 4 Discussion

The objective of the present study was to better understand how sequential dependencies in a non-random perceptuo-motor event series are learned and neurally represented. In particular, the relative contributions of perceptual and motor processes to this type of learning were analysed.

Behavioral data

Behavioral data indicate that both groups of subjects learned the underlying sequential regularities despite the fact that in each chain of 8 events one regular element was always replaced by a deviating letter. The acquisition of sequence knowledge is reflected by two facts: First, a prolongation of average RT in unstructured (i.e. pseudorandom) compared to structured stimulus blocks, and second, by an overall decrease of RT during the total course of the experiment. Learning is also reflected by a higher error rate for motor deviants in the second half of the experiment. These findings are in line with the results of other invesitgators who also reported learning of sequential regularities, even if these were disrupted from time to time by irregular elements (Eimer, Goschke, Schlaghecken, & Stürmer, 1996, Jiménez, Méndez, & Cleeremans, 1996; Stadler, 1993).

Although both groups of subjects showed a substantial decrease in RT to standards from the beginning to the end of the experiment, the gain in response speed was almost twice as large in the group of subjects with explicit knowledge (about 250 ms) compared to the group with implicit knowledge (about 125 ms). This indicates that explicit learners were more disturbed when the stimuli were determined randomly rather than according to the repeating sequence. This finding is in line with previous studies in which subjects who possess verbalize sequence knowledge show a larger RT benefit (e.g. Curran & Keele, 1993; Mayr, 1996). With respect to this difference one could argue that subjects with explicit knowledge acquire a more complete representation of the regularities of an event sequence.

Further information can be gained from RT to standard letters: A performance advantage for explicit learners compared to implicit learners started to develop from block 24 onwards (see fig. 7). In the final blocks, the average RT of implicit learners was about 100 ms longer than that of explicit learners. However, in the first half of the experiment, the RT-pattern was reversed: Between blocks 9 and 18, explicit learners were about 100 ms slower than implicit learners. A possible explanation for this RT-pattern is that explicit learners noticed regularities fairly early on in the sequence. From that time onward, they might have tried to figure out the exact sequential rules and, therefore, might have acted as in a dual task situation - the primary task being the choice RT-task and the secondary task comprised the extraction of the sequential rules. If this holds true, the secondary task will have captured some of the available processing resources and this resource trade-off seems to be reflected by the prolongation of the choice RTs. Later on, explicit learners had acquired complete knowledge about the event sequence and then could predict the next event much more effectively than implicit learners, which is reflected in their faster RTs.

Furthermore, in the explicit group, response time to both perceptual and motor deviants was prolonged in comparison to standards at the end of the training phase. However, this prolongation was twice as large for motor deviants than for perceptual deviants. Two factors may contribute to this effect pattern. Responses to perceptual deviants may have been prolonged because the subjects recognized a difference between an expected and an actually presented stimulus. This mismatch interrupts a primed perceptual set and as a consequence, the stimulus is analysed more thoroughly. For motor deviants an additional factor may be relevant. Subjects with explicit knowledge can predict the next response from the preceding sequence with high accuracy; therefore it is most likely that not only the perceptual set for the next stimulus but also the associated motor program will be primed. In case of a motor deviant, however, this primed response pattern has to be inhibited and the system must activate a different response instead. It is most likely that this switch from a primed to an unprimed response causes the additional increase of response time to motor deviants in comparison to perceptual deviants. This post hoc analysis suggests that subjects with explicit knowledge developed a memory trace of the sequence structure which represents both perceptual and motor dependencies.

Subjects who had implicit knowledge only showed a different pattern of RT changes. In this group, the change of response time throughout the training session was the same for both perceptual and standard stimuli. Even at the end of the training session no reliable difference emerged between these two stimulus categories. This suggests that standards and perceptual deviants were processed in the very same manner, or, in other words, that the perceptual deviance was not recognized by the system at all. On the other hand, motor deviants prolonged the RT in this group of subjects, too. However, the overall difference between standards and motor deviants was smaller than in the group of subjects with explicit knowledge. This delay of the response to motor deviants could be due again to the fact that an already primed motor program has to be inhibited and that another one has to be activated. However, in this group of subjects the effect must be independent from a perceptual representation of the stimulus sequence. These subjects were not able to recognize sequence fragments of two, three, or four elements. Thus, these subjects must have developed a memory trace of the sequence which is not accessible by consciousness but which nevertheless represents dependencies between successive responses. This suggests that implicit knowledge about sequential regularities may be represented directly in the motor system. This would be compatible with other observations on motor behavior, i.e. that we can acquire complex motor skills like riding a bicycle without being able to give a concise and complete description of what our muscles are actually doing.

A similar pattern of results for implicit learners was observed by Nattkemper & Prinz (1997). They, too, found RT costs for motor but not for perceptual deviants in a group of subjects without explicit sequence knowledge.

Other studies addressing the contribution of perceptual and motor processes to the implicit acquisition of stimulus-response sequences found that both processes may be involved (e.g. Cohen, Ivry, & Keele, 1990; Hoffmann & Sebald, 1996). However, many of these studies used spatial rather than symbolic sequences as perceptual input and such an arrangement may provoke "perceptual" effects which are actually represented as eye-movement patterns and thus have to be attributed to the motor system as well. Stadler (1989), for example, used a complex speeded visual search task and provided evidence for implicit perceptual learning of the position of target stimuli. Most likely, an orientation of attention to the location of the next stimulus is learned in such a situation and this knowledge might be encoded as a sequence of eye movements (Mayr, 1996; Posner & Rothbart, 1992). In contrast, associations between consecutive elements of a letter sequence, as used in the present study, must be formed on a more abstract code level and this code may not be directly linked to the motor system, at least for explicit learners.

It is surprising that implicit learners acquired only knowledge of the response dependencies although the response sequence was more complex than the stimulus sequence (see methods). This failure to extract the regularities of the "directly visible" stimulus sequence suggests that these subjects did not pay attention at all to the repeating sequence of letters. They performed the choice RT task as such and they acquired knowledge of the response dependencies just "by doing", not by "thinking about regularities". This gives further support to the notion that the two groups of subjects must have handled the task in a different manner.

It is important to notice that all of these RT-changes cannot be attributed to a speed-accuracy trade-off: Error rates were very small and hardly differed between conditions, and the only case in which error rates increased (motor deviants in the second half of the experiment) coincided with an increase of RT.

To summarize: The behavioral data of the present study suggest that explicit learners seem to represent both stimulus and response dependencies, while implicit learners seem to have acquired knowledge about response dependencies only. Therefore, explict learners have more complete knowledge about the sequential dependencies. This enables an accurate prediction of the next response due to two types of associations: First, the associations between sucessive stimuli (S_{t-1} - S_t) which trigger directly the a priori given association between a particular stimulus and a particular response (S_i - R_i), and second, associations between one or more successive responses (R_{t-1} - R_t). The combination of both effects causes a substantial gain of RT speed in case of regular elements. In contrast, implicit learners seem to have stored sequential dependencies of motor acts only, i.e. the associations R_{t-1} - R_t. Since this is the only basis for anticipating the next response, the gain in RT speed is less pronounced on the average in implicit than in explicit learners. One could speculate that the associations between successive responses are implicit in both groups, i.e. not available to consciousness. In that case the stimulus-stimulus associations would be the only basis for so-called explicit knowledge.

The conclusion that implicit sequence learning consists of response-response associations is in line with those obtained in recent PET studies (Grafton, Hazeltine, & Ivry, 1995, 1998; Hazeltine, Grafton, & Ivry, 1997). They found increased rCBF in contralateral motor areas during implicit spatial sequence learning, whereas no learning-related rCBF-increase was found in sensory areas (see 1.4.3).

ERP-data

The conclusion that subjects with implicit and explicit knowledge represent different aspects of the regularities of a stimulus-response sequence in memory is further supported by the ERP data of the present study. The two types of deviant stimuli left different signatures in the ERPs and these signatures also had a different expression in the two groups.

To begin with, all three types of stimuli evoked ERPs which had by and large the same general outline. The most prominent feature of the stimulus-locked ERP was a pronounced positivity which reached its maximum at about 500 ms poststimulus over the parietal cortex. Latency and topography of this positivity suggest that it is a member of the P300 family. Functionally, this component has been associated with processes of stimulus evaluation and "context updating" (Donchin & Coles, 1988; Johnson, 1986). The P300 was preceded by a negative shift, the expression of which varied with the stimulus type and the learning stage. If present, it peaked at about 300 ms poststimulus and it had a parieto-central maximum. Latency and topography of this negativity suggest that it is the N200 component which is functionally related to processes of stimulus discrimination (Lawson & Gaillard, 1981; Ritter, Simson, & Vaughan, 1983; Towey, Rist, Hakerem, Ruchkin, & Sutton, 1980).

In the group of implicit learners both components were evoked with the same latency and amplitude by each of the three stimuli - standards, perceptual, and motor deviants. Since both components are assumed to reflect stimulus evaluation processes, this finding suggests that all three types of stimuli were processed in the very same manner. Obviously, the brain of implicit learners made no difference between these three stimuli, or, in other words, the fact that the otherwise regular sequence was interrupted by a different letter was not recognized at all by those processors which evaluate the perceptual input and which perform an update of the internal model of the environment.

In the group of explicit learners the situation is different. Here, both types of deviants evoke a much more pronounced N200 than standards in the second half of the experiment, i.e. when explicit knowledge about the stimulus sequence has been accumulated. The N200 effect indicates that any perceptual inconcistency in the stimulus sequence is now readily noticed by the system. A comparable N200 effect was described by Eimer, Goschke, Schlaghecken, & Stürmer (1996) for subjects categorized as explicit learners. These authors suggested that the N200 effect could reflect the amount of consciously available sequence knowledge. This is a strong conclusion and due to the subjectivity of the hypothetical construct difficult to objectify. However, even if the effect is not functionally related to the subjective domain of consciousness, the data provide converging evidence for a weaker conclusion, i.e. that a memory trace of the stimulus sequence must be stored which represents stimulus attributes as such.

Visual inspection of fig. 9 shows that perceptual and motor deviants are also reliably more negative in amplitude compared to standard stimuli at electrode Fz (200-300 ms poststimulus) in the explicit group. Again, this effect was larger after a considerable amount of experience with the sequence learning task. This negativity has a different waveform than the centro-parietal N200, starts slightly earlier and has a centro-frontal topography. In previous research, a comparison of Go- and NoGo- trials in RT-tasks revealed an enhanced amplitude of the N200-component for NoGo-trials at fronto-central electrode sites (e.g. Kok, 1986; Pfefferbaum & Ford, 1988; Thorpe, Fize, & Marlot, 1996) even if Go- and No/Go- trials appeared equally often (Eimer, 1993; Jodo & Kayama, 1992; Schröger, 1993). Fronto-central N200-amplitude enhancement was also found for covert cognitive responses (Pfefferbaum, Ford, Weller, & Kopell, 1985), which shows that it does not seem to be confined to the necessity to withhold a motor response but may appear whenever either overt or covert response preparation has to be interrupted.

Gehring, Gratton, Coles, & Donchin (1992) found the fronto-central N200 to be sensitive to flanker compatibility in a flanker task. It has been proposed that the sensitivity of the fronto-central N200 to the compatibility of the flanker stimuli has is associated with the necessity to interrupt the activation of incorrect reactions when competetive responses are primed (Kopp, Rist, & Mattler, 1996). 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 (note that activation of the expected but incorrect response is indicated by the positive-going 'dip' in the LRP). 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 deviance of the presented stimulus from the expected one might initiate an inhibition of the response to be executed. After an additional check of the correctness of the prepared response, this inhibition is released and the correct response is executed. This process might be indicated by the enhanced frontal N200. This interpretation would also account for the enhancement in RT to perceptual deviants for explicit learners and the difference in onset-latency for perceptual deviants compared to standards in the second half of the experiment (see table 6).

Most interestingly, the group of implicit learners does not show an enhanced frontal N200 amplitude for motor deviants despite a prolonged RT and an activation of the incorrect response hand for these stimuli. Thus, the fronto-central N200 seems to be no prerequisite for the inhibition of a primed response.

Response inhibition processes have been linked to executive control functions (Kopp, Rist, & Mattler, 1996). Thus, the present results suggest that executive control processes play a different role in explicit and implicit sequence learning. One could speculate that conscious awareness of the sequence emerges only if executive control processes are involved. Taken the other way round, the involvement of executive control processes in the processing of a task might be a prerequisite for the acquisition of explicit, verbally recallable knowledge.

The stimulus-locked ERPs of explicit learners revealed another systematic effect. The amplitude of the P300 was reliably larger for motor deviants than for perceptual deviants or standards respectively. This effect, too, emerged in the second half of the experiment, i.e. when knowledge about the event sequence was clearly available. Since the centro-parietal N200 was affected by both types of deviants and the P300 by motor deviants only, one has to conclude that the generating mechanisms are functionally distinct. Assuming that the system continuously generates and updates a model which comprises all perceptual features of the next stimulus to be expected, Gehring, Gratton, Coles, & Donchin (1992) argued that the N200 component could reflect a process which is sensitive to any deviation of an actually perceived stimulus from such a model. In the present experiment, both, perceptual and motor deviants, differed perceptually from the next most likely, regular stimulus. Thus, it makes sense that both bear an effect on the N200. In this respect the centro-parietal N200-effect observed here with visual stimuli would be at least in part functionally comparable to the mismatch negativity effect observed in the auditory modality. This effect is sensitive to any change in an ongoing stimulus sequence (Näätänen, 1992).

The motor deviant, on the other hand, forms not only a mismatch with an expected stimulus template, but in addition it transmits task-relevant information, because after perceiving it the subject has to change a primed action or motor program. Task relevance in this shade of meaning has been found to be one of the most potent antecedent conditions for the P300 component (Donchin & Coles, 1988; Johnson, 1986). For example, the amplitude of P300 is larger for stimuli which require an overt behavioral response compared to a silent counting response, and P300 amplitude is also 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 the increase of P300 amplitude.

The lateralized readiness potential provides further insight into the mechanisms of sequence learning. As mentioned above, the polarity of the stimulus-locked LRP reveals if the centrally initiated motor program is correct or incorrect, and the onset latency indicates when such a motor program is initiated. Both parameters of the stimulus locked LRP were systematically affected in this study. Modifying factors were the type of stimulus and the learning stage but not the factor group, i.e. the criterion of explicit vs. implicit learning. With respect to the LRP, both groups revealed the very same response pattern.

In the second half of the experiment the LRPs following motor deviants were clearly different from those following standards or perceptual deviants, respectively. Two features of the motor deviant LRP are striking during this stage of the experiment. First, in the initial part of the LRP the polarity goes in the incorrect direction. This suggests that the program for the expected but inappropriate hand is at least partially activated. Most likely, this is an automatic effect which has to be counteracted after a full analysis of the stimulus (Gratton, Coles, Sirevaag, Eriksen, & Donchin, 1988). Second, and due to the initial incorrect activation, the LRP-onset for the correct side is slightly delayed compared to standard letters.

A more detailed analysis of the LRP-onset times in the present study reveals that the pronounced difference between standards and motor deviants in the second half has two causes. On the one hand, LRP-onset for standards starts earlier in the second than in the first half of the experiment. This decrease of LRP onset latency amounts to about 100 ms and reflects the shortening of RT. On the other hand, LRP-onset for motor deviants is delayed compared to standards reflecting the delay in RT. Thus, there are two effects: a positive priming effect - standards activate their associated responses faster after some training - and a negative priming effect - unexpected responses are delayed after acquisition of the sequence. LRP onset latency of perceptual deviants showed not much of a change from the first to the second half. On average, the latency for perceptual deviants was somewhat longer than for standards. In total, this pattern of effects is similar to the pattern of response times. The main difference between these two sets of data is, however, that the LRP effects are the same in both groups of subjects while the RT effects are dependent on whether a subject has verbalizable knowledge or not. The fact that the LRP to motor deviants is delayed in both groups for about the same amount of time and, most importantly, that both groups show an initial activation of the incorrect hand is further evidence for the claim that priming of the next response depends in both groups on the same type of response-to-response association.

The present experiment differs from others in the sequence learning domain in that subjects had to perform many more trials than in most other experiments. In most studies, learning is observed after a much smaller number of training blocks (e.g. Perruchet, Bigand, & Benoit-Gonin, 1997). However, the RT results of the present study show that the conclusions with respect to implicit learning are valid: A comparison between mean RT in the random block and the standard letters of the preceding structured stimulus block (20 vs. 19) shows non-significant learning for the implicit subject group in the first half of the experiment ($t(9)=1.25$, $p > .24$). Furthermore, in an experiment using only motor deviant letters, Eimer, Goschke, Schlaghecken, & Stürmer (1996) obtained learning effects for their implicit subjects which are comparable to the effects presented here. Cleeremans & McClelland (1991) showed that it is much harder for subjects to learn probabilistic material and, therefore, more practice is needed to learn regularities inherent in it. The introduction of deviant stimuli in the present study can be compared with using probabilistic material as there are disruptions of the sequence at unpredictable positions. Thus, it is more difficult to detect the sequential regularities and longer training is required before an (implicit) learning effect emerges.

Taken together, the observed pattern of RT and ERP results supports the idea that implicit learners represent mainly, if not solely, R-R- dependencies, whereas explicit learners represent both stimulus- and response- based dependencies. This seems to be the case at least for event sequences in which symbols and not spatial positions are used as stimuli (spatial sequences are studied in experiment 3). These results converge with recent PET-studies in which rCBF increased substantially during implicit sequence learning in the motor areas contralateral to the performing hand while not much blood flow change could be observed in the sensory association areas (Grafton, Hazeltine, & Ivry, 1995; Hazeltine, Grafton, & Ivry, 1997).

III. EXPERIMENT 2: A DIRECT COMPARISON OF EXPLICIT AND IMPLICIT SEQUENCE LEARNING

III. 1 Introduction

In experiment 1, ERPs were used to study the role of perceptual and motor processes in implicit and explicit sequence learning (see also Eimer, Goschke, Schlaghecken, & Stürmer, 1996). Letters were presented according to a repeating sequence. Subjects had to respond to a letter with a lift of the appropriate finger. Two letters each were related to one response finger. Thus, it was possible to introduce two deviant events into the sequence: Perceptual deviants changed the perceptual but preserved the response sequence whereas motor deviants violated both response and stimulus sequences (see also Nattkemper & Prinz, 1997). Two groups of subjects were formed according to their postexperimental verbalizable sequence knowledge. A striking difference between implicit and explicit learners was found: Explicit learners showed an enhanced negativity 250-350 ms poststimulus for perceptual and motor deviants as well as an enhanced positivity for motor deviants in the second half of the experiment (i.e. after a considerable amount of practice). Furthermore, for motor deviants an activation of the incorrect response prior to execution of the correct response was found (positive LRP). In contrast, for implicit learners no ERP-effect of stimulus deviance emerged. However, the LRP was sensitive to stimulus deviance for implicit learners: Motor deviants again activated the incorrect response before the correct response was executed. These findings are in line with the view that implicit sequence learning is primarily response-based.

In experiment 1, the formation of postexperimental groups was based on the results of tests of explicit knowledge administered after completion of the SRT-task. This procedure is problematic because it involves the use of an arbitrarily chosen criterion for categorization of the participants. In the present experiment, instructional manipulations are used to induce explicit and implicit learning, respectively: the explicit group is informed about the presence of a sequence prior to performing the SRT-task whereas the implicit group is not.

Baldwin & Kutas (1997) recorded ERPs during implicit learning in a variant of the SRT-task (adapted from Cleeremans & McClelland, 1991). Subjects had to respond to a specified movement of a square in a 3*3 grid of locations. The position of the next square was determined according to an artificial grammar. In 15 % of all cases, a grammatically incorrect location replaced a grammatically correct one. The detection of the violation of the grammatical structure was reflected in a larger positivity 200-500 ms after stimulus presentation for grammatical targets compared to ungrammatical ones. Thus, it was shown that ERPs are sensitive to deviations of implicitly acquired expectations. In a second experiment, Baldwin & Kutas (1997) directly compared ERPs for groups of subjects learning implicitly and explicitly by varying the instructions the participants received prior to the sequence learning task to address the question whether different neuronal structures are involved in both forms of learning. Again, they found a larger positivity 200–500 ms for grammatical compared to ungrammatical target movements for explicit as well as implicit learners. Furthermore, explicit learners showed a larger frontal negativity than implicit learners starting 500 ms prior to response execution for grammatical movements. This finding was interpreted as reflecting the intentional aspect of response preparation. The difference between both groups of learners is taken as support for the view that explicit and implicit learning depend – at least partly – on different neuronral systems.

In Exp. 2 of Baldwin & Kutas (1997), the movement of the square was determined according to a repeated sequence of the four possible movements of a square through a 3*3 grid (horizontal-diagonal-vertical-knight’s move). Explicitly instructed subjects always saw the sequence of movements presented in the corner of the monitor (abbreviation of the sequence (letters h-d-v-k) always present) whereas implicit learners received the information that the movements would occur randomly. Thus, it cannot be ruled out that the explicit subject group did not learn the construction rule of the sequence but applied the given rule to enhance performance. The performance increase for explicit subjects could reflect increasing proficiency in applying the rule. The implicit group, on the other hand, did not know about the presence of a sequence and, therefore, had to learn it to increase performance. Thus, the larger frontal negativity for explicit learners could reflect the process of actively using a rule rather than a learning process or intentional response preparation.

To examine this alternative account of the Baldwin & Kutas (1997) results, in the present experiment sequence learning for a group of subjects who received the information that a sequence is present in the material (explicit group) and a group which did not know about the presence of a sequence (implicit group) is compared. In contrast to the Baldwin & Kutas (1997) - study, the participants in the explicit group did not know the actual sequence. To this end, the modification of the SRT-task which was also used in experiment 1 is employed. It is expected that explicitly instructed subjects exhibit larger sequence learning and more verbalizable postexperimental knowledge than implicit learners. Most importantly, different patterns of ERPs sensitive to sequence learning for the two groups are expected.

Two further aspects of the results of the first experiment are examined in more detail in experiment 2: First, the relationship between different measures of explicit knowledge is analysed in more detail. In experiment 1, the assessment of reproducable knowledge about the motor sequence was not included. This is done in the present study.

Secondly, a different, more complex letter sequence is used to provide evidence that the results with respect to the brain systems involved in explicit and implicit sequence learning can be generalized to a variety of sequence types.

III. 2 Method

Subjects. 32 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 (8 female; age 23-29) participated in the implicit and 14 (6 female; age 24-34) in the explicit 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 implicit sequence learning before.

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 (1.45^0 visual angle) on a computer display served as stimulus material. From a constant viewing distance of 100 cm letters subtended a visual angle of 0.58^0 (height) and 0.28^0 (width). Letters were presented in 46 blocks of 72 stimuli each. The letters remained on the screen until a response was executed. The RSI was held constant at 500 ms. Correctness of the response and response time (to the nearest 5 ms) were recorded.

Procedure. Subjects placed their left and right middle and index fingers in a circular cavity of a light gate. They were instructed to respond to letters appearing on the screen by 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, respectively (see fig. 13).

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 (i.e. the first letter was a Z, the second an N and the 13th a Z again). 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 related to the same response (e.g. the perceptual deviant for Z is N, for T it is R). 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 (see fig. 13).

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 (2 * D, T, L and N, 1 * Z, V, X and R).

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

To assess the amount of explicit sequence knowledge, all participants had to complete three tasks after the 46th stimulus block. In the free letter sequence recall task, subjects had to write down as many consecutive letters as possible. In the free movement recall task, the participants had to place their fingers in the light gates and execute the finger lifts in the same order as they did during the experiment proper. In a recognition task, 24 letter bigrams and 24 trigrams were presented on the screen (see appendix B). Subjects had to indicate whether these sequence fragments were part of the previously presented sequence.

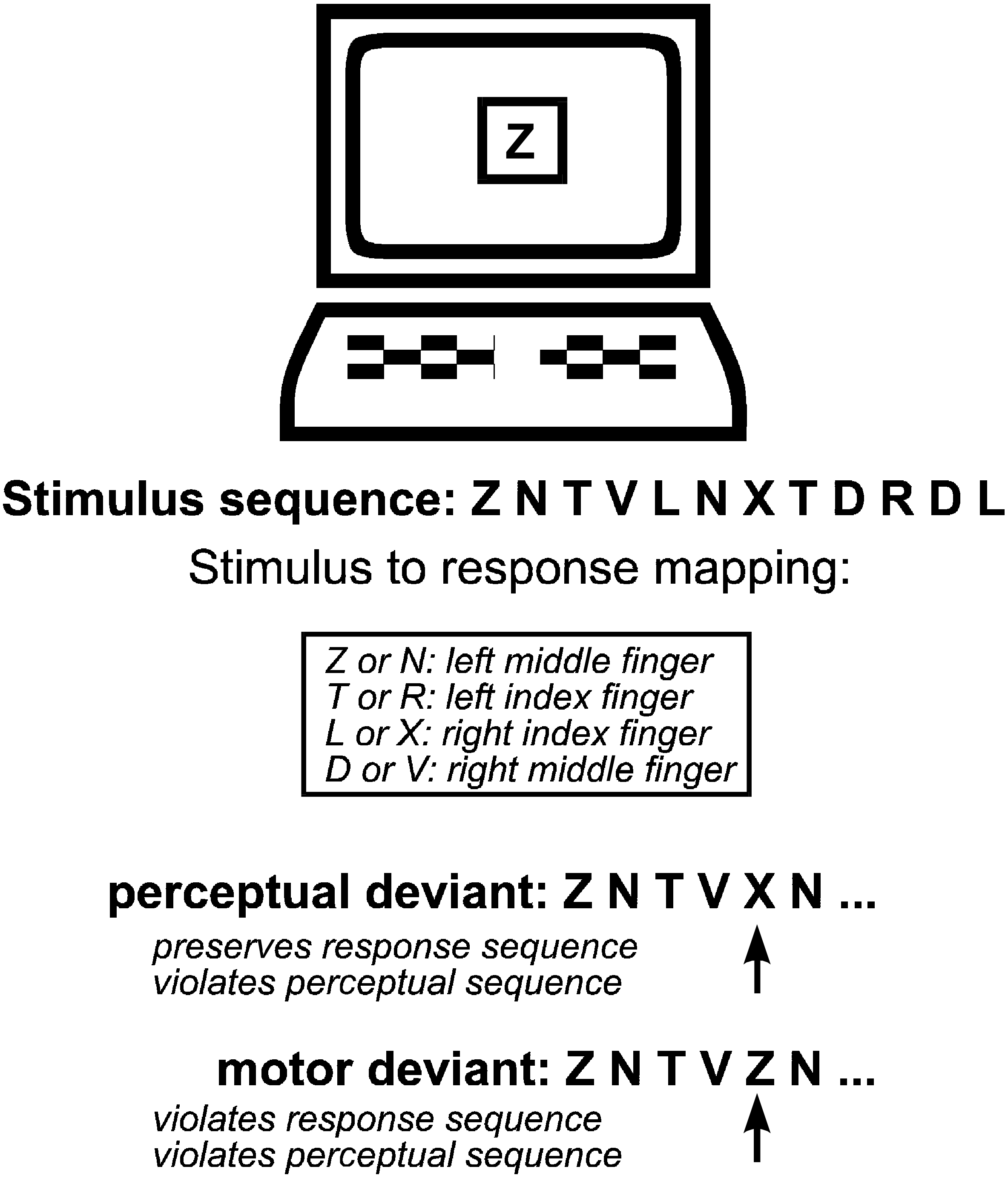


Figure 13: Stimulus-response mapping and construction of the two types of deviant stimuli used in experiment 2.

EEG recording. The electroencephalogram (EEG) was recorded as described in the methods section of experiment 1.

Data analysis. *Behavioral data.* Data of the explicit knowledge tests for both experimental groups were compared by means of pairwise t-tests. In the free recall tasks, the number of correctly recalled consecutive elements was taken as dependent measure whereas for the recognition test, the percentage of correctly categorized sequence fragments was used.

RT and errors were analysed as described in the methods section of experiment 1.

Stimulus-locked event-related potentials. EEG and EOG were divided off line 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 µV, horizontal EOG exceeding 100 µV) or an amplitude range of more than 100 µV 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 (N200: 250-350 ms, P300: 450-600 ms, late positivity: 650-900 ms). For these analyses, only the 18 electrode sites of the standard 10-20-system (Jasper, 1958) were used.

To determine whether the experimental manipulations had different effects on ERPs for explicit and implicit learners, an overall repeated measures ANOVA with factors GROUP, ELECTRODE SITE, HALF and STIMULUS TYPE was conducted 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 (Huynh & Feldt, 1980). Degrees of freedom are reported before, p-values after the adjustment.

Response-locked event-related potentials. Artefact rejection and averaging of response-locked ERPs was performed as described for the stimulus-locked data with the following exception. ERPs were averaged in the time-period 1000 ms before to 100 ms after response execution and related to a baseline of mean voltage 700 - 600 ms prior to response execution. Statistical analyses were comparable to those of the stimulus-locked ERPs. Mean voltage 450 - 150 ms before response execution was taken as the dependent measure.

Topographical maps of the difference potential between explicit and implicit learners for standards, perceptual deviants and motor deviants were computed using all 61 scalp electrodes.

Lateralized readiness potential. LRPs were computed separately for each stimulus type, first and second half of the experiment and group from epochs starting 500 ms prior to and ending 1500 ms after stimulus onset. Computation of the LRP was performed as described in the methods section of experiment 1.

Differences in LRP-onset latency for standards and perceptual deviants in the first and second half were examined separately for both groups by using the jackknife method (Miller, Patterson, & Ulrich, 1998). This method is the most sensitive procedure available to detect onset-latency differences. 50 % of the amplitude maximum were taken as criterion to determine the onset latency. LRPs were computed relative to a baseline starting 500 ms and ending 400 ms prior to response execution.

To test whether motor deviants activated the incorrect response prior to execution of the correct reaction after a considerable amount of learning (positive-going LRP), t-tests were computed for the initial portion of the LRP for motor deviants in the second half of the experiment.

III. 3 Results

Behavioral Performance. *Tests of explicit sequence knowledge.* To test whether the instructional manipulation was successful, performance in the explicit knowledge measures for implicitly and explicitly instructed subject groups was compared. In the free letter and movement recall tasks, explicit subjects performed significantly better than implicit learners (letter sequence recall: 2.07 vs. 6.64 letters, $t(26) = 3.305$, $p < .0028$; movement sequence recall: 3.5 vs. 7.14 movements, $t(26) = 2.725$, $p < .0113$). Thus, the instructional manipulation was successful. However, in the recognition task no significant difference in explicit knowledge between both groups emerged (implicit: 56.4 % correctly classified sequence fragments, explicit: 62.5 %; $t(26) = 1.4$, $p < .174$; see table 7 for results of the individual subjects).

Pearson correlation coefficients were computed for the three explicit knowledge tests to evaluate whether the different measures tap the same or different knowledge bases. The correlational patterns revealed differences between the two groups: No significant correlations between the three measures were found for implicit learners whereas for the explicit group, the three measures were highly correlated ($r_{\text{free recall letter sequence - movement sequence}} = .978$, $p < .0001$, $r_{\text{free recall letter sequence - fragment recognition}} = .796$, $p < .0007$, $r_{\text{free recall movement sequence - fragment recognition}} = .812$, $p < .0003$).

Table 7: Performance in free letter and movement recall and recognition tests for each subject. Subjects # 1-16: implicit group, # 21-35: explicit group. For the free letter and movement recall tasks, the number of correctly recalled letters/movements is given (max. 12). For the recognition task, the number of correctly classified sequence fragments is given (max. 48). See method section for details.

Subject #	*Letter recall*	*Movement recall*	*Recognition score*
1	0	3	30
4	0	0	23
5	3	7	25
6	0	0	27
7	7	3	35
8	2	3	23
9	3	0	28
10	2	5	28
11	4	5	22
12	0	4	30
13	2	6	22
14	2	4	30
15	2	4	32
16	2	5	24
21	12	12	38
22	12	12	41
23	11	12	30
24	2	5	31
25	8	8	33
26	12	12	33
27	0	0	21
28	4	5	34
30	10	10	29
31	2	3	25
32	3	2	24
33	0	2	19
34	12	12	38
35	5	5	24

To determine whether the amount of verbalizable knowledge in the free recall tests is different from the guessing probability, a simulation of subjects' performance in these tests was conducted. First, the mean number of letters reported by implicit subjects in the free letter recall task was computed. On average, 7 letters were reported by implicit learners. Consequently, in the first simulation (see table 8), sequences of 7 letters length were drawn out of a pool of 12 letters (N,N,D,D,T,T,L,L,Z,X,V,R; pairs of letters (e.g. NN) allowed, with repetition). Using a pool of 12 letters rests on the assumption that subjects realized that four letters appeared twice in each repetition of the sequence (letters N, D, T and L). This is not necessarily the case. Therefore, a second simulation with the stimulus pool N,D,T,L,X,Z,V,R was conducted (see table 9).

In all simulations, it was first tested whether the drawn seven-element sequence was part of the stimulus sequence used in the experiment. Next, it was tested whether one out of all possible six-letter sequences inherent in the drawn seven-letter train was part of the stimulus sequence, and so on. The program stopped when the first correct sequence was found (Hennighausen & Rüsseler, 1998). The percentage of correct sequences of length 2,3,4,5,6 and 7 was computed. This measure is equivalent to the probability of guessing correctly for a correct sequence of the relevant length. Furthermore, the mean number of correctly recalled letters in the simulation was computed. In all reported simulations 1000000 sequences were drawn out of the relevant stimulus pool.

Table 8: Results of simulation 1. 1000000 draws of a seven letter sequence out of a pool of 12 letters. See text for details.

Mean sequence length	*1.91169*
Probability for 2 correct elements	0.6543
Probability for 3 correct elements	0.1072
Probability for 4 correct elements	0.0124
Probability for 5 correct elements	0.0012
Probability for 6 correct elements	0.00014
Probability for 7 correct elements	0.00004

Table 9: Results of simulation 2. 1000000 draws of a seven letter sequence out of a pool of 8 letters. See text for details.

Mean sequence length	*1.81838*
Probability for 2 correct elements	0.5999
Probability for 3 correct elements	0.09282
Probability for 4 correct elements	0.00950
Probability for 5 correct elements	0.00096
Probability for 6 correct elements	0.00008
Probability for 7 correct elements	0.00007

Irrespective of the stimulus-pool used, guessing probability for two correct consecutive elements was above 50 %. Therefore, it is likely that subjects who recalled sequences of more than two consecutive elements have at least some explicit knowledge about the stimulus regularities (subjects 5, 7, 9 and 11 of the implicit group). Likewise, four explicit learners (24, 27, 31 and 33) did not recall more than two consecutive sequence elements. Nevertheless, these subjects were not excluded from their respective samples as the purpose of the present experiment was to assess the effect of the instructional manipulation on RT and ERPs. Nevertheless, all reported statistical analyses were also computed using only the data of the ten 'truly implicit' and the ten 'truly explicit' subjects. The pattern of results remained the same.

On average, implicit learners recalled 10 consecutive elements of the movement sequence. Therefore, the simulation was computed by drawing a ten-element sequence out of a pool of the four different movements. Results are shown in table 10.

Table 10: Results of simulation 3. 1000000 draws of a ten-element sequence out of a pool of 4 movements. See text for details.

Mean sequence length	*2.95811*
Probability for 2 correct elements	0.3271
Probability for 3 correct elements	0.4529
Probability for 4 correct elements	0.1669
Probability for 5 correct elements	0.0409
Probability for 6 correct elements	0.0091
Probability for 7 correct elements	0.0019

Guessing probability for three or fewer correct consecutive movements was 77 % (32.71 % + 45.29 %). Subjects who recalled more than three consecutive movements acquired at least some reproduceable knowledge about the movement sequence. This is the case for 8 implicit and 10 explicit subjects. However, these subjects were not excluded from their respective samples because it is not clear what exactly is measured in free movement recall tasks. Fendrich, Healy, and Bourne (1991) argued that movement recall tasks tap implicit rather than explicit knowledge. This is in line with the non-significant correlations between the explicit knowledge tests for implicit learners in the present experiment.

Reaction time (RT). RTs for the different stimulus types were different for explicit and implicit learners as indicated by a STIMULUS TYPE by GROUP interaction ($F(2,52) = 5.37$, $p < .0228$, $\varepsilon = 0.5857$). Therefore, separate analyses for explicitly and implicitly instructed subjects were conducted.

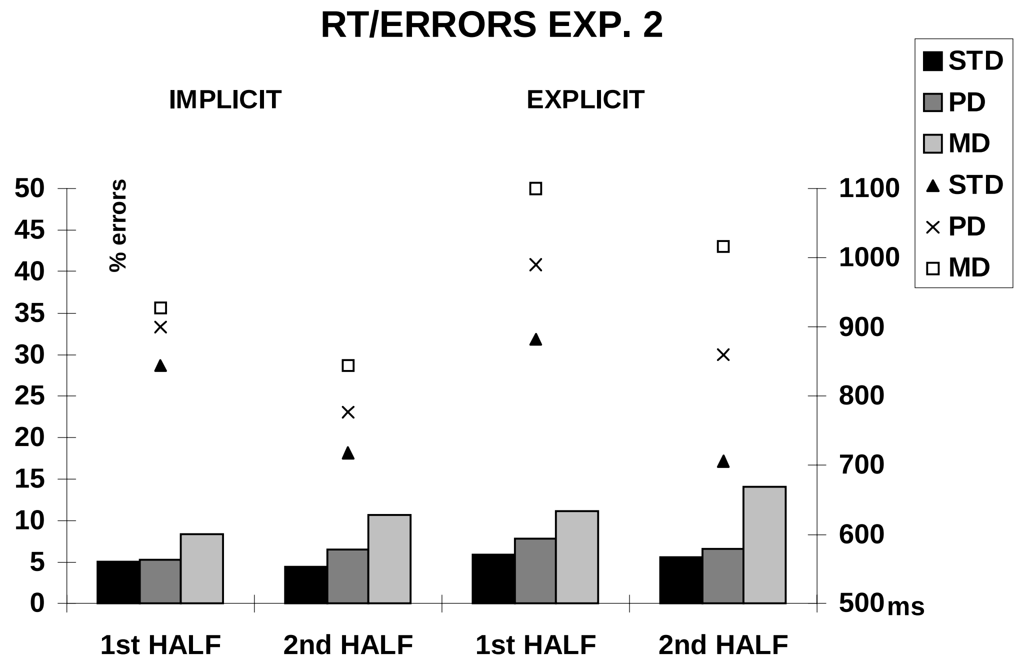


Figure 14: RT in ms (top) and errors (percentage) for standard, perceptual and motor deviant letters for explicit and implicit learners in the first and second half in the experiment. Note the shortening of RT from the first to the second half and the differences between standard and both types of deviant letters in the second half of the experiment for both groups.

Both groups learned the sequential structure of the material as reflected in a significantly prolonged RT for random compared to structured blocks (random - structured block, explicit: first half (block 23-22) 192.97 ms, t(13) = 2.506, p < .0262, second half (block 43-44) 258.9 ms, t(13) =4.14, p < . 0012, implicit first half: 13.86 ms, n.s., second half: 87.7 ms, t(13) = 3.5, p < .0039) and a shortening of RT for standard letters in the second compared to the first half of the experiment (explicit: 882 vs. 706 ms, F(1,13) = 14.46, p < .0022, implicit: 844 vs. 718 ms, F(1,13) = 50.7, p < .0001; see fig. 14).

Responses to standard letters were significantly faster than to perceptual deviants (second half, explicit: 706 vs. 860 ms, F(1,13) = 16.09, p < .0015, implicit: 718 vs. 777 ms, F(1,13) = 13.5, p < .0028) or motor deviants (second half, explicit: 706 vs. 1016 ms, F(1,13) = 21.31, p < .0005, implicit: 718 vs. 844 ms, F(1,13) = 24.7, p < .0002), respectively.

Accuracy data revealed the same pattern of significant results as RT data and are not reported in detail.

Stimulus-locked 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 member of the P300 family. The rising flank of this positivity is modulated by the experimental manipulations, especially 250-350 ms after letter presentation (N200 latency range).

ERPs for deviant letters elicited an enhanced negativity 250-350 ms after stimulus presentation (N200 latency range) for explicit learners which is more pronounced in the second half of the experiment. No effect of stimulus deviance is obtained for implicit learners in the N200 latency range (see fig. 15). Statistically, this group difference is reflected by a three-way interaction STIMULUS TYPE by HALF by GROUP ($F(2,52) = 4.79$, $p < .0124$, $\varepsilon = 0.9969$).

The N200-effect for explicit learners has a broad scalp distribution with a centro-parietal maximum (see fig. 16). Separate ANOVAs for single electrode sites revealed significant interactions of HALF and STIMULUS TYPE which show that the deviance effect emerges with training (frontal: Fz ($F(2,26) = 6.38$, $p < .0081$, $\varepsilon = 0.8773$; central: Cz ($F(2,26) = 7.04$, $p < .0042$, $\varepsilon = 0.9581$; parietal: Pz $F(2,26) = 5.42$, $p < .0140$, $\varepsilon = 0.892$).

ERPs for explicit and implicit learners also differed in the P300 latency range (450-600 ms) as reflected in a STIMULUS TYPE by GROUP interaction in the four-way ANOVA ($F(2,52) = 3.55$, $p < .0358$, $\varepsilon = 1.0604$). Stimulus deviance had no significant effect on the ERP amplitudes for the implicit group although a slightly enhanced positivity for motor deviants can be seen in fig. 15. However, for explicit subjects P300 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 (see fig. 16). Statistically, it is significant at frontal (Fz: main effect STIMULUS TYPE, $F(2,26) = 4.37$, $p < .0232$, $\varepsilon = 1.0315$), central (Cz: STIMULUS TYPE by HALF interaction, $F(2,26) = 5.22$, $p < .0124$, $\varepsilon = 1.0676$) and parietal electrode sites (Pz: standard letters, second half: 3.9 µV, perceptual deviants: 4.54 µV, motor deviants 5.74 µV, STIMULUS TYPE by HALF interaction, $F(2,26) = 6.9$, $p < .0005$, $\varepsilon = 0.8690$). However, only the contrasts between standards and motor deviants turned out to be significant.

To summarize: As in experiment 1, stimulus deviance had no effect on the ERP-waveforms of implicit learners. However, for explicit learners, 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 P300 amplitude.

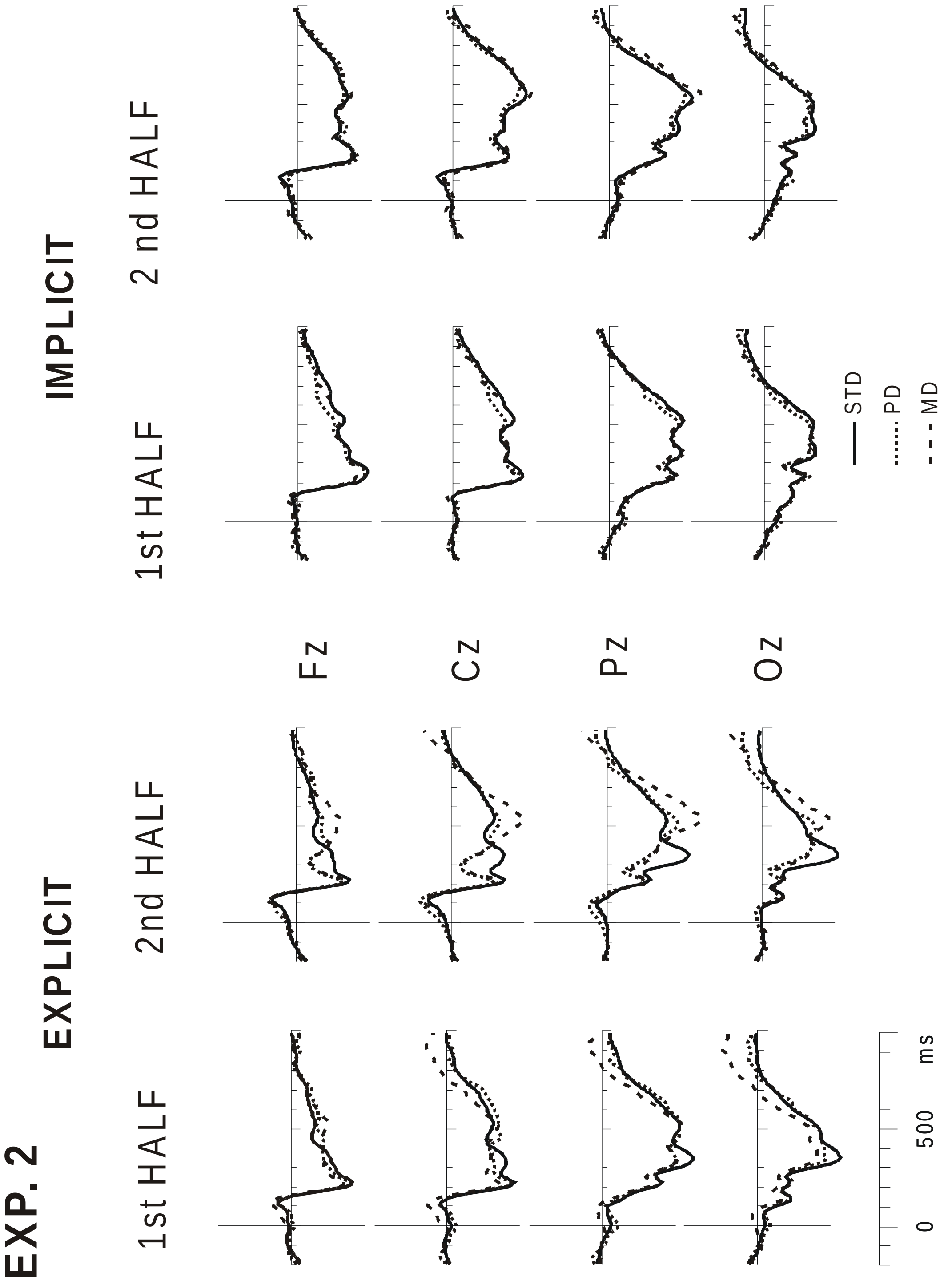


Figure 15: ERPs of experiment 2 at midline electrode sites (Fz, Cz, Pz and Oz) for standard (solid line), perceptually deviant (dotted line) and motorically deviant letters (dashed line) separately for both experimental groups (implicit left, explicit right) and first and second half of the experiment (first: top, second: bottom). Note the absence of a deviance effect for implicit subjects.

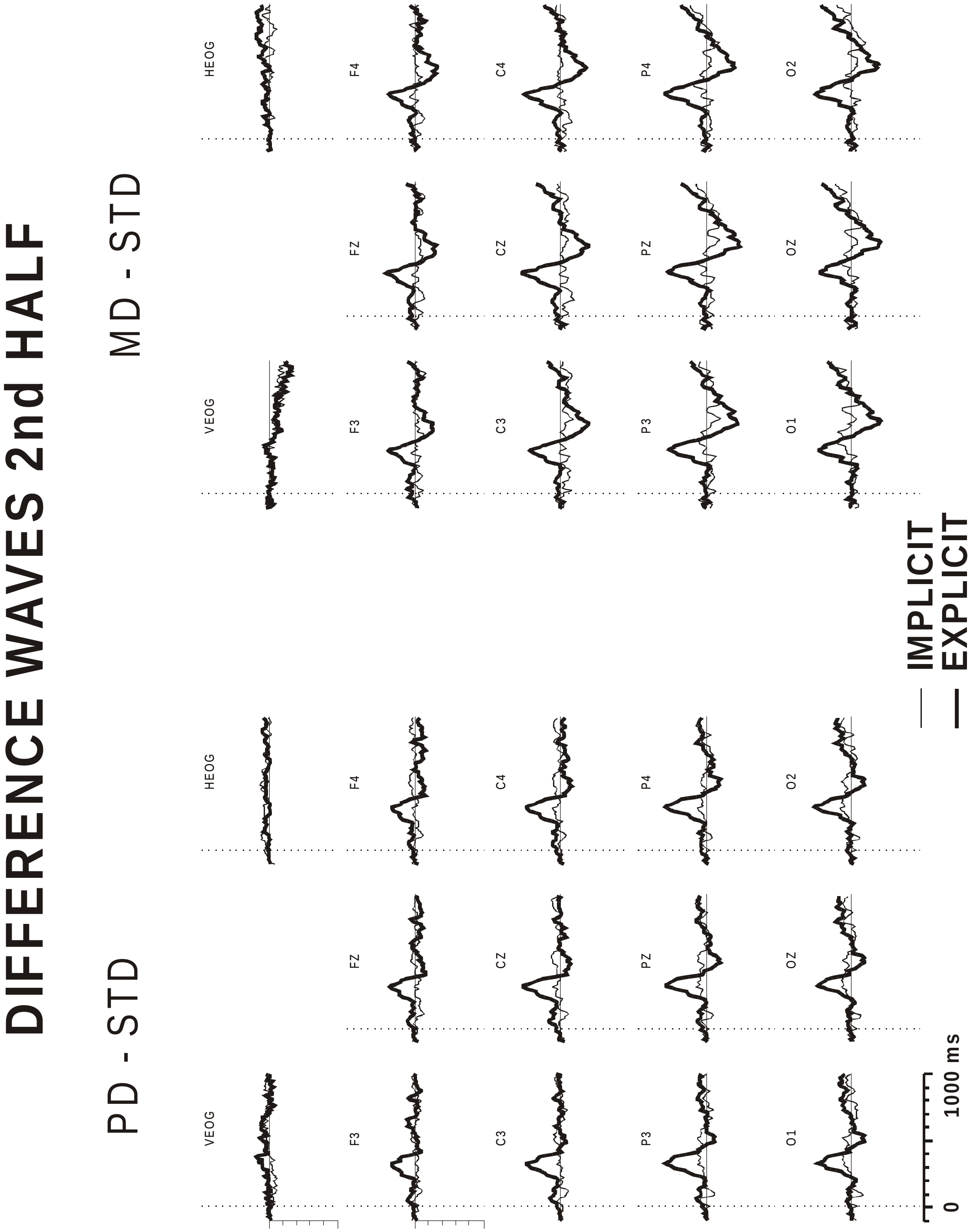


Figure 16: Difference waveforms for the second half for explicit (thick lines) and implicit subjects (thin lines) obtained by substracting from ERPs elicited by perceptual deviants the ERPs elicited by standard letters (left side) and by substracting from ERPs elicited by motor deviants the ERPs evoked by standard letters (right side). Note the deviance effects for explicit learners in the N200 (250-350 ms) and P300 (450 - 600 ms) latency ranges.

Response-locked ERPs. Experimental group had a significant effect on the amplitude of the response-locked ERPs for standard stimuli. Explicit learners had a larger negativity 450 - 150 ms prior to response execution on frontal and central electrode sites (see figs. 17 and 18). The effect was greater in the first HALF. Statistically, this is reflected in a three-way interaction GROUP by HALF by ELECTRODE SITE for standard letters ($F(17,442) = 3.67$, $p < .0031$, $\varepsilon = 0.3126$). No significant effects of experimental group could be found for perceptual or motor deviant letters.

For response-locked ERPs, the choice of the baseline is critical. As mean RT in the first half of the experiment for both groups is in the vicinity of 850 ms, on average the baseline of the response-locked ERP is 150-250 ms after stimulus presentation in the first half. As can be seen in fig. 19, the stimulus-locked waveforms are the same for both groups in this time-window. Thus, it can be concluded that the differences in the response-locked ERPs are not due to different baseline potentials.

The difference between explicit and implicit learners in the stimulus-locked ERPs was also analysed. In the time-window of the late positivity (650-900 ms), explicit learners showed a larger fronto-central negativity for standard letters than implicit learners. Statistically, this is reflected in a marginally significant interaction between ELECTRODE SITE and GROUP ($F(17,442) = 2.22$, $p < .0512$, $\varepsilon = 0.3169$).

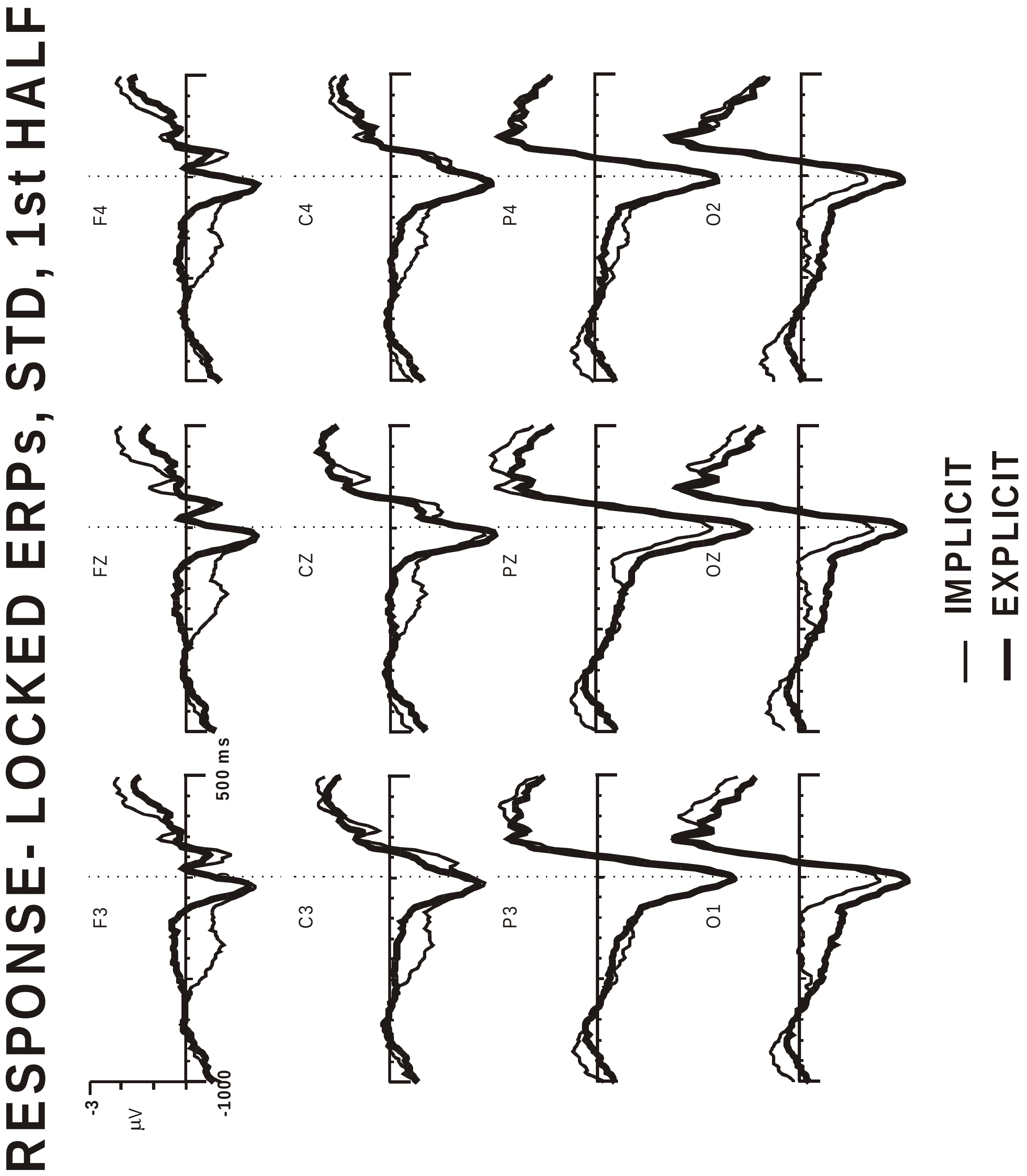


Figure 17: Response-locked ERPs starting 1000 ms prior to and ending 500 ms after response execution for implicit (thin lines) and explicit (thick lines) learners in the first half of the experiment. Note the larger left fronto-central negativity for explicit learners.

DIFFERENCE MAPS EXPLICIT - IMPLICIT, STD

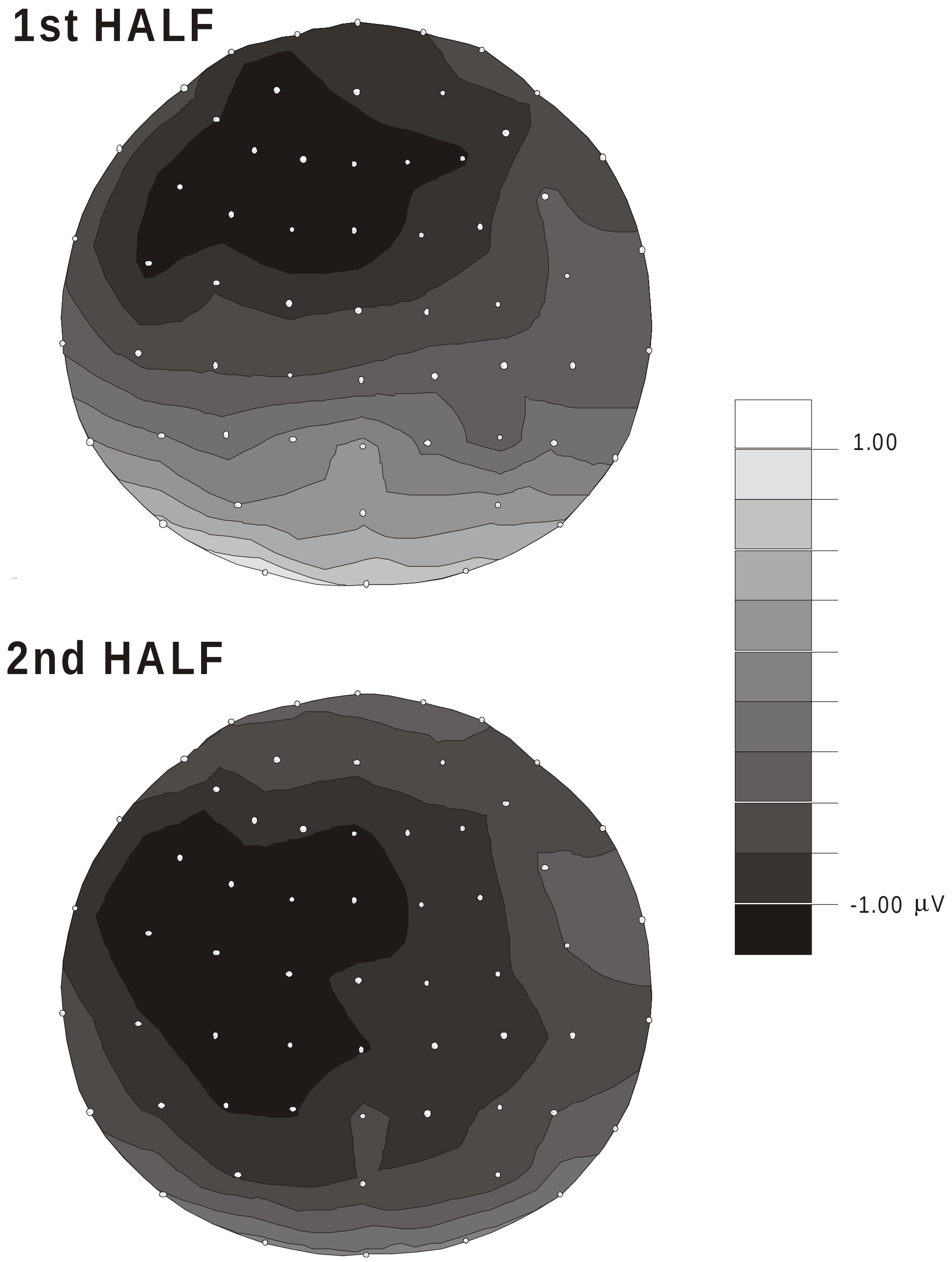


Figure 18: Topography of the difference waves explicit - implicit learners for standard letters separately for the two experimental halves. Darker shading indicates a larger negativity for explicit subjects. Note the larger left fronto-central negativity for explicit learners. Maps were computed by using the difference waveforms at all 61 scalp electrodes in the time-window 450 - 150 ms prior to response execution.

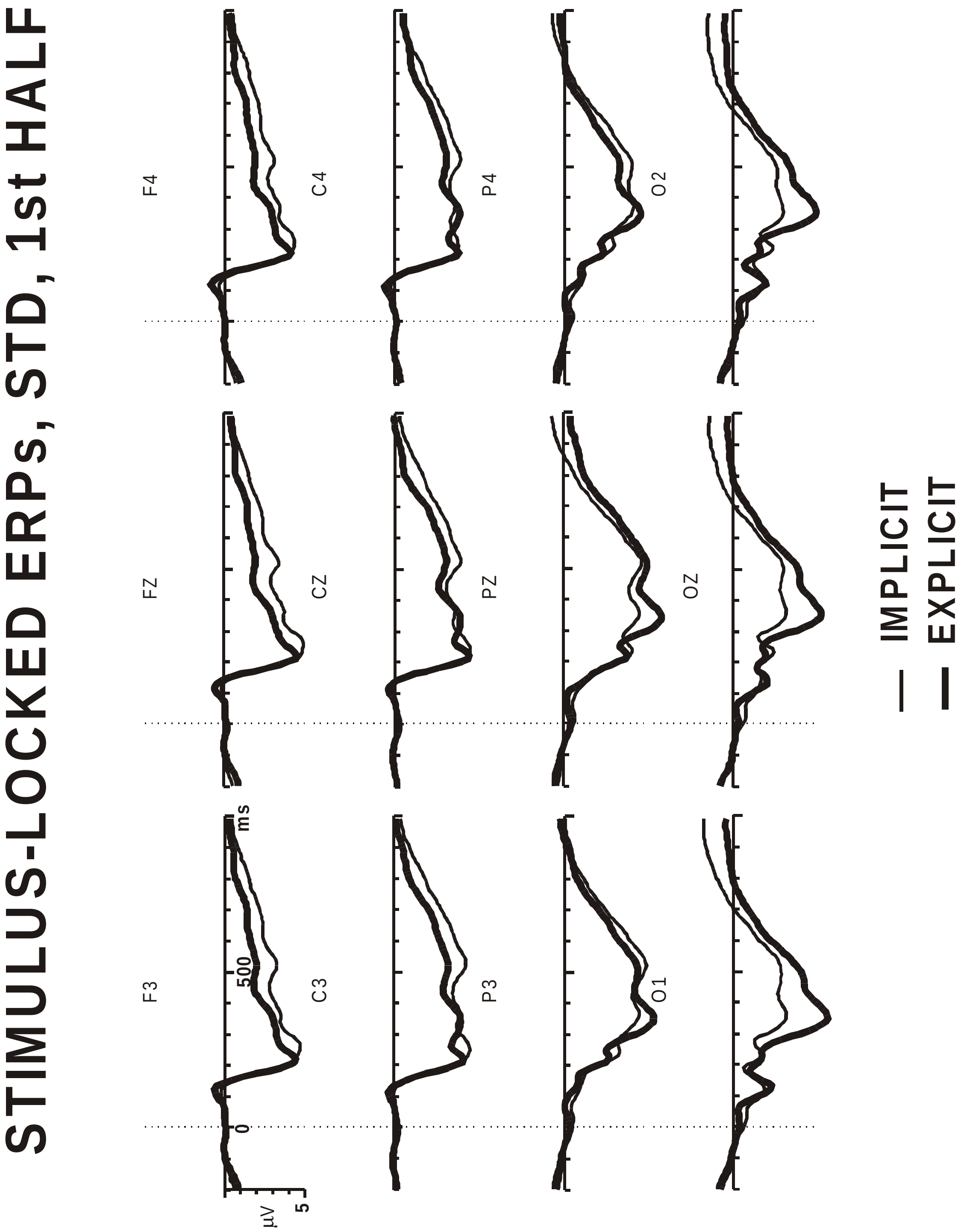


Figure 19: Stimulus-locked ERPs for standard letters in the first half of the experiment for implicit (thin lines) and explicit learners (thick lines). Note the larger frontal negativity for explicit learners starting about 250 ms after letter presentation.

Lateralized readiness potential. LRPs were analysed separately for explicit and implicit learners respectively. Note that data of four explicit and four implicit subjects had to be discarded because these subjects failed to show a lateralization of the readiness potential. First, it was tested whether LRP-onset latency for standard letters was different in the second compared to the first half of the experiment: This was the case for explicit learners (first half: 401.41 ms, second half: 279.42 ms, t(9) = 3.51), but the effect failed to reach significance for implicit learners (405.05 ms vs. 350.67 ms, t(9) = 1.782. The critical t-value at the α = 5 %-level for two-tailed testing is t(9) = 2.262 for this and subsequent comparisons). Onset-latency for perceptual and motor deviants did not differ between both halves (perceptual deviants, explicit, first half: 494.42 ms, second half: 457.55 ms, t(9) < 1, implicit: 475.48 ms vs. 343.62 ms, t(9) = 1.448; motor deviants, explicit: 831.12 ms vs. 905.82 ms, t(9) < 1, implicit: first half 444.1 ms, second half 450.22 ms, t(9) < 1).

A comparison of LRP-onset latency for standard letters and motor deviants yielded a significant prolongation for motor deviants in the second (std: 279.42 ms, motor deviants: 905.82 ms, t(9) = 6.307) but not in the first half (401.41 ms vs. 831.12 ms, t(9) = 1.04) for explicit subjects and a nonsignificant tendency in the same direction for the implicit group (first half, std: 405.05 ms vs. 444.1 ms, second half: 350.67 ms vs. 450.22 ms).

The same pattern of results emerged when a 25 %-criterion for determining LRP-onset latency in the jackknife procedure was used.

To test whether motor deviants activated the incorrect reaction prior to the activation and execution of the correct response, t-tests for every sampling point starting 500 ms prior to and ending 1500 ms after stimulus presentation were computed. No significant positivity was found for motor deviants for implicit or explicit learners in the first or second half of the experiment.

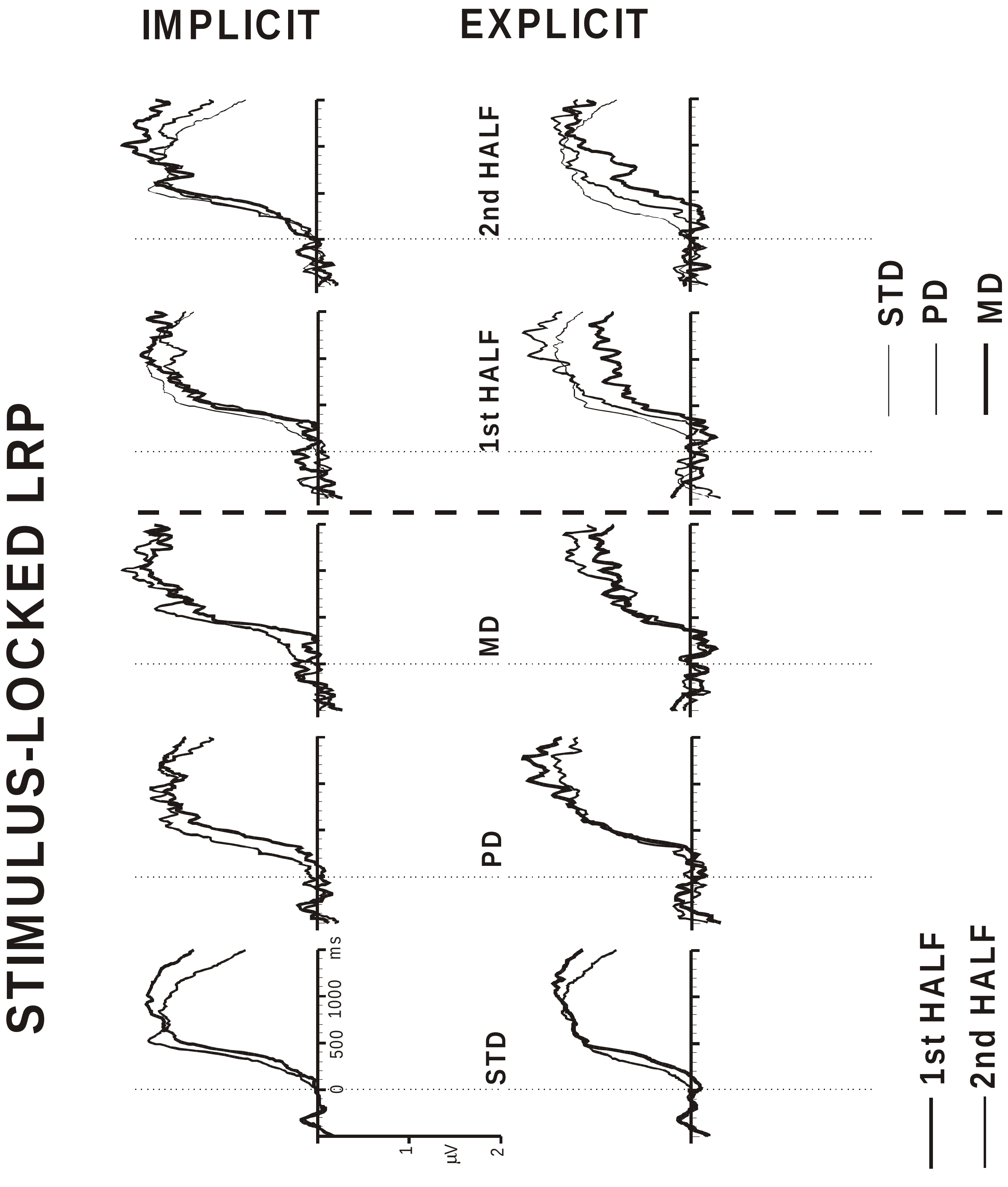


Figure 20: Stimulus-locked lateralized readiness potential for implicit (top row) and explicit learners (bottom row). The first three columns depict LRPs for standards (first column), perceptual deviants (second column) and motor deviants (third column) in the first (thick line) and second half (thin line) of the experiment. Columns four (first half) and five (second half) show the same LRPs in a direct comparison of the different stimulus types (standards (thin line), perceptual (medium line) and motor deviants (thick line)).

III. 4 Discussion

The present research investigated (i) the role of perceptual and motor processes in learning in the SRT-task, and (ii) whether different neuronal systems are involved in explicit and implicit learning. To this end, ERPs were recorded while a group of implicitly and a group of explicitly instructed subjects performed a sequence learning task. In an otherwise repeating sequence, two types of deviant letters replaced standards in 16.6 % of all cases. Perceptual deviants violated the stimulus sequence but preserved the response sequence, whereas motor deviants violated both stimulus and response sequences. Performance in tests of explicit knowledge showed that the instructional manipulation was successful: In both the free movement and the free letter recall task, explicit learners exhibited more verbalizable knowledge than implicit learners. Both groups of subjects learned the stimulus sequence as indicated by a prolonged RT for random compared to structured stimulus blocks and a shortening of RT for standard letters throughout the experiment. Stimulus deviance had different effects on the ERP-waveforms of explicit and implicit learners: For explicit learners, deviants elicited a larger negativity 250-350 ms poststimulus and a larger P300, especially for motor deviants. In contrast, no ERP-effects of stimulus deviance were found for implicit learners. Furthermore, ERPs to standard letters showed a larger left-frontal negativity for explicit compared to implicit learners. The LRP did not differ between both experimental groups. Sequence learning was reflected in a significantly shorter LRP-onset latency for standard letters and perceptual deviants in the second compared to the first half and a non-significant prolongation of onset-latency for motor deviants.

Tests of explicit knowledge

In all three measures of explicit knowledge, performance of explicit learners was superior to that of implicit learners, although this effect failed to reach significance for the recognition test. The simulations of the probability of guessing correctly for the free recall tasks showed that, on average, implicit learners did not exhibit knowledge which is different from guessing in either the free letter or movement recall tasks. However, performance of explicit learners in these tasks clearly indicated that they did not guess but acquired an explicit knowledge base during performance of the SRT-task. Thus, it seems to be that the instructional manipulation was successful. Baldwin & Kutas (1997), in their comparison of explicit and implicit learning, also found superior performance for explicit learners in a postexperimental prediction task. In this test, subjects were given two sequence elements and had to predict the position of the next stimulus.

Behavioral data

RTs indicate that both groups did learn the sequential regularities inherent in the stimulus material: (1) mean RT in the random stimulus blocks was prolonged in comparison to standard letters in the non-random blocks, (2) RT for standard letters decreased with practice, and (3) RT for deviant letters was longer than RT for standard letters, and this difference was much more pronounced in the second half of the experiment. As in other studies (Curran & Keele, 1993, Exp. 1; Frensch & Miner, 1994, Exp. 1), explicit learners showed more learning than implicit learners.

Both groups were sensitive to perceptual as well as motor deviance of a presented letter (longer RT for perceptual and motor deviants compared to standard letters in half 2). In experiment 1, groups were formed according to performance in postexperimental tests of explicit sequence knowledge. In contrast to the present results, RT for implicit learners was enhanced for motor deviants only. In the present study, however, groups were formed according to an instructional manipulation prior to the SRT-task and, thus, implicit learners could have acquired some explicit, verbalizable sequence knowledge which could explain the enhanced RT for perceptual deviants. To test this possibility, RT for standard letters and perceptual deviants for those subjects who were not able to recall any consecutive letters or movements in the free recall tasks and performed at chance level in the recognition task was analysed. Only two subjects of the implicit group fulfilled these criteria. For these subjects, the RT-difference between standard letters and perceptual deviants in the second half of the experiment was still present (703 vs. 751 ms), but the contrast was not significant.

ERP differences between explicit and implicit learners

ERPs elicited by standard letters, perceptual and motor deviants did not differ for implicit learners. In contrast, for explicit learners, both deviant types evoked a larger N200 and motor deviants showed an enhanced positivity in the P300 latency range. This replicates earlier findings of experiment 1 as well as those obtained by other researchers (Eimer, Goschke, Schlaghecken, & Stürmer, 1996).

Both the N200 and the P300-effects were larger in the second half, i.e. when a significant amount of learning had taken place. N200-amplitude was affected by both deviant types which violate the perceptual sequence. In contrast, P300 amplitude was only affected for those deviants which violate the response sequence (motor deviants). The finding that N200 and P300 show a difference in their sensitivity to motor and perceptual deviance suggests that they reflect two functionally distinct processes.

Visual inspection of fig. 15 suggests that, apart from the centro-patietal N200, a larger negativity for deviant stimuli was also present at frontal electrodes. This replicates the results obtained in the previous study (see exp. 1 for a discussion of this effect).

The centro-parietal N200-effect could indicate that after a considerable amount of learning, a detection of a perceptual inconsistency between the actually presented letter and the letter which is expected is possible on the basis of acquired sequence knowledge. The P300-effect for motor deviants might indicate that after a considerable amount of training subjects are also detecting task-relevant changes in the sequence: A motor deviant requires a change of the response which might have been prepared on the basis of acquired sequence knowledge. Task-relevant, deviating events are known to elicit larger positivities in the P300-latency range (Donchin & Coles, 1988).

P300 is also known to be sensitive to the stimulus probability of task relevant events. The probability of perceptual and motor deviants did not differ (8.33 %) but a deviant letter was presented in only 16.66 % of all cases. Thus, an enhanced P300 for deviant compared to standard letters was expected which should reflect this probability difference. A slight tendency towards a larger positivity for perceptual deviants is seen in fig. 15 (for explicit learners) which could reflect this probability difference but it failed to reach significance. However, as in experiment 1, motor deviants evoked a larger P300 compared to standard letters. Task-relevance of the stimulus-change in the sense that the actual letter required a response-change in comparison to the expected response seems to be additionally needed to obtain a significant amplitude enhancement.

There is a striking difference between the sensitivity of RTs to stimulus (and response) deviance and the lack of a deviance effect in the ERP-data of implicit learners. In contrast to explicit learners, implicit learners showed no awareness of the deviance. Thus, it seems possible that a N200 or P300-effect only emerges if subjects show some degree of awareness for the deviance.

The LRP is commonly viewed as an index of response preparation and response selection (e.g. Coles, 1989). This index shows some sensitivity to sequence learning in the present study: LRP-onset-latency for standard letters shortened in the second compared to the first half of the experiment. The effect was significant for explicit learners only. For implicit learners, a strong tendency in the same direction is evident. Knowing which letter will be presented next may have led to speed-up of processes prior to response execution (stimulus identification, stimulus evaluation, response selection). Similar results were reported by Eimer, Goschke, Schlaghecken, & Stürmer (1996). Furthermore, for both implicit and explicit learners, LRP-onset latency for motor deviants was prolonged compared to standard stimuli after some learning experience (i.e. in the second half). Thus, a violation of an expectation about the upcoming letter led to a delay in LRP-onset latency, indicating a delay in response preparation processes.

In several ERP-studies, short-term memory for verbal material was accompanied by an enhanced frontal negativity (e.g. Gevins, Smith, Le, Leong, Bennett, Martin, McEvoy, Du, & Whitfield, 1996; King & Kutas, 1995; Kluender & Kutas, 1993a,b; Lang, Starr, Lang, Lindinger, & Deecke, 1992; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992; Ruchkin, Johnson, Canoune, & Ritter, 1990). For example, Ruchkin, Johnson, Canoune, & Ritter (1990) presented consonant sequences in the visual modality and compared brain activity under two different conditions: In one condition, subjects had to retain the letter train in working memory for 2450 ms before they had to decide whether or not a test letter had been present in the sequence. In a second condition, the decision had to be made immediately after letter presentation. Memory-load was manipulated by varying the number of letters in the train to be remembered. A frontal negative slow wave which was specifically associated with the retention of verbal material in short-term memory was found. In the present experiment, a larger negativity for explicit compared to implicit learners prior to response execution was present in the response-locked ERPs for standard letters. This effect had a fronto-central topography and was slightly lateralized to the left hemisphere. Baldwin & Kutas (1997) and Grafton, Hazeltine, & Ivry (1995) reported comparable results. This larger negativity for explicit learners might reflect a larger involvement of short-term memory in learning for this group. It might have been that subjects who knew that they had to discover a regularity in a letter-sequence tried to remember as many consecutive letters as possible. This process should involve verbal short-term memory. In contrast, subjects who did not know that a sequence was present were less likely to store consecutive letters. Thus, a difference in short-term memory involvement for implicit and explicit learners seems to be reasonable. This could be reflected in the larger frontal negativity for explicit learners.

IV. EXPERIMENT III: IMPLICIT AND EXPLICIT LEARNING OF A SPATIAL SEQUENCE

IV. 1 Introduction

In experiments 1 and 2, symbolic stimulus material (letters) served as response cue in an SRT-task to explore differences in neural involvement in implicit and explicit learning. By introducing a many-to-one mapping of stimuli onto responses it was possible to insert deviant letters into an otherwise regular sequence. With this technique, stimulus- and response-based processes could be disentangled. In experiment 3, the same manipulation was used in a situation which is more similar to the original Nissen & Bullemer-task, i.e. a location served as imperative stimulus.

To this end, a stimulus was presented at one out of eight different positions. Two circles were each placed at the same horizontal position. Both circles differed in vertical location only (see fig. 21). Whenever a stimulus appeared at one of the two locations which shared one vertical position, the subject had to press a corresponding key, i.e. as in the previous experiments, two different stimuli were related to one response. With this setting, it was possible to introduce two types of deviant events in an otherwise regular spatial sequence: Perceptual deviants (the stimulus appeared below or above the expected position) preserved the response sequence but violated the perceptual sequence whereas motor deviants (the stimulus appeared at a location which required a response with the opposite hand in comparison to the expected response) violated both, response as well as perceptual sequences. As in the previous experiments, RTs, errors, ERPs and the LRP were measured to examine (1) whether response-based or stimulus-based learning (or both) is of prime importance in the SRT-task, (2) to analyse differences in explicit and implicit sequence learning and, (3) to examine whether learning of a sequence of spatial locations involves different brain systems than learning of a sequence of symbols (e.g. letters).

Several researchers have proposed that different brain systems exist for the learning of sequences of different stimulus aspects (e.g. spatial location, objects, tones, responses, colors). Mayr (1996), for example, showed that subjects are able to learn two independent sequences simultaneously (objects and locations, respectively). Goschke (1998) found that in a visual search task, independent sequences of letters and locations can also be learned simultaneously. In a recent PET-study, Hazeltine, Grafton, and Ivry (1997) found that different brain systems were involved in learning of a color- and a spatial sequence (see I.4.3). In the "color task", rCBF was enhanced in Brodman areas 24, 37, 10, 6, 40 and 9 while in the "spatial task" enhanced activity was found in Brodman areas 19, 39, 40, 17 and 6. These differences emerged more clearly under single-task (explicit) learning conditions. These studies provide at least suggestive evidence for the idea that sequence learning depends on experience-dependent modifications in different domain-specific brain structures. Possible candidates include those structures that are involved in the initial, perceptual processing of the information to be learned (e.g. sequences of locations, colors, linguistic symbols or motor responses).

A comparison of the topography of learning-related ERP-effects in the present experiment with the topography of the effects obtained for explicit learners in experiment 1 (enhanced N200 for perceptual and motor deviants, enhanced P300 for motor deviants, letter sequence) was planned to test the hypothesis that different brain systems are involved in spatial and symbolic sequence learning. It is expected that, at least for explicit learners, sequence learning should be modality specific and, therefore, different brain systems should be involved.

If it holds true that different, modality-specific brain systems for sequence learning exist, it is possible that stimulus- and response- based processes play a different role for different stimulus domains. Therefore, in the present experiment, the role of stimulus- and response- based processes in sequence learning was studied using a spatial rather than a letter sequence.

It is still an open question which types of representations are formed during implicit learning. To date, the available evidence is contradictory, indicating either learning of response-response (R-R), stimulus-stimulus (S-S) or stimulus-response (S-R)- associations.

Willingham, Nissen, & Bullemer (1989) suggested that associations between stimuli and responses are of primary importance for the acquisition of sequence knowledge. In their study, subjects responded to the color of stimuli appearing at different locations. Subjects failed to show an RT-advantage for structured blocks, if the task-relevant sequence of colors and responses was unpredictable although the locations of the stimuli followed a repeated sequence. In contrast, if the sequence of colors and the related responses were predictable but the stimuli appeared at randomly determined locations, performance improved. However, if subjects were instructed to respond to the location of uncolored stimuli that followed the same sequence as before no transfer was found. Thus, the authors concluded that stimulus structures are learned only if they can be mapped directly onto motor responses.

Mutter, Howard, & Mutter (1992) presented evidence compatible with the stimulus-stimulus association learning view. They showed that subjects who simply observed sequentially structured stimuli learned as much as subjects who responded to the stimuli with key-presses throughout the learning phase.

Finally, Nattkemper & Prinz (1997) obtained evidence in favor of a motor learning perspective. In their studies, pairs of letters were always assigned to one response.Unexpected manipulations of the stimulus sequence that did not interrupt the response sequence were not accompanied by an RT increase whereas violations of both, stimulus and response sequences, led to a prolonged response latency.

The strongest evidence in favor of a response-response association learning view had been obtained using symbolic stimulus material. Therefore, it is interesting to examine whether similar results can be obtained if spatial location of a stimulus is used as the task-relevant domain.

With respect to the hypotheses reviewed above, the following predictions can be made for the present study: If S-S-associations are learned in an implicit sequence learning task, RT for perceptual as well as motor deviants should be prolonged compared to standards. No difference should emerge between both deviant types.

If R-R- associations are of prime importance for sequence learning, RT for motor deviants should be enhanced whereas no difference between RT for standards and perceptual deviants should be present. Furthermore, an activation of the incorrect response prior to execution of the correct response should be found in the LRP.

Amplitude of ERP-components reflecting stimulus evaluation pocesses should be affected only if stimulus-stimulus- or stimulus-response associations are learned.

ERPs should exhibit a difference in their sensitivity to the deviance of a stimulus between implicit and explicit learners, if the two forms of learning rely on different neuronal structures.

IV.2 Method

Subjects. 36 subjects participated in the study for course credit or monetary compensation. Data of 8 participants had to be discarded because these subjects did not show any lateralization of the readiness potential. All of the remaining 28 participants were students at the Philipps-University Marburg. They had normal or corrected to normal vision. 15 subjects were female; all participants were right-handed according to self-report. Mean age was 22.3 years (range 19-27). None of the subjects had participated in prior experiments concerned with sequence learning.

Stimuli and Apparatus. The experiment took place in an electrically shielded, sound attenuated and dimly lit room. The stimulus material consisted of an array of eight circles arranged in two horizontal rows of four circles each. The circles were always visible during an experimental block (see fig. 21). The circles (0.61^0 of visual angle) were drawn in white on a dark grey background. The vertical and horizontal extension of the grid subtended 2.85^0 and 7.5^0 of visual angle from a constant viewing distance of 75 cm, respectively, center-to-center distance of two circles amounted to 2.3^0. A plus-symbol which served as fixation point was presented in the center of the display. Task-relevant stimuli were black circles which filled one of the eight white circles completely. These were presented in 64 blocks of 52 stimuli each. The black circle remained on the screen until a response was executed. The response-to-stimulus interval was held constant at 500 ms. Correctness of the response and RT (to the nearest 5 ms) were recorded.

Procedure. Subjects placed their left and right middle and index fingers in the circular cavity of a light gate. They were instructed to briefly lift the relevant finger whenever a black circle appeared at one of the eight possible locations. For a circle appearing at the upper or lower left location, a response with the left middle finger was required, upper or lower second from the left locations required a response with the left index finger, upper or lower second from the right locations a lift of the right index finger and upper or lower rightmost locations required a response with the right middle finger.

Stimuli were presented in 64 blocks of 52 stimuli each (blocks 1-32: first half, blocks 33-64: second half). In each block, locations for trials 1 - 4 were determined randomly with the restriction that no position could occur twice. These trials served as a 'warm-up' to ensure that subjects paid attention to the task and were not analysed (see, for example, Mayr, 1996). Locations of trials 5-12 were determined pseudorandomly with the restrictions that each of the eight location had to occur once in these eight trials and that no response repetition could occur for trial 4/5 and 12/13, respectively. This procedure was similar to the one used in Frensch & Miner (1994) and made it more difficult for participants to detect the sequence consciously. For the sake of simplicity, these trials are termed random in the remainder of this chapter (see table 11).

Table 11: Trial structure and labels of the events in one block of experiment 3. See text for details.

Trial #	*Event*	*Label*
1 - 4	random warm-up trials	warm-up (not analysed)
5 - 12	pseudorandom trials	random
13 - 44	structured trials: sequence and interspersed deviants	std: standard pd: perceptual deviants md: motor deviants
45 - 52	pseudorandom trials	random

Locations in trials 13-44 of each block followed a repeating sequence of eight positions: 1 6 5 2 4 7 0 3 (Resulting response sequence: M m i I i m M I, capital letters indicate left hand responses, i/I denotes the index finger, m/M the middle finger). According to Cohen, Ivry, & Keele (1990), the stimulus sequence is unique in structure (i.e. it only contains unique pairwise associations) whereas the response sequence is hierarchical (i.e. it contains only ambiguous pairwise associations). In each of the four replications of the sequence in one block, one standard position was replaced randomly by one of two deviant locations: Perceptual deviants were constructed by presenting the circle at the second location that required a response with the same hand as the respective standard location (e.g. for location 0, the perceptual deviant is location 1). Thus, perceptual deviants violated the sequence of positions but not the sequence of responses. In contrast, motor deviants violated both the spatial and the response sequence as a response with the opposite hand (compared to the standard) was required.

Motor deviants were constructed in the following way: To exclude the possibility of a response repetition for motor deviants, for each standard position one location (of the four theoretically possible) was always used as the motor deviant for that particular location (see fig. 21; table 12). For example, the motor deviant for position 0 was position 5 which required a response with the right index finger (instead of the expected left middle finger for the standard). Note that all motor deviants had the same distance (5.4^0) from their respective standard stimulus. In each of the two experimental halves, both deviant types were presented with equal probability.

Finally, Trials 45-52 of each block were pseudorandom again with the restrictions that each of the eight locations had to occur once and no response repetition occurred for trials 44/45.

Prior to the first block of the SRT-task, all participants performed one training block to become familiar with the task. In this training block, all stimulus locations were determined randomly.

Table 12: Construction of motor deviants. The location of a standard stimulus (left column) is given together with the location of the motor deviant for that location (middle column) and the response that is required for the motor deviant. See fig. 21 for an illustration of the spatial layout of the display.

Stimulus position of standard	*Motor deviant*	*Response required for motor deviant*
0 (upper left)	5	right index finger
1 (lower left)	4	right index finger
2 (upper second from the left)	7	right middle finger
3 (lower second from the left)	6	right middle finger
4 (upper second from the right)	1	left middle finger
5 (lower second from the right)	0	left middle finger
6 (upper right)	3	left index finger
7 (lower right)	2	left index finger

After performing the 64 blocks of the SRT-task, all participants were informed about the presence of a repeating sequence and tested to assess their amount of explicitly available, verbalizable knowledge about the stimulus sequence. First, a free sequence recall task was administered. Subjects had to indicate the sequence of locations on a sheet of paper which contained eight circles arranged in the same way as in the experiment proper. They were prompted to number the positions from 1 - 8 according to the sequence they saw. Second, subjects had to reproduce the movement sequence. To this end, they placed their fingers in the light gates and lifted the fingers in the same way as they presumedly did in the SRT-task. Third, in a prediction task, eight bigrams of positions were shown to the subjects who had to predict where the next stimulus will be presented. After a delay of about 15 minutes to remove the electrodes from the subjects' head, a recognition task concluded the experiment. 16 bigrams and 16 trigrams of circles were presented and subjects had to indicate whether they had been part of the sequence or not (see appendix C).

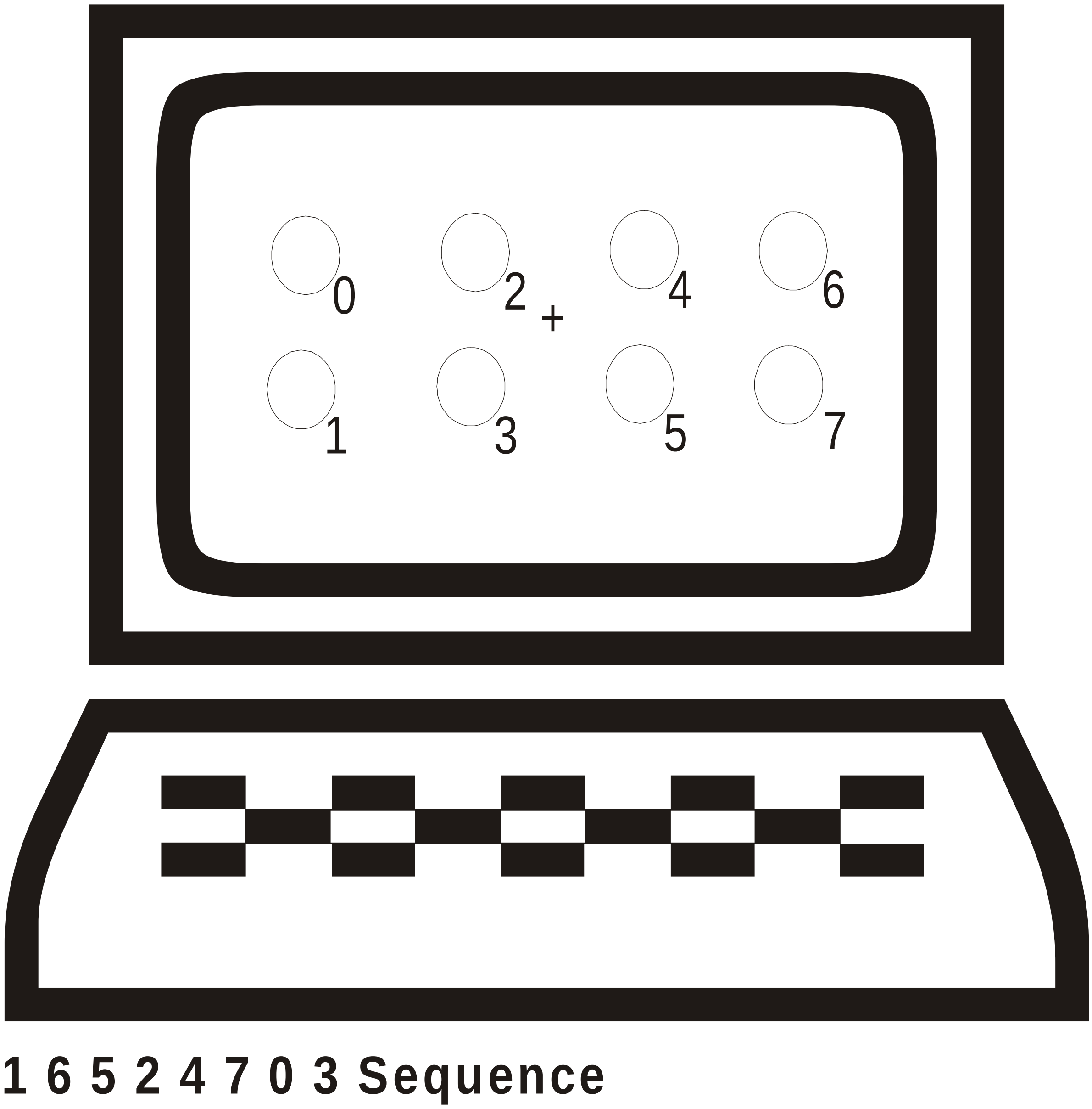


Figure 21: Setup of experiment 3. Note that the digits denoting the stimulus locations are not present during the experiment.

EEG recording. As in the previous experiments, the electroencephalogram (EEG) was recorded with 61 Ag-AgCl-electrodes placed on the subjects' head by means of an elastic cap (Gaggl-system, Graz, Austria). Further details of the recording method are described in the methods section of experiment 1.

Data analysis. *Tests of explicit sequence knowledge.* For the free sequence recall and free movement recall tasks, the number of correctly recalled consecutive elements of the sequence was counted. To determine whether the amount of verbalizable knowledge in the free recall tests is different from guessing probability, a simulation of subjects' performance in the free recall tasks was computed. For the prediction- and recognition-tasks, the number of correct predictions or correctly recognized items was computed. In all simulations, it was first tested whether the drawn sequence with n elements was part of the stimulus sequence. Next, it was tested whether one out of all possible n-1 sequences inherent in the drawn eight element train was part of the stimulus sequence and so on. The program stopped when the first correct sequence was found (Hennighausen & Rüsseler, 1998). The percentage of correct sequences of length 2,3,4,5,6,7 and 8 which is equivalent to the probability of guessing for a correct sequence of the respective length was determined. This was done without repetition as the participants saw the eight-location display on paper during the free sequence recall task. Furthermore, the mean number of correctly recalled letters in the simulation (and for the experimental subjects) was computed.

For the free movement sequence recall task, the average number of produced movements for the participants was computed (6). The simulation of subjects' performance was conducted by drawing sequences of 6 elements length out of a pool of four stimuli (0, 1, 2, 3; the digits represent the four response buttons). In this simulation, pairs were allowed (e.g. 0, 0) and it was performed with repetition. This seems to be equivalent to the situation of the participants in this task. In all reported simulations 1000000 sequences were drawn out of the respective stimulus pool.

Behavioral data. Mean RT and error rate were computed separately for random stimuli, standards, perceptual and motor deviants for each of the 64 blocks. Data of the first four stimuli of each block were discarded. For the sake of comparison with the ERP-data, RT and errors of blocks 1-32 (first half) and 33-64 (second half) were averaged. These data were submitted to a 2 (HALF) by 4 (STIMULUS TYPE, std, pd, md, random) by 2 (GROUP; explicit vs. implicit) repeated measures ANOVA to determine whether the participants learned the sequence. Preplanned contrasts were computed to see whether RT for the four stimulus types differed in the second half of the experiment.

Event-related potentials. EEG and EOG were divided off-line into periods of 800 ms starting 100 ms prior to stimulus-presentation and ending 700 ms after stimulus onset. Mean voltage 100 ms before stimulus presentation to stimulus-onset was taken as a baseline for ERP-computation. Trials with eye-blinks or horizontal eye-movements (vertical EOG or horizontal EOG exceeding 80 µV) or an amplitude range of more than 100 µV at one of the 63 electrode locations in the 800 ms epoch were excluded. Trials with response errors, RT less than 100 ms and trials immediately following a deviant stimulus were also discarded. ERPs were computed separately for each of the four stimulus types (std, pd, md, random) in the first and second half of the experiment.

To determine whether the experimental manipulations had an effect on ERP-amplitude, mean amplitude values were computed in time-windows from 150-200 ms (N1) and from 250-450 ms (N2/P3-complex), respectively. Furthermore, a negative-going flank of the P300 (500-600 ms) was analysed. These data were submitted to a 2 (HALF) by 4 (STIMULUS TYPE) by 6 (ELECTRODE; Fz, Cz, Pz, Oz, O1, O2) by 2 (GROUP) repeated measures ANOVA for each of these time windows. For significant, learning-related ERP-effects, a topographical analysis using data of all 61 scalp electrodes was conducted. Furthermore, several subordinate ANOVAs were run to qualify the results.

Where appropriate, the degrees of freedom in the ANOVAs were adjusted to control violations of the sphericity-assumption (Huynh & Feldt, 1980). Degrees of freedom are reported before, p-values after the adjustment.

Lateralized readiness potential. Stimulus-and response-locked LRPs were computed separately for each stimulus type and half of the experiment. LRPs were computed as described in the methods section of experiment 1. Stimulus-locked LRPs were computed from 400 ms pre- to 900 ms post- stimulus presentation relative to mean voltage in the interval 400 to 300 ms prior to stimulus onset (baseline). Response-locked LRPs (see Miller, & Ulrich, 1998) were computed using a time-interval 800 ms prior to and ending 200 ms after response execution (baseline: 700 - 600 ms prior to response execution).

Onset-latency for stimulus-locked LRPs was determined as the time-point at which the respective grand-average LRP reached 50 % of their maximal peak amplitude. Differences in LRP-onset latency between the experimental conditions were examined by using the jackknife-method proposed recently by Miller, Patterson, & Ulrich (1998; see also Miller, 1998). Simulations comparing this method to other common measures of LRP-onset latency indicate that this is the best available technique for estimating and testing the significance of onset-latency differences between conditions (Miller, Patterson, & Ulrich, 1998).

Separate t-tests for consecutive intervals of 50 ms were used to determine whether motor deviants lead to an activation of the incorrect response ('positive dip') prior to activation of the correct response. Further t-tests were employed to determine whether standard stimuli and perceptual deviants activated the correct response prior to the presentation of the stimulus.

IV. 3 Results

Tests of explicit knowledge. Table 13 shows the results of the tests of explicit sequence knowledge.

Table 13: Results of the tests of explicit knowledge in experiment 3. For spatial and movement sequence recall, the number of correctly recalled consecutive sequence elements is shown. For the generate- and recognition tasks, the number of correct items is displayed (maximum 8 for the generate, 32 for the recognition task). Status I = implicit, E = explicit.

Subject #	*spatial sequence recall*	*Movement sequence recall*	*Generate task*	*Recognition task*	*Status*
1	8	7	7	32	E
3	2	4	5	18	E
5	2	3	1	24	I
6	0	2	3	14	I
9	0	3	2	19	I
10	2	3	4	18	I
11	3	3	3	20	E
12	5	5	2	17	E
14	1	0	2	18	I
15	2	3	3	20	I
16	0	4	1	20	I
17	0	2	2	18	I
18	3	3	2	19	E
19	3	3	1	19	E
20	2	3	2	21	I
21	0	2	1	16	I
22	2	2	2	17	I
23	2	3	1	20	I

24	3	0	2	23	E
26	4	4	6	24	E
27	0	0	0	15	I
28	2	7	4	16	I
30	4	4	1	18	E
31	0	6	3	16	I
32	3	8	5	30	E
33	2	4	2	19	I
35	5	7	3	19	E
36	2	2	1	19	I

To determine whether the amount of verbalizable knowledge in the free recall tests is different from guessing, a simulation of subjects' performance in the free recall tasks was conducted. In the first simulation (see table 14), sequences with a length of 8 were drawn out of a pool of eight positions (0,1,2,3,4,5,6,7; without repetition). In the second simulation, sequences of 6 elements were drawn out of a pool of four different movements (see table 15).

Table 14: Results of simulation 1. 1000000 draws of an eight-element sequence out of a pool of 8 different items. Note that if seven elements are correct, only one element remains in the stimulus pool. Consequently, the eighth element must be correct, too.

Mean sequence length	*1.7698*
Probability for 2 correct elements	0.5176
Probability for 3 correct elements	0.0959
Probability for 4 correct elements	0.0157
Probability for 5 correct elements	0.0027
Probability for 6 correct elements	0.0006
Probability for 7 correct elements	0.000196
Probability for 8 correct elements	0.000196

Guessing probability for two correct consecutive elements is 51 %. Therefore, subjects who recall more than two elements of the sequence correctly must have at least some explicit knowledge of the stimulus sequence and are categorized as explicit learners.

On average, implicit subjects reported 1.23 consecutive elements correctly whereas explicit subjects reported 3.91 consecutive elements.

Table 15: Results of simulation 2. 1000000 draws of a six element sequence out of a pool of four elements. See text for details.

Mean sequence length	*2.4429*
Probability for 2 correct elements	0.5878
Probability for 3 correct elements	0.3032
Probability for 4 correct elements	0.0639

Probability for 5 correct elements	0.0118
Probability for 6 correct elements	0.002

Guessing probability for two correct consecutive movements was 58 %. Therefore, it is concluded that subjects who recalled more than two consecutive movements correctly have at least some reproduceable knowledge about the movement sequence. This is the case for 11 implicit subjects. However, as in the previous experiment, these subjects were not excluded from the sample as it is not clear what exactly is measured in a free movement recall task (see Fendrich, Healy, & Bourne, 1991). Note that all explicit subjects recalled more than two correct consecutive movements.

Taken together, 11 subjects were categorized as explicit and 17 subjects as implicit on the basis of the reported tests of explicit knowledge (see table 13).

Behavioral data. Response accuracy. Overall error-rate was 7.86 % and did not differ between explicit and implicit learners (no significant main effect or interaction with factor GROUP). Therefore, error data for all subjects was collapsed for subsequent analyses.

Learning of the sequential structure was reflected in an increasing difference in errors for standard and random stimuli in the first and second half, respectively (first half: std: 7.39 %, random: 9.64 %; second half: std: 5.55 %, random: 9.7 %, ($F(1,27) = 52.51$, $p < .0001$).

Subjects comitted more errors in motor deviant and random trials compared to standards and perceptual deviants. This is indicated by a main effect STIMULUS TYPE ($F(3,78) = 12.53$, $p < .0003$, $\varepsilon = 0.4937$; see fig. 22). A marginally significant STIMULUS TYPE by HALF interaction ($F(3,78) = 3.15$, $p < .052$, $\varepsilon = 0.6562$) indicates that this effect increased after a considerable amount of training (i.e. in the second half of the experiment).

RT. RT did not differ between explicit and implicit learners (no significant main effect or interaction with factor GROUP). Therefore, RT-data of both groups were collapsed for further analyses.

Subjects learned the regularities inherent in the stimulus material: First, the difference between RT for standard and random stimuli increased in the course of the experiment (see fig. 22). Second, responses to standard stimuli were significantly faster than responses to motor deviants (see below). Statistically, this is reflected in a main effect of STIMULUS TYPE (F(3,78) = 37.26, $p < .0001$, ε = 0.5727) and a HALF by STIMULUS TYPE interaction (F(3,78) = 11.61, $p < .0001$, ε = 0.6834).

As can be seen in fig. 22, RT for standards and perceptual deviants did not differ (first half: 415 ms vs. 420 ms, second half: 369 ms vs. 371 ms, contrast in the second half: F(1,27) = 0.44). Responses to motor deviants and random stimuli were slower than those to standards (contrasts in half 2: std vs. md: 369 ms vs. 425 ms, F(1,27) = 48.9, $p < .0001$; std vs. random: 369 ms vs. 408 ms, F(1,27) = 84.04, $p < .0001$). RT to motor deviants was even longer than RT for randomly presented stimuli (425 ms vs. 408 ms, F(1,27) = 8.15, $p < .0082$).

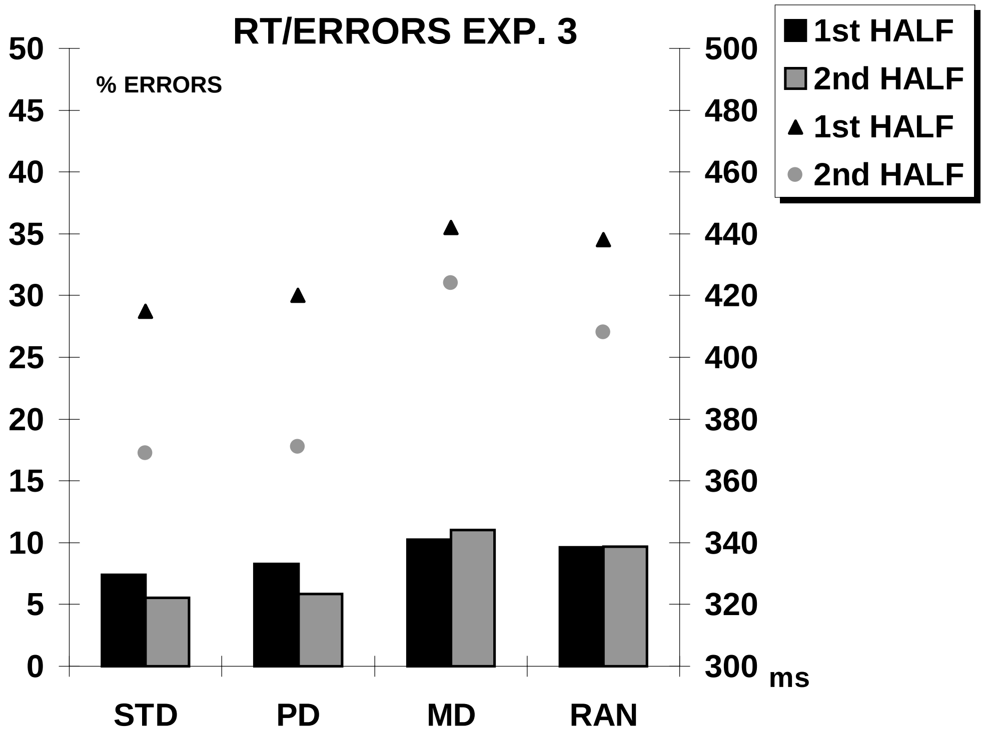


Figure 22: RT (lines) and errors (bars) for standards (std), random stimuli (ran), perceptual (pd) and motor deviants (md) in the first (black) and second (grey) half of experiment 3 averaged over all 28 subjects. Note that RT for std and pd is not different in the 2nd half, whereas RT for md and random is longer than for std.

ERPs. Two distinctive features were prominent in the ERP-waveforms: First, a negative going component at occipital electrodes between 150 and 200 ms and a positive peak at about 350 ms with a parietal maximum (see fig. 23). Topography and latency of these components suggests that these are the N1 and P3-complex respectively. The negative-going resolution of the P3 from 500 - 600 ms poststimulus showed also amplitude modulations as a function of stimulus type and was analysed separately.

N1. No significant difference of mean ERP-amplitude was found for implicit or explicit learners 150-200 ms poststimulus. For both groups of learners, no signifcant differences of the ERPs for the four stimulus types were found.

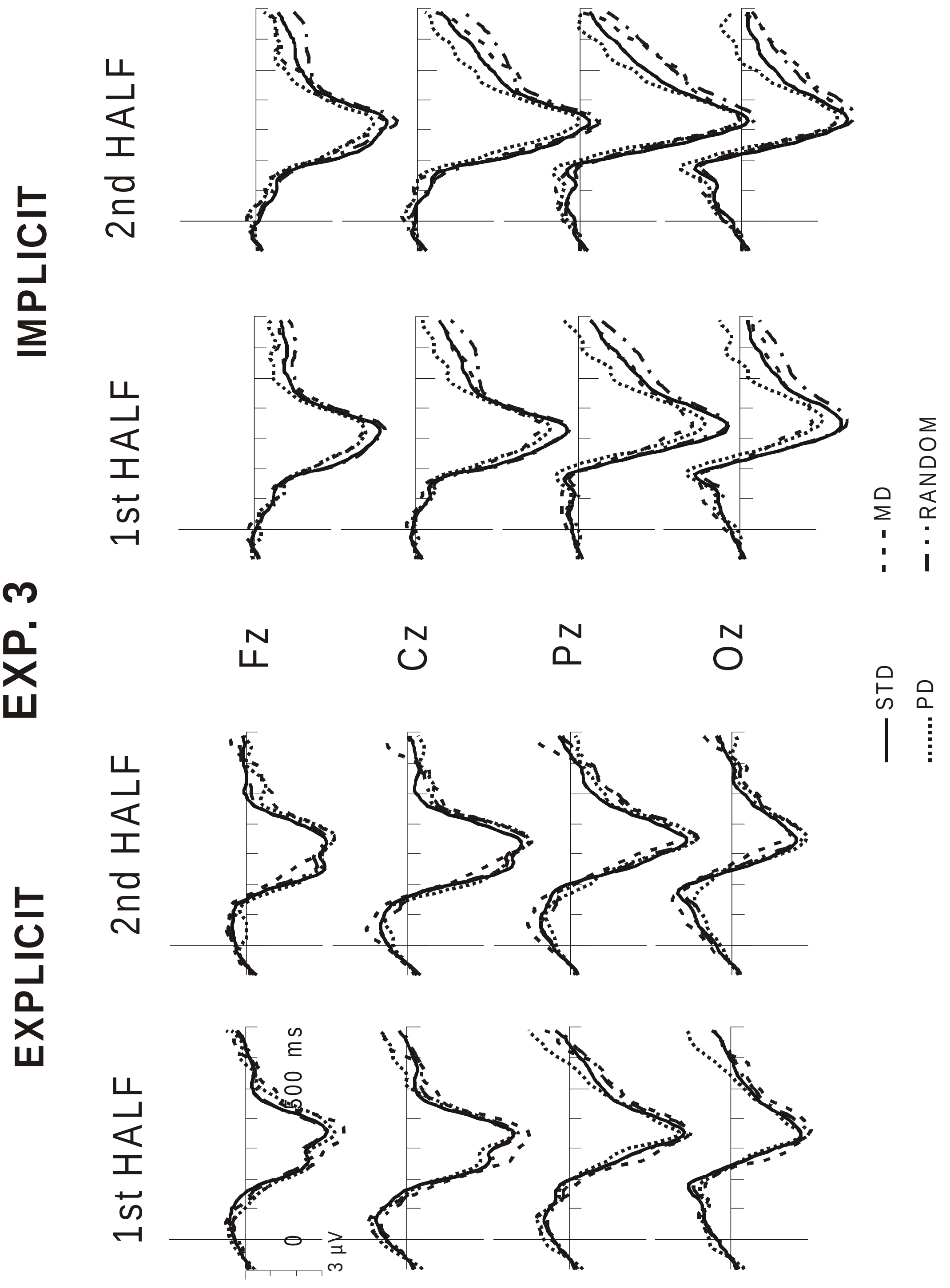


Figure 23: ERPs of experiment 3 at midline electrodes (Fz, Cz, Pz Oz) for standard (std, solid line), perceptual deviants (pd, dotted line), motor deviants (md, dashed line) and random stimuli (random, dashed and dotted line) in the first and second half of the experiment separately for explicit (left) and implicit learners (right).

P3. Mean ERP-amplitude 250-450 ms poststimulus differed for implicit and explicit learners for the four stimulus types (STIMULUS TYPE by GROUP-interaction, F(3,78) = 3.09, $p < .0438$, ε = 0.7977). Consequently, data for both groups were analysed separately. For the implicit group, ERPs evoked by perceptual and motor deviants were more negative (or less positive) than ERPs for standards and random stimuli (main effect STIMULUS TYPE, F(3,48) = 5.32, $p < .0053$, ε = 0.8436). This effect had a maximum at electrode Pz (std: 4.77 µV, pd: 3.91 µV, md: 3.69 µV, random: 4.79 µV; F(3,48) = 3.32, $p < .0374$, ε = 0.8196). Note that the effect of STIMULUS TYPE did not vary with training (STIMULUS TYPE by HALF: F(3,48) = 0.64, $p < .5526$, ε = 0.751).

In contrast, for explicit learners the effect of stimulus type on ERP-amplitude was not significant (main effect STIMULUS TYPE: F (3,30) = 0.15; STIMULUS TYPE by HALF -interaction, F(3,30) = 3.4, $p < .0645$, ε = 0.5601).

Negative-going resolution of P3. The four stimulus types differed in amplitude in the resolution phase of the P3 (500 - 600 ms poststimulus; main effect STIMULUS TYPE: F(3,78) = 5.24, $p < .0039$, ε = 0.8749) and this effect did not differ for explicit and implicit learners (no significant STIMULUS TYPE by GROUP- interaction or main effect GROUP). However, the effect was different at the various electrode locations (STIMULUS TYPE by ELECTRODE: F(33,858) = 2.33, $p < .0326$, ε = 0.1896). At central and parietal electrode sites, amplitude for perceptual deviants was more negative compared to the other three stimulus types (e.g. at Cz: std: 1.29 µV, pd: 0.49 µV, md: 1.49 µV, random: 1.71 µV; F(3,81) = 4.39, $p < .0129$, ε = 0.764). Note that the effect did not vary as a function of practice with the sequence learning task (STIMULUS TYPE by HALF: F(3,78) = 1.42, $p < .2484$, ε = 0.8151).

Taken together, no learning-related ERP-effects were found (the effects for implicit learners did not vary as a function of training and cannot be interpreted as learning effects). Thus, no topographical analysis could be computed and the planned comparison between the results of experiment 1 and the present study could not be made.

Stimulus-locked LRP. A GROUP (explicit vs. implicit) by STIMULUS TYPE (std vs. ran vs. pd vs. md) by HALF by TIME repeated measures ANOVA of mean LRP-amplitude in 19 consecutive time-windows of 50 ms length from 250 ms prior to until 700 ms after stimulus presentation indicated that the stimulus-locked LRP did not differ between implicit and explicit learners (no main effect or significant interaction with factor GROUP). Consequently, data of explicit and implicit learners were collapsed for further analysis.

A main effect of STIMULUS TYPE ($F(3,78) = 6.3$, $p < .0047$, $\varepsilon = 0.6079$) indicates that the experimental manipulations influenced LRP- amplitude (see fig. 24). This finding is qualified by a three-way interaction HALF by TIME by STIMULUS TYPE ($F(54, 1404) = 2.21$, $p < .049$, $\varepsilon = 0.1049$) which shows that differences in LRP-amplitude changed over the course of the experiment.

Separate one-tailed t-tests were run for 10 consecutive time-windows of 50 ms length starting 250 ms pre- and ending 250 ms poststimulus to examine response activation processes. These tests revealed that standard stimuli led to an activation of the correct response which emerged as early as 0 - 50 ms after stimulus presentation ($t(27) = 2.16$, $p < .02$; see table 16). Most importantly, motor deviants lead to an activation of the incorrect (but expected) response ('positive dip') prior to the activation and execution of the correct response. This effect is more pronounced in the second half of the experiment (-100 .. - 50 ms, second half: $t(27) = 1.91$, $p < .0335$). These results indicate that motor anticipation is one important factor in implicit as well as explicit learning of a spatial, perceptuo-motor sequence.

Table 16: Mean LRP-amplitude (µV) for standards (std), perceptual deviants (pd), motor deviants (md) and random stimuli in five consecutive time-windows of 50 ms length in the first and second half of experiment 3. Note that a positive amplitude indicates activation of the incorrect, a negative amplitude of the correct response. * indicates an amplitude significantly different from zero as indicated by one-tailed t-tests. Time denotes the beginning of the respective time-frame.

Time	*Std*		*pd*		*Md*		*random*	
	half 1	half 2	half 1	half 2	half 1	half 2	half 1	half 2
-100	-0.016	-0.0967	0.0248	-0.2011*	0.0276	0.3333*	0.0331	-0.0386
-50	-0.054	-0.1334	-0.1207	-0.3316*	0.0224	0.2825	-0.0021	-0.0423
0	-0.1156*	-0.2013*	-0.269*	-0.3268	0.2561*	0.3245*	0.0146	-0.0162
50	-0.1544*	-0.2104*	-0.174	-0.1539	0.3681*	0.4274*	0.0441	-0.0711
100	-0.7802*	-0.8944*	-0.8041*	-0.8971*	-0.1106	0.1055	-0.601*	-0.6927*

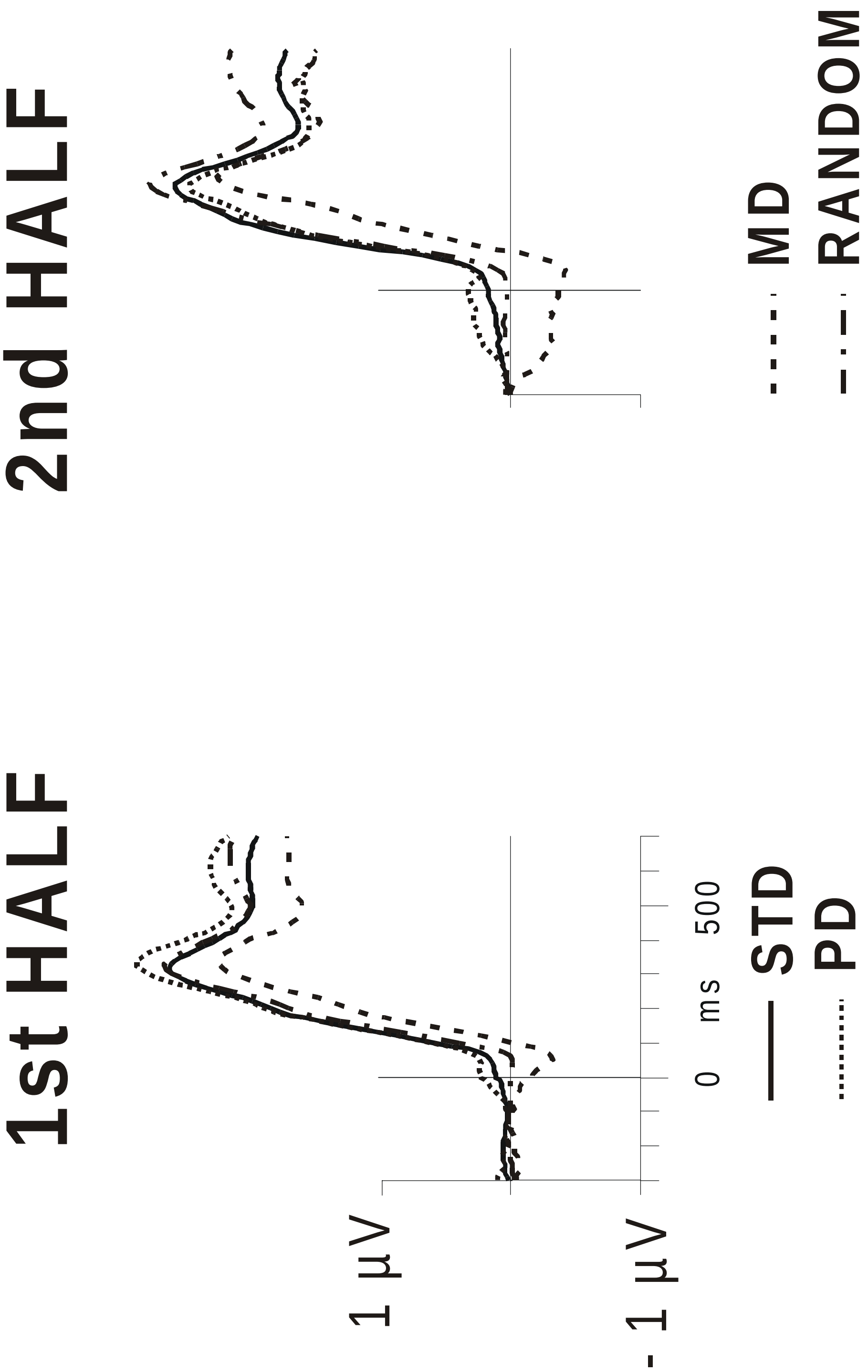


Figure 24: Stimulus-locked LRP for all 28 subjects in the first (left) and second (right) experimental half separately for standards (std, solid line), perceptual deviants (pd; dotted line), motor deviants (md; dashed line) and random stimuli.

Of the 17 subjects categorized as implicit learners, 11 exhibited significant "explicit" knowledge about the motor sequence as measured with the free movement sequence recall task. Furthermore, all 11 subjects categorized as explicit learners showed significant knowledge about the response sequence. Thus, it is possible that motor anticipation as revealed by the LRP-data is due to reproducable knowledge about the response sequence. To examine whether motor anticipation also played a role for subjects without movement sequence knowledge, the LRP for the six implicit subjects (6,14,17,21,22,36) which did not show any response-related sequence knowledge was averaged separately (see fig. 25). Although the 'positive dip' for motor deviants failed to show significance, a tendency towards activation of the incorrect response for motor deviants and a very early activation of the correct response for standards are evident. Thus, response anticipation might be important for implicit learners as well as for explicit learners.

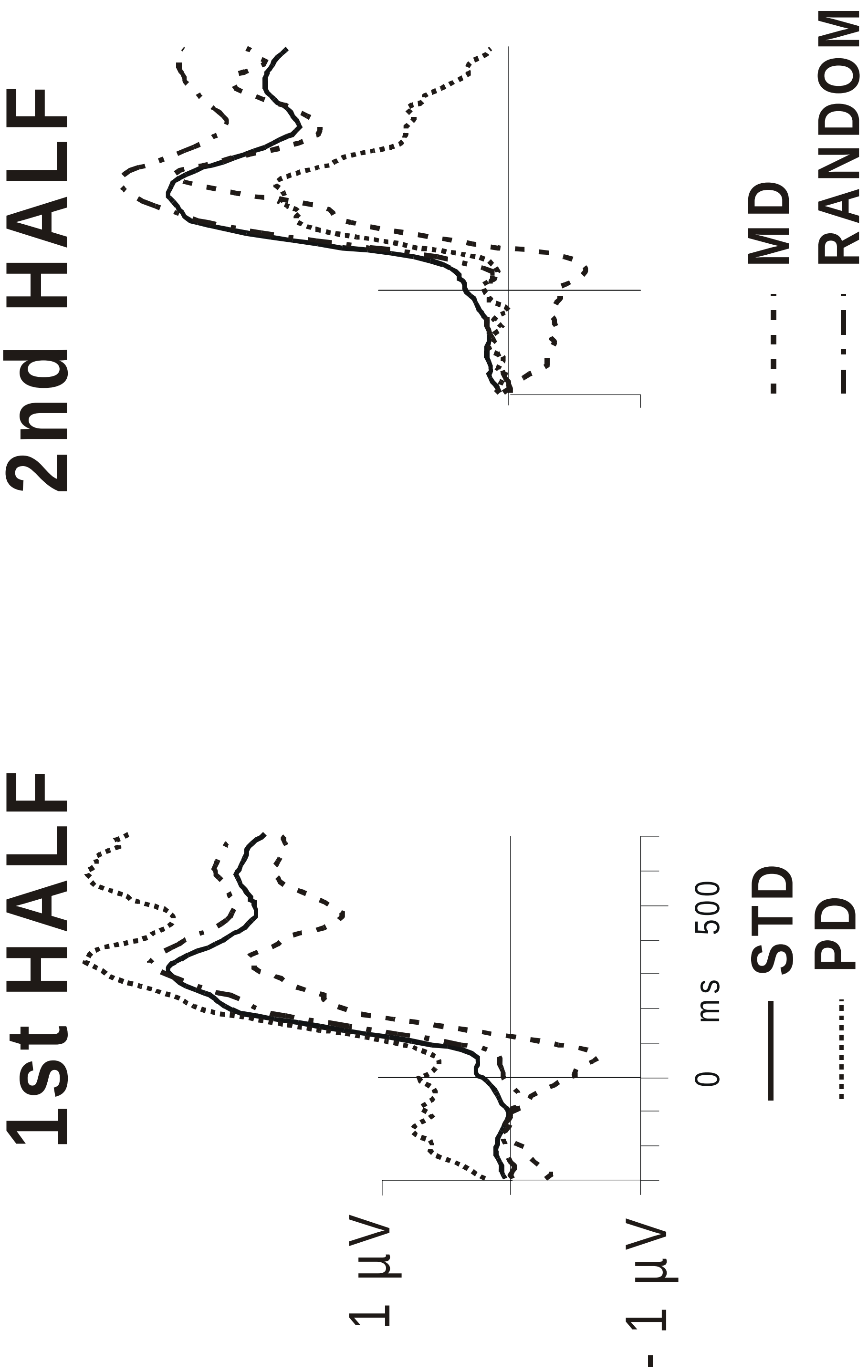


Figure 25: Stimulus-locked LRP for six subjects without reproducable knowledge about the response sequence for the first and second half of the experiment and for standards (std; solid line), perceptual deviants (pd; dotted line), motor deviants (md; dashed line) and random (dotted and dashed line) stimuli, respectively.

Response-locked LRP. Amplitude of the response-locked LRP did not differ between the two groups (no significant main effect or interaction with factor

GROUP) and was not influenced by the experimental manipulations (no main effect or interaction with factor STIMULUS TYPE; see fig. 26).

LRP-onset latencies. Onset of the stimulus-locked LRP for standard letters was earlier than onset for motor deviants or random letters in the second experimental half (std. vs. md: 135.19 vs. 233.8 ms, T(27) = 13.325; std vs. ran: 135.19 vs. 145.83 ms, T(27) = 3.42; Tcrit(27) = 2.052 two-tailed at $\alpha = 5$ % level for these comparisons). In contrast, onset-latencies for response-locked LRPs did not differ. Note that effects of LRP-onset latency are similar to the effects of RT.

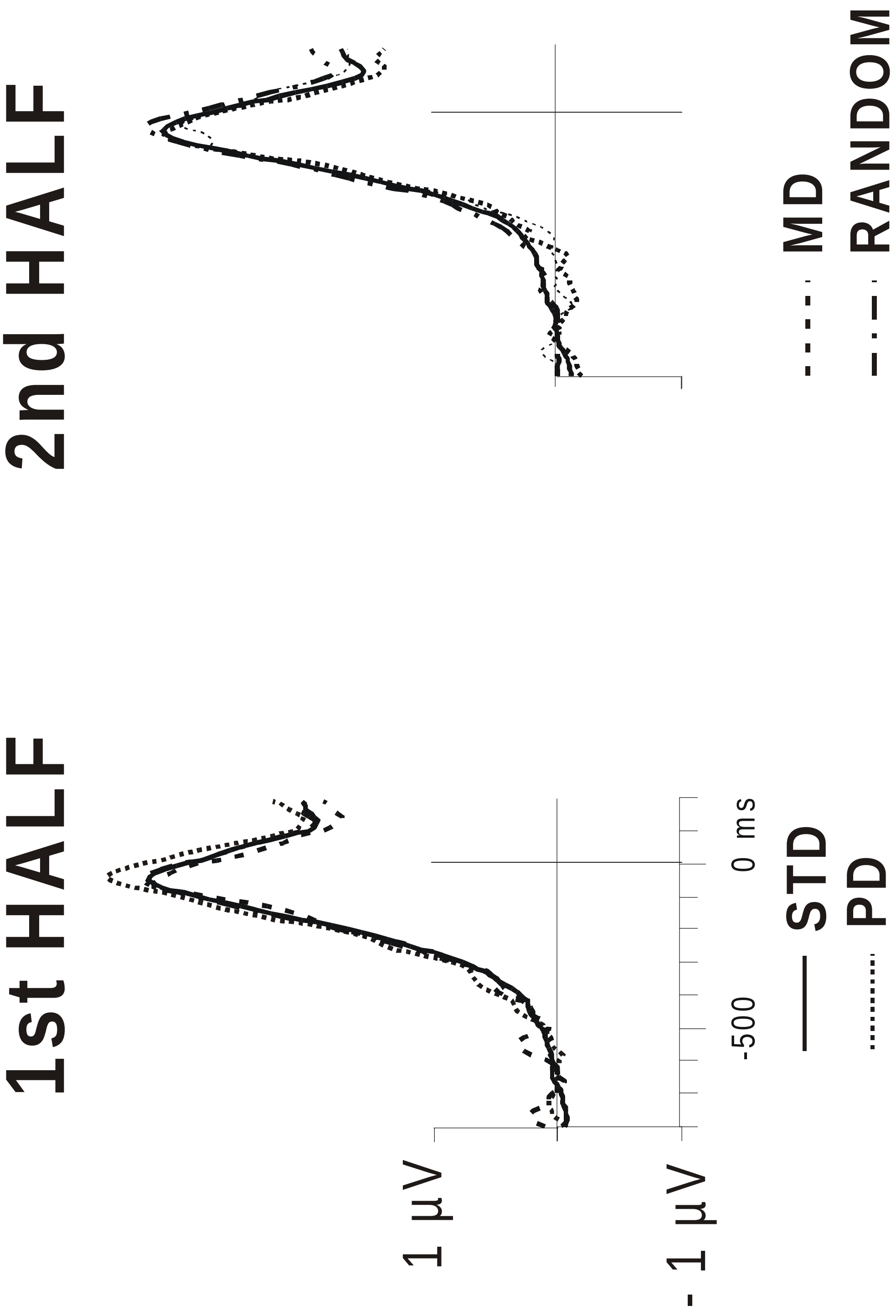


Figure 26: Response-locked LRP for for all 28 subjects for the first and second half of the experiment and for standards (std; solid line), perceptual deviants (pd; dotted line), motor deviants (md; dashed line) and random stimuli (dotted and dashed line), respectively.

IV. 4 Discussion

The present study examined implicit and explicit learning of a sensorimotor skill. Specifically, the role of perceptual processes (S-S-learning) and motor processes

(R-R-learning) in a variant of the SRT-task was explored. Furthermore, differences in the neuronal structures involved in explicit and implicit learning were analyzed.

Subjects performed a four-choice reaction time task. Eight locations were arranged so that two locations each shared the same horizontal position and differed only with respect to their vertical location. Subjects had to respond according to the horizontal position of the stimulus with a finger lift, i.e. two locations each were mapped onto one response finger. Unknown to subjects, the stimuli followed a sequence of eight elements which was interrupted occasionally by one of two types of deviant stimuli. Perceptual deviants violated the perceptual sequence but required the same response as a regular stimulus whereas motor deviants required a response with the opposite hand, and thus violated both the response as well as the perceptual sequence. Several tests of explicit sequence knowledge were administered after completion of the SRT-task to assess the amount of verbalizable knowledge about the stimulus regularities. On the basis of these results two groups of subjects were formed. Implicit learners did not exhibit sequence knowledge different from the probability of guessing correctly, whereas explicit learners were able to recall at least three consecutive elements of the sequence correctly.

The basic findings obtained by other researchers in the SRT-paradigm were replicated: Both groups of subjects learned the regularities inherent in the stimulus sequence. This is reflected in a decrease of errors for responses to standard stimuli in the course of the experiment. Furthermore, subjects made more erroneous responses to random stimuli compared to standards in the second half of the SRT-task. Likewise, RT to standard stimuli decreased from the first to the second half and was faster than responses to random stimuli. At least for those subjects who are categorized as implicit, this learning most likely took place without the development of concurrent awareness of the stimulus structure (see, for example, Nissen & Bullemer, 1987). However, the present study differed from the standard SRT-task in several respects: First, rather than using one block of random stimuli as a control condition which can be compared to the structured stimulus blocks, random stimuli were introduced at the beginning and at the end of each block (see Frensch & Miner, 1994). This manipulation served to diminish sequence learning effects as it is more difficult for subjects to detect the beginning and the end of the structured parts in each stimulus block. Indeed, the learning effect in the present study was small compared to other SRT-studies. Second, the introduction of deviant stimuli should further enhance the difficulty of sequence learning. Finally, the subjects had much more experience with the task than in most other studies (each subject was confronted with 256 replications of the sequence, compared to 100 in Nissen & Bullemer (1987)). Using probabilistic rather than deterministic sequences, Cleeremans & McClelland (1991) found implicit learning of structural regularities after subjects practiced for 60000 trials (see also Jiménez & Méndez, 1999). Thus, it seems to be justified to draw conclusions concerning the mechanisms involved in sequence learning from the present results.

Response- or stimulus- based learning ?

Behavioral results indicate that both explicit as well as implicit learners were sensitive to the violation of the response sequence. Error rate as well as RT did not differ for standard stimuli and perceptual deviants but were enhanced for motor deviants. These effects emerged in the first half of SRT-performance and increased towards the end of the experiment. These results replicate and extend those of Nattkemper & Prinz (1997) who found prolonged RTs for deviants violating the response sequence for symbolic stimulus material (letters) in a group of implicit learners. These results are compatible with the idea that R-R associations might be the major component of implicit sequence learning (Hoffmann & Koch, 1997; Nattkemper & Prinz, 1997).

This idea is further supported from stimulus-locked LRP data. Selective activation of the correct response started immediately after the onset of a standard stimulus. LRPs for perceptual deviants (which violated the stimulus-, but not the response sequence) showed by and large the same pattern as those to standards, that is, an early activation of the correct response. In contrast, a significant activation of the correct response for randomly presented stimuli emerged approximately 100 ms after stimulus onset (see table 16). This indicates that selective anticipation may influence the motor system very early. Furthermore, for both explicit as well as implicit learners an activation of the incorrect but expected response hand was found for motor deviants prior to the execution of the correct response (positive 'dip' in the stimulus-locked LRP). In the second half of the experiment, this started to develop as early as 100 ms prior to stimulus onset indicating that subjects expected the upcoming response already before the imperative stimulus was presented. Taken together, these findings show that specific anticipations about the upcoming response may have been induced by the presence of the sequence. These expectations seem to have an immediate influence on the response execution stage. Similar findings were reported by Eimer and colleagues (1996) for symbolic stimulus material (letters). However, in their study, participants who were unable to recognize any regularities in the stimulus material did not show an activation of the incorrect response hand. In contrast, in the present study, anticipatory response activation was present for subjects who did not exhibit explicit knowledge about the response sequence in a movement sequence recall task (see fig. 25). Thus, it seems reasonable to conclude that conscious awareness of the sequence structure or of the movement sequence is not necessary for the development of response anticipation.

Onset latencies of the stimulus-locked LRP were longer for motor deviants than for standards in the second, but not in the first half of the experiment. This indicates that response anticipation developed with increasing experience of the task.

Learning in the SRT-task, whether accompanied by the development of accessible knowledge of the sequence or not, could consist of changes in the motor related systems itself. This is consistent with PET data which show that procedural learning of a motor skill involves modifications in the same brain areas as those mediating the execution of the skill (Grafton, Mazziotta, Presty, Friston, Frackowiak, & Phelps, 1992). Furthermore, sequence learning has been found to be impaired in patients with degenerative changes in brain structures mediating motor behavior such as Parkinson's disease (Ferraro, Balota, & Connor, 1993) or Huntington's disease (Knopman & Nissen, 1991).

In contrast to the stimulus-locked LRP, no difference in amplitude or onset-latency was evident in response-locked LRPs. This indicates that response execution processes were most likely not influenced by sequence learning.

Differences between explicit and implicit learning

ERPs were also influenced by stimulus deviance, and this effect differed as a function of accessible sequence knowledge. For implicit learners, mean ERP-amplitude 250 - 450 ms poststimulus was more negative for stimuli presented at deviant locations compared to those at standard and random positions. This effect could reflect either a confirmation or a violation of sequential expectancy of the upcoming stimulus. However, several aspects of the data suggest that this effect was not related to sequential learning itself. First, the ERP-effect of stimulus deviance was not reliably affected by the amount of training (no STIMULUS TYPE by HALF interaction). However, RT and errors were larger for motor deviants and random stimuli compared to standards, and this behavioral effect was affected by the amount of practice. Thus, if the ERP-effect were learning related, one would also expect a statistically reliable interaction with factor half, i.e. with the amount of practice. This is not in line with the data. Secondly, visual inspection of fig. 23 reveals an unexpected trend: If at all, the deviance effect for ERP-amplitude for implicit learners was larger in the first half of the experiment, not in the second as one would expect from RT data. Finally, ERPs were of the same amplitude for standards and random stimuli. However, behavioral data (RT and errors) were significantly different for these two stimulus types. If the ERP-effect would reflect sequence learning, and if sequential and non-sequential stimuli are processed differently in the human brain, one would expect an ERP for random stimuli which is similar to that of deviant events. This is not in line with the data. Thus, it is concluded that the ERP-effect (250-450 ms poststimulus) for implicit learners is most likely not related to sequence learning.

For both, implicit as well as explicit learners, amplitude of the negative-going flank of the P300 (500-600 ms poststimulus) was reliably more negative for perceptual deviants compared to the three other stimulus types (see fig.23). However, this effect did not vary as a function of training.

Due to the lack of an ERP-effect related to sequence learning it was not possible to look at topographical differences in learning of a symbolic and learning of a spatial sensorimotor sequence.

Taken together, behavioral and ERP-data of the present experiment are more in line with a model which does not assume different cortical structures to be involved in explicit and implicit sensorimotor sequence learning, at least if spatial stimulus sequences are involved.

V. GENERAL DISCUSSION

V.1 Summary of the results

The most important results of the three experiments presented here can be summarized as follows:

(i) As already shown previously, learning of sensorimotor sequences was possible with and without concurrent development of consciously accessible, verbalizable knowledge about the regularities inherent in the stimulus material. This has been found for symbolic (experiments 1 and 2) as well as spatial sequences (experiment 3).

(ii) Implicit as well as explicit learners seem to have learned response-response-associations (prolongation of RT for motor deviants (experiments 1 and 2); significant activation of the incorrect response-hand prior to activation and execution of the correct response (experiments 1 and 3)). Furthermore, explicit learners showed additional stimulus-based learning (RT-increase for perceptual deviants relative to standard letters (experiments 1 and 2).

(iii) The experiments provide evidence in line with the hypothesis that implicit and explicit learning rely on different neuronal structures, at least if symbolic stimulus material is used (reliable difference of ERPs for implicit and explicit learners (experiments 1 and 2), i.e. larger negativity for perceptual and motor deviants relative to standards (N200) and larger positivity to motor deviants (P300-effect) for explicit learners, but not for implicit learners).

(iv) With a spatial sequence, both explicit as well as implicit learners seem to acquire response-response-associations (RT and error rate were enhanced only for deviants violating the response sequence). ERPs showed some sensitivity to stimulus deviance for implicit learners, but this did not interact with the amount of training. LRP data indicated an early activation of the correct response hand for standard stimuli and an activation of the incorrect response hand prior to activation and execution of the correct response for motor deviants (experiment 3). However, in contrast to the experiments using symbolic stimuli, the ERP of explicit learners did not show any sensitivity to stimulus deviance.

V.2 Discussion

The results of the three experiments are discussed with respect to the two main issues under examination: First, are different brain systems involved in implicit and explicit sequence learning ? and, second, which type of representation results from implicit learning of sensorimotor sequences ?

Are different brain systems involved in explicit and implicit learning ?

In all three experiments, a free recall and several recognition tasks were used to assess the amount of verbalizable sequence knowledge subjects acquired during performance of the SRT-task. Subjects were divided into groups of explicit or implicit learners either on the basis of their results in these tests (experiments 1 and 3) or according to the instructions they had received. The criteria used for the categorization are in line with those used by other researchers (e.g. Eimer, Goschke, Schlaghecken, & Stürmer, 1996). Furthermore, it was shown that performance of implicit learners in the explicit knowledge tasks was not different from guessing (experiments 2 and 3). In all three experiments, reliable differences in the amount of acquired verbalizable knowledge for both groups of learners were observed. Thus, conclusions with respect to differences between the two forms of learning seem to be warranted.

Previous studies concerned with differences of explicit and implicit learning focused on the neuronal systems involved. This line of research was inspired by the multiple systems view in implicit memory research. Dissociations between explicit and implicit memory are explained by postulating that different brain structures subserve these two memory systems (see, for example, Schacter, 1987, 1993; Squire & Cohen, 1984). In implicit learning research, attempts have been made to identify brain systems which are involved in implicit and explicit learning. For example, PET-studies yielded two different hypotheses with respect to the involved brain structures. Rauch, Savage, Brown, Curran, Alpert, Kendrick, Fischman, & Kosslyn (1995) proposed that implicit learning is mediated by a distributed system encompassing the right ventral premotor cortex, right ventral striatum, right thalamus and bilateral visual association cortices, whereas explicit learning is mediated by a subsystem relevant for motor learning (cerebellum, thalamus, brain stem) and subsystems which may reflect the implementation of conscious strategies like language or visual imagery (see 1.4.3). Grafton, Hazeltine, & Ivry (1995, 1998; see also Hazeltine, Grafton, & Ivry, 1997) provided evidence for the involvement of a cortical-subcortical loop in implicit learning encompassing the sensorimotor cortex, SMA and putamen. Brain structures involved in explicit learning seem to be parietal/prefrontal cortical areas.

In the present series of studies, results are ambiguous: In experiment 1, implicit learning seemed to be primarily based on response-response contingencies, whereas explicit learning seemed to be stimulus-based, too (prolonged RT for perceptual deviants for explicit, but not for implicit learners; prolonged RT for motor deviants for both groups; sensitivity of ERP-amplitude to stimulus deviance for explicit learners only). ERP-results of experiment 2 replicated those of experiment 1. However, implicit learners seemed to be also sensitive to the perceptual deviance of a stimulus (prolonged RT for perceptual deviants compared to standards). In experiment 3, no difference emerged for implicit and explicit learners in case of a spatial sequence. Learning for both groups seemed to be primarily based on the response sequence. Taken together, the studies presented here provided an incoherent picture with respect to differences in the brain systems that are involved in both forms of learning.

A critical point in these experiments concerns the procedure used for dividing the participants into groups of implicit and explicit learners. The reliability of the tests used to assess explicit, verbalizable knowledge about the stimulus sequence has been criticised (e.g. Perruchet & Amorim, 1992; see 1.3.1). Furthermore, it is assumed that these tests are not "process pure", i.e. not only explicit, but also implicit knowledge might be measured. Despite these criticisms, the free recall-, the generate- and the recognition task have been used to test explicit sequence knowledge in the present experiments due to the lack of alternative tests.

The use of deviant stimuli might have led to an additional problem for the explicit knowledge tests in the present studies: Subjects were confronted with a variety of different bigrams and had to recall only those stimuli which appeared more often than others (i.e. the sequential stimuli). It cannot be ruled out that they remembered some of the deviants which occurred in the last block prior to the explicit knowledge tests and reproduced these sequence fragments.

In the light of these concerns, it might be that the incoherent picture concerning differences between implicit and explicit learning is due to differences in the quality of the tests used to assess explicit knowledge. In experiments 1 and 2, subjects had to recall a letter sequence. In experiment 3, they had to indicate the sequence of locations on a sheet of paper which contained eight circles. They had to write numbers into these circles which indicated the position of that location in the sequence. This procedure might involve more transfer of knowledge compared to the free letter sequence recall, and, thus, might further lower the reliability of this test procedure.

Explicit subjects in experiment 3 on average reported 3.91 consecutive locations correctly. In experiment 1 (which also employed a sequence of 8 elements length) explicit learners reported at least 7 out of 8 consecutive elements correctly. Thus, it seems that explicit learners in experiment 3 had less explicit sequence knowledge than those in experiment 1. This difference in the amount of verbalizable sequence knowledge (which is also apparent in the recognition task) could also explain the lack of a difference in ERPs and RTs in experiment 3 and the emerging incoherent picture regarding differences in explicit and implicit learning.

Multiple systems for implicit sequence learning ?

Several researchers claimed that implicit learning might occur in different, independent brain systems (e.g. Goschke, 1998; Mayr, 1996). For example, Keele, Ivry, Hazeltine, Mayr, and Heuer (1998) proposed the existence of two qualitatively different systems of sequential representation: The first extracts domain-specific information. "Domain" refers to stimulus location, color, tones or responses. According to the model, potentially confusing information coming from other, extradimensional sources is filtered out by the domain-specific system. Such filtering would be especially useful if information from other dimensions were presented randomly as in most dual-task experiments. The second, so-called multidimensional learning system allows information to be integrated across dimensions or modalities. It will be operational in situations where cross-dimensional information improves sequential predictability. The theory further assumes that the unidimensional system operates in an entirely implicit mode, whereas learning in the multidimensional system can occur outside of awareness, but the development of explicit knowledge appears to be dependent on the content of this system.

Evidence supporting this claim comes from experiments which show that simultaneous learning of two uncorrelated sequences is possible (e.g. Mayr, 1996). However, behavioral results alone are not sufficient to show that multiple, domain-specific systems underlying different forms of implicit learning do indeed exist. Simultaneous learning of two independent sequences may, in principle, be mediated by a unitary system with the capacity to learn sequences in parallel. Neuropsychological and neurophysiological data are needed to evaluate the hypothesis of domain-specificity of implicit, sequential learning. In the present experiments, symbolic (experiments 1 and 2) and spatial (experiment 3) imperative stimuli were used. From a domain-specificity point of view, one would predict that different brain systems are involved in implicit learning for the two types of stimulus material. This should be reflected in topographical differences of learning-related ERP-effects for these two types of imperative stimuli. However, in these experiments, learning-related effects for implicit learners were found only in the LRP which reflects response-preparation processes, but not in ERP-components which reflect stimulus evaluation processes. Thus, it seems that irrespective of the domain of the stimulus material, implicit serial learning might have been mainly based on the regularities inherent in the response sequence. This finding is not in line with the domain-specificity hypothesis. Other neuroimaging studies yielded comparable results: Grafton, Hazeltine, and Ivry (1995) and Hazeltine, Grafton, and Ivry (1997) compared implicit learning of a sequence of colors and a sequence of locations. In both cases, learning-related rCBF-enhancement was found mainly in the striatum and areas of motor control. Differences between the two tasks were also found, but the interpretation of these findings with respect to sequence learning is not clear.

On what is learned in implicit sequence learning

The present series of experiments was concerned with the role of stimulus-based and response-based learning in variants of the SRT-task. In experiments 1 and 3, RT and error rate increased only for motor deviants compared to standard stimuli. This indicates that the sequence of responses seems to be of prime importance for the development of implicit sequence learning.

This conclusion is further supported by data from stimulus-locked LRPs: In all three experiments, a shortening of LRP-onset latency for standard letters in the second half of the experiment was found. Furthermore, onset latency for motor deviants was later compared to standards. Most importantly, in experiments 1 and 3, motor deviants showed an activation of the incorrect response hand prior to activation and execution of the correct response. Thus, after considerable learning experience, subjects seem to have developed (non-conscious) expectations about the upcoming response which led to the activation of the expected (but in case of a motor deviant wrong) response. Furthermore, standard stimuli showed a very early activation of the correct response after training. In experiment 3, a reliable LRP was present as early as 0 - 50 ms after stimulus presentation. Thus, response selection may be influenced by learning about the regularities inherent in a sensorimotor sequence. More precisely, experience with a perceptuo-motor sequence may lead to the development of motor anticipations and to faster response selection. Results of Keele, Jennings, Jones, Caulton, and Cohen (1995) suggest that this type of response selection may take place at a non-effector specific level. In their study, a change of the response modality in a sequence learning task from key-pressing to verbal responses resulted in reliable transfer of sequence knowledge.

Behavioral results of experiment 2 are at odds with the idea that the regularities inherent in the response sequence are of prime importance for sequence learning: In this experiment, RT for perceptual deviants was longer and error rate larger compared to standards for the group of implicit learners. This experiment differed in some respects from experiment 1, which might be responsible for the differences obtained in the results. First, subjects were categorized as implicit and explicit groups on the basis of the instruction they received prior to performing the SRT-task. Second, the used sequence was longer and the statistical structure of both response as well as stimulus sequences was more complex. Third, more deviant stimuli were used than in experiment 1. In each replication of the sequence, two deviants were inserted. This made it more difficult to capture the structure which is reflected in a smaller learning effect for both groups in experiment 2. Recently, Thomas and Mayr (1999) tried to replicate the results of the Nattkemper and Prinz (1997) experiments. Most importantly, they changed the statistical complexity of the response and of the stimulus sequence. Enhanced RTs were found for deviant events violating the response- as well as for deviants violating the stimulus sequence. Remember that in the Nattkemper and Prinz (1997) study, only motor deviants led to enhanced RTs. Thus, it is possible that the differences in the statistical structure of the response- and the stimulus sequence may account for the different results of experiments 1 and 2. Systematic studies which manipulate complexity of the response- as well as of the stimulus sequence are needed to resolve this issue.

However, the behavioral differences between the three stimulus types in experiment 2 are not reflected in ERP-components known to be sensitive to stimulus identification and evaluation processes (N200, P300). One possible explanation is that subcortical processing of stimuli which cannot be measured with the ERP-methodology may be involved in implicit learning. Hazeltine, Grafton, and Ivry (1997), for example, found an involvement of the left thalamus in implicit learning of a sequence of colors.

One of the main driving forces for research on implicit learning has been an interest in dissociable forms of learning, one of which might be associated with control and, at a phenomenological level, consciousness, and another with an automatic, often called unconscious, mode of knowledge acquisition. It has been proposed that this distinction must be (a) empirically validated by showing that qualitatively different learning processes are involved in the two forms of learning, and (b) captured theoretically by developing models of the different learning processes. Research with the SRT-paradigm has contributed to both issues, but the results are ambiguous. Empirically, a convincing dissociation of the two forms of learning has not been found until now. The results of the present experiments were also incoherent with respect to differences in the processes and brain systems involved in implicit and explicit learning. Thus, it might be helpful to shift the focus in sequence learning research from the conscious/unconscious- dichotomy to a characterization of the learning systems involved. A closer interaction between the psychological analysis of the processes involved in sequence learning and a functional analysis of different brain areas may contribute to delineate the many functions provided by different brain systems involved in sequential learning.

VI. ABSTRACT

The ability to recognize sequential dependencies in the continuous stream of information is fundamental to the nervous system. When subjects are asked to respond to one of several possible stimuli, reaction times (RT) and errors decrease when the stimuli and responses form a predictable sequence. This learning can occur both with and without awareness of the stimulus regularities and has been termed explicit and implicit learning.

The present experiments used event-related brain potentials (ERPs) to examine whether different brain systems are involved in the two types of learning. Furthermore, the role of stimulus- and response-based processes in learning of sensorimotor sequences was analysed.

In three experiments, explicit and implicit learning of symbolic (experiments 1 and 2) and spatial sequences (experiment 3) were studied using a variant of the serial reaction time (SRT) task. In otherwise regular, repeating event- sequences, two types of deviant stimuli occasionally replaced standard events: Perceptual deviants violated the stimulus- but preserved the response sequence, whereas motor deviants violated both the stimulus- as well as the response sequence. This allowed the separation of stimulus- and response- based learning. Subjects were categorized as groups of implicit and explicit learners either according to their performance in tests which probed explicit sequence knowledge (experiments 1 and 3) or according to the instruction they had received in advance (experiment 2).

Implicit learning proved to be primarily response- based in two of the three experiments. This was indicated by motor deviants which prolonged the RT and which activated the incorrect, but expected response-hand prior to the execution of the correct response in the group of implicit learners. This effect became evident in the lateralized readiness potential (LRP). ERPs did not show any other effects related to implicit learning processes.

In contrast, explicit learning proved to be response- as well as stimulus-based. In the group of explicit learners, events violating the stimulus sequence only prolonged RT relative to regular events and for motor deviants a further increase in

RT was present. Stimulus deviance per se influenced ERPs in explicit learners, but only if symbolic stimulus sequences were used (experiments 1 and 2): In this case, an enhanced negativity, peaking 250-350 ms after stimulus presentation (N200) was observed. In addition, motor deviants evoked a larger positivity 350-650 ms poststimulus (P300).

These results provide only weak evidence for the involvement of different brain systems in explicit and implicit learning.

VI. ZUSAMMENFASSUNG

Die Verarbeitung sequentiell strukturierter Information ist eine grundlegende Fähigkeit der menschlichen Verhaltenssteuerung. Sollen Versuchspersonen auf einen von mehreren möglichen Reizen reagieren, so sinken Fehlerrate und Reaktionszeit, wenn der imperative Stimulus ein Element einer sich regelhaft wiederholenden Sequenz ist. Dieser Lerneffekt kann mit der Entwicklung von verbalisierbarem Wissen über die dem Stimulusmaterial zugrundeliegenden Regularitäten einhergehen (explizites Lernen). Für Subgruppen von Versuchsteilnehmern ist derartiges Lernen auch ohne gleichzeitigen Erwerb von explitzitem Wissen möglich (implizites Lernen).

In drei Experimenten wurde mit Hilfe von ereigniskorrelierten Gehirnpotentialen (EKPs) untersucht, ob implizites und explizites Lernen (a) auf unterschiedlichen Prozessen beruhen, und (b) ob daran unterschiedliche neuronale Strukturen beteiligt sind. Dabei wurde insbesondere die Bedeutung von reizbasierten und motorischen Prozessen beim Erlernen sensumotorischer Ereignissequenzen analysiert.

Explizites und implizites Lernen von symbolischen Reizsequenzen (Experimente 1 und 2) bzw. räumlichen Reizsequenzen (Experiment 3) wurde mit einer Variante der seriellen Wahlreaktionsaufgabe untersucht. In reguläre, sich wiederholende Reizsequenzen wurden zwei Arten von abweichenden Ereignissen eingefügt: Perzeptuelle Abweichler verletzten die sequentielle Abfolge der Reize, nicht aber die Reaktionsfolge während motorische Abweichler die sequentielle Abfolge sowohl der Reiz- als auch der Reaktionssequenz verletzten. Dadurch wurde es möglich, Reiz- und Reaktionsbasiertes Lernen voneinander zu trennen.

Aufgrund der in expliziten Wissenstests gezeigten Leistungen wurden die Versuchsteilnehmer in Gruppen impliziter und expliziter Lerner aufgeteilt (Experimente 1 und 3). In Experiment 2 wurde implizites und explizites Lernen durch eine Variation der Instruktion induziert.

In zwei von drei Experimenten zeigte sich, daß implizites Lernen vor allem durch den Erwerb von Kontigenzen aufeinanderfolgender Reaktionen bedingt ist.

Reaktionszeit und Fehlerraten waren für motorische Abweichler im Vergleich zu Standardreizen erhöht. Zudem zeigte sich eine Aktivierung der antizipierten, aber falschen Reaktionshand vor Ausführung der korrekten Reaktion im lateralisierten Bereitschaftspotential (LRP). Die Abweichung eines Reizes spiegelte sich bei impliziten Lernern allerdings nicht im EKP wieder, was auf gleiche kortikale Verarbeitungsmechanismen für alle präsentierten Reize, Standards und Abweichler, schließen läßt.

Explizites Lernen von sensumotorischen Sequenzen scheint dagegen sowohl auf dem Erwerb von Kontigenzen in der Reiz- als auch in der Reaktionsfolge zu beruhen: Perzeptuelle Abweichler verlängerten die Reaktionszeiten und Fehlerraten. Für motorische Abweichler fand sich eine weitere Erhöhung des Effektes. Die perzeptuelle Abweichung eines Reizes von der Erwartung führte im EKP bei Verwendung von symbolischen Sequenzen (Experimente 1 und 2) zu einer stärkeren Negativierung 250-350 ms nach Reizdarbietung (N200). Motorische Abweichler evozierten zusätzlich eine stärkere Positivierung 350-650 ms (P300).

Die Ergebnisse liefern nur schwache Hinweise darauf, daß unterschiedliche neuronale Strukturen an explizitem und implizitem Lernen beteiligt sind.

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Appendix A

List of bigrams, trigrams and quadrupels used for the recognition procedure in experiment 1.

Regular bigrams, trigrams and quadrupels which were part of the sequence:

TX
KT
XS
MR
SM

VLK
TXS
SMR
KTX
RVL

VLKT
KTXS
TXSM
XSMR
LKTX

Irregular bigrams, trigrams and quadrupels which were not part of the sequence:

LT
VS
KX
MV
SK

VSL
KSR
LKS
SMX
XSR

VTXM
VLTR
LKXM
TXSR
KTLV

Appendix B

List of bigrams and trigrams used for the recognition task in experiment 2.

Regular bigrams and trigrams which were part of the sequence:

ZN	ZNT
NT	NTV
TV	TVL
VL	VLN
LN	LNX
NX	NXT
XT	XTD
TD	TDR
DR	DRD
RD	RDL
DL	DLZ
LZ	LZN

Irregular bigrams and trigrams which were not part of the sequence:

ZT	ZLT
NL	NXV
TR	TDL
VD	VXN
LX	LTX
NR	NRT
XV	XTZ
TZ	DRX
DN	RDR
RV	DLX
DT	LZV
LV	TDX

Appendix C

List of bigrams and trigrams used for the recognition task in experiment 2. = denotes the upper left circle, 1 the lower left, 7 the lower right circle.

Regular bigrams and trigrams which were part of the sequence:

1/6
6/5
5/2
2/4
4/7
7/0
0/3
3/1

4/7/0
7/0/3
0/3/1
3/1/6
1/6/5
5/2/4
6/5/2
2/4/7

Regular bigrams and trigrams which were not part of the sequence:

3/2
2/7
1/0
0/6
4/3
5/1
6/4
7/5

1/3/5
5/7/0
2/1/6
0/2/4
4/5/7
7/6/1
6/0/3
3/4/2

ACKNOWLEDGEMENTS

Finally, it is a great pleasure for me to thank all the people who supported me in writing this thesis.

I am grateful to Prof. Dr. Frank Rösler for providing the possibility to conduct this work and for the continuous support during the preparation of this thesis.

I thank Prof. Dr. Harald Lachnit for his willingness to give an experts opinion on this thesis as a second advisor.

I am also indebted to Dipl.-Phys. Erwin Hennighausen who helped me a lot with the development of the software necessary to conduct the experiments and the simulations.

Dr. Martin Heil provided his support with insightful discussions on LRP-methodology. Thanks for that.

I also wish to thank Dipl.-Psych. Jasmin Bajric for many hours of discussion which provided a great source of enjoyment and inspiration. You made working in the lab much more fun.

Mustafa Öczan, Kristina Nielsen, Ina von Ceumern-Lindenstjerna, Martin Hefner, and Maren Struve helped in data collection. Dipl.-Phys. Hansjerg Gölz developed the EEG-analysis software. Thanks a lot.

I would also like to thank all other members of the workgroup "Cognition and Brain Activity": Dr. Hubertus Haan, Dr. Brigitte Röder, Dipl.-Psych. Kerstin Jost, Dipl.-Biol. Bettina Rolke, and Dipl.-Psych. Judith Streb.

Last but not least, I wish to express my gratitude to my wife Annette and my parents for their love and understanding during the last years.