Rapid acquisition of long spatial sequences in long-term memory

Johannes Drever

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Direktorin: Prof. Dr. med. Marianne Dieterich

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Berichterstatter: Prof. Dr. med. Andreas Straube

Mitberichterstatter: apl. Prof. Dr. Frank Weber
Priv. Doz. Dr. Ingo Borggräfe

Mitbetreuung durch den
promovierten Mitarbeiter: Dr.-Ing. T. Eggert

Dekan: Prof. Dr. med Dr.h.c. Maximilian Reiser, FACR, FRCR

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Contents

1 Introduction

It is common in everyday life that complex and long sequential movements have to be learned. Skills that require a long sequence of movements to be acquired include dancing, diving, karate, gymnastics or playing an instrument. For example, when learning to dance, a long and complex sequence of steps has to be acquired. This sequence is acquired by concentrating on only a few steps in the first attempt to perform the sequence. In successive attempts more steps are learned, the control of the center of mass improves and the positioning of the steps gets more accurate until the whole sequence is learned[1]. Importantly, such sequences are too complex to be learned in a single go because there are too many aspects to focus on. Thus, complex movement sequences have to be acquired by concentrating on specific aspects of the movement at a time. In many situations movement sequences are demonstrated by a teacher and are learned by deferred imitation, i.e. after the teacher has finished the demonstration (e.g. a combination of dance steps). For some movement sequences a partitioned presentation of the movement sequence is not possible. In these situations, it is the task of the learner to decide to which part of the sequence attention should be paid.

Since this aspect of learning has not been investigated in previous studies, we developed a learning task in which the movement sequence is too complex to be learned without such an attentional selection. In this task long sequences of spatial locations are learned by deferred imitation. A long sequence of 20 spatial positions is presented on a graphic tablet and reproduced after presentation by manual pointing. Hereafter, the learning task is referred to as “deferred imitation learning of long spatial sequences”. We used this task to investigate the acquisition and memory representation of complex movement sequences.

1.1 Learning paradigms

> When the crude beginnings of this research have been improved and replaced by more in-genious and adroit experimenters, the results ought to be very valuable. (Edward L. Thorndike, 1898)

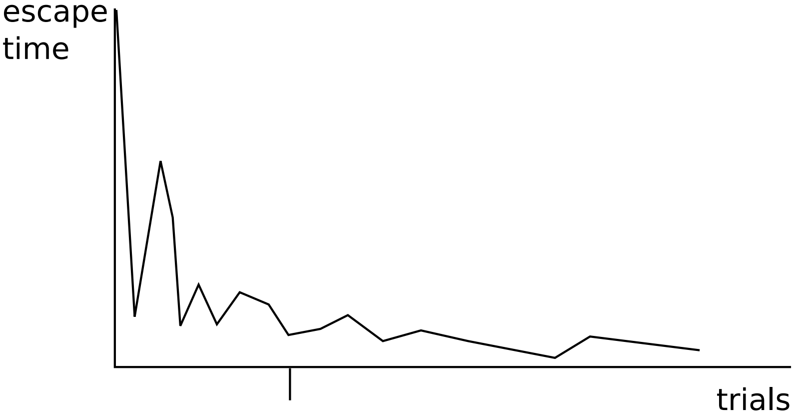

Figure 1.1: The learning curve introduced by Thorndike in the puzzle-box experiments. The time to escape is plotted as a function of trials. With repeated performance of the task the escape time decreases, indicating learning in the animal. (Adopted from Chance & Delaware, 1999).

1.1.1 The historical origin of learning paradigms

Since learning is the most remarkable ability of animals and humans it has attracted interest since the beginning of psychological research. In the early days, evidence on learning was gathered by introspection and anecdotal observations rather than by a scientific method. In his dissertation “Animal intelligence: An experimental study of the associative processes in animals” (Thorndike, 1889; Chance & Delaware, 1999), Edward L. Thorndike introduced a scientific method to study learning with a paradigm in which animals were put into puzzle boxes. He was the first to introduce a formal measure that defines a *learning curve* (Figure 1.1) by measuring the escape time as a function of trials. Based on his observations he formulated the *law of effect* (Thorndike, 1927) which states that the animal initially performs random acts and that those acts which are recognized as leading to success would be more likely to be chosen. The scientific investigation of learning with a specific apparatus and procedure was further developed and refined, leading to well known learning paradigms such as classical (Pavlov, 1927; reprinted 2010)[2] and operand conditioning (Skinner, 1945). A key feature of these paradigms is an objectively measurable variable that quantifies the learning progress. In classical conditioning the successful association of an unconditioned stimulus with a conditioned response is quantified by the strength of the response, e.g. the amount of saliva produced in response to a bell tone in the famous Pavlovian experiments. In operand conditioning changes in behavior are quantified by the frequency of responses, e.g. specific button presses in

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[1] An interesting aspect is generalization of motor learning. For example, learning a new dance is facilitated by the previous acquisition of another dance. This phenomenon, known as structural learning (Braun, Mehring & Wolpert 2010, Cleeremans & McClelland 1991), is not subject of the thesis.

[2] Pavlov was ignorant of the work by Thorndike when he started to investigate classical conditioning (Pavlov, 1927).

operand conditioning chambers.

These paradigms are used to investigate **which** behaviors are formed and which reflexes or actions are associated with specific stimuli or rewards[3]. Another line of research is motivated by the question **how** skilled actions are learned and which mechanisms are involved in the learning process. Skill learning paradigms range from parametric adaptation learning paradigms, such as saccadic gain adaptation (McLauglin, 1967; Straube, Fuchs, Usher & Robinson, 1997; Ethier, Zee & Shadmehr, 2008), prism adaptation (Redding, Rossetti & Wallace, 2005), classical conditioning of eye blink reflexes (Napier, Macrae & Kehoe, 1992) and force field adaptation (Shadmehr & Mussah-Ivaldi, 1994) to complex skill learning paradigms.

Sequence learning is a growing sub-field of skill learning in which the acquisition of complex movement sequences is studied (Rhodes, et al. 2004). An important distinction of sequence learning paradigms is whether the sequence production is *stimulus guided* or whether it occurs in the absence of stimuli in *deferred imitation learning* paradigms (McDonough, Mandler, McKee & Squire, 1995). Stimulus-guided learning paradigms do not capture the natural learning situation in which sequences are too complex to be learned without attentional selection in the early learning phase. In the following sections the concepts of stimulus-guided learning and deferred imitation learning paradigms are explained in more detail.

1.1.2 Stimulus-guided learning

In stimulus-guided learning a sequence of responses to a recurring sequence of training stimuli is learned. Typically a single stimulus is presented until the subject responds to the stimulus. The next stimulus is presented after the subject's response. This procedure is repeated until the whole sequence has been presented. In this situation the subject is able to reproduce the whole sequence because of the guiding stimuli, regardless of the acquisition of an internal representation. The buildup of an internal representation is inferred from improvements in performance measures, such as reaction time or accuracy over repeated sequence presentations. A diverse set of paradigms developed for stimulus-guided learning.

The serial reaction time task is used to investigate *implicit learning* (Nissen & Bullemer, 1987). In this task, a sequence of stimuli to which the subject has to perform a matched response was presented. The stimulus was a repeating sequence of 10 elements and subjects were not made aware of the repetition. The reaction time to stimuli of the repeated sequence, typically about 200 ms, decreased by 50 % and was significantly shorter than the reaction time to random sequences. Thus, an implicit learning process, indicated by a shift from stimulus-response movements to anticipatory movements, must have been taken place. Some subjects showed sequence learning although they were not aware of the sequential structure, as assessed by a verbal report after the experiment.

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[3] Classical conditioning has also been proven to be a fruitful paradigm to investigate mechanisms involved in learning. For example learning was investigated on a neuronal level in eye-blink conditioning (Gerwig et al., 2007) and on a molecular level with the siphon withdrawal reflex in aplysia (Kandel, 2001).

Interestingly, although awareness is not necessary for sequence acquisition, disturbance of performance in dual task conditions strongly suggest that attention is required for sequence acquisition.

The shift from stimulus response movements to stimulus anticipation movements was also characteristic for serial reaching tasks (Ghilardi et al., 2009; Park & Shea, 2005). In these tasks a manipulandum was moved to a sequence of target positions that were all simultaneously visible during sequence production. The sequence order was indicated by illuminating the current target. At the beginning of learning the movements were reactive and became anticipatory with repeated reproduction, as indicated by shorter movement times. The accuracy (Ghilardi et al., 2009) or the smoothness (Park & Shea, 2005) of the movement was used as a continuous variable in order to quantify the acquisition of metric information. Ghilardi et al. (2009) also quantified the acquisition of order with the number of anticipatory movements per trial. Depending on the measure used to quantify learning, different aspects were investigated. In general, ordinal measures (e.g. the number of anticipations) quantifying the number of correct reproductions reflected the acquisition of sequence order and continuous measures quantifying the reproduction quality (e.g. the accuracy) reflected the acquisition of metric information.

The acquisition of order information is also the main aspect of investigation in the so-called 2x5 task (Hikosaka, Rand, Miyachi & Miyashita, 1995). In this paradigm a sequence of 2x5 (=10)[4] button presses on 16 buttons arranged on a 4x4 grid was learned by discovery. Two buttons were simultaneously illuminated and had to be pressed in a predefined order that was not known to the subject. Once the buttons were pressed in the correct order the next two buttons were illuminated. If the buttons were pressed in the wrong order the procedure started over with the first two buttons. By completing 5 button choices the subjects performed a sequence of 10 button presses. The acquisition of sequence order was measured by the number of trials needed to complete a set. At the beginning of learning the sequence had to be discovered, leading to a high number of trials needed to complete the sequence. With repeated performance the sequence was learned and could be performed on the first attempt. A further improvement of sequence performance was indicated by the movement speed. Movement speed increased further after the sequence order was learned, indicating the development of a highly automated effector specific representation (Rand et al., 1998).

In conclusion, the main feature of stimulus-guided learning tasks is that the stimulus is present during task reproduction. The present stimulus can be used as a recall cue for the next items. Thus, it is not necessary to recall the sequential context from memory and sequences may be learned without the acquisition of a long sequential context.

1.1.3 Deferred imitation learning

Deferred imitation learning refers to the ability to see actions in other subjects and then learn the movement sequence (McDonough, Mandler, McKee & Squire, 1995). In learning paradigms for deferred imitation learning a sequence of stimuli is presented in

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[4] In a variant of this task longer sequences of 2x10 items are learned.

a presentation phase. Then, the stimulus sequence is reproduced after the presentation is finished in the absence of stimuli. In contrast to stimulus-guided learning, the whole sequence has to be recalled from memory requiring the involvement of vision, attention, motor planning and control during learning.

In typing, a short sequence of key presses was first instructed and than reproduced following a GO-signal. It allows the investigation of mechanisms of motor control (e.g. Sternberg, Monsell, Knoll & Wright, 1978; Verwey, 1996) and the influence of higher order concepts, such as knowledge of words, on motor control (e.g. Crump & Logan, 2010). The key dependent measure in studies of the production of short sequences were the latency of movement production and the latencies between the single movements. Typically, the length of the sequence was manipulated and the key findings were sequence length effects on latency (sequence length effect on latency) and on inter-response intervals: The latency of sequence production increased and the inter-response intervals were prolonged with increasing sequence length. A key finding on learning is that the sequence length effect on latency disappears with extensive practice (Verwey, 1996). These timing properties give valuable insights into the mechanisms involved in sequence production and learning (Verwey, 2003) and constrain quantitative modeling studies (Boardman & Bullock, 1991; Rhodes et al., 2004).

Deferred imitation of spatial sequences was first investigated in the Corsi Block-tapping task (see Berch, Krikorian & Huha, 1998 for a review). In this task blocks were touched in a specific sequence by the examiner and the subject had to imitate the behavior by touching the blocks in the correct sequential order. This task has been used to measure the span of spatial memory by systematically increasing the length of the sequence until the sequence could no longer be directly reproduced, serving as a tool for clinical diagnosis of working memory disorder (Berch, Krikorian & Huha, 1998). A similar paradigm in which not only the spatial memory span but also the accuracy of reproduction could be measured was introduced by Sekuler, Siddiqui, Goyal & Rajan (2003). In this paradigm a short sequence of 3 to 7 line segments was presented by a moving disc. The subject reproduced the trajectory of the disc with a pen on a graphic tablet. The accuracy of reproduction was measured by the angular difference between the stimulus and the reproduction, whereas the acquisition of order was quantified by omissions and order errors. Deferred imitation of sequences has not only been investigated in hand movements but has also been studied in eye movements (Ditterich, Eggert and Straube, 1998). In this task a sequence of up to 5 target positions was presented. The sequence was reproduced by the subject with saccadic eye movements to the memorized target positions.

In all these paradigms deferred imitation learning of short sequences is investigated, whereas deferred imitation learning of longer sequences has, to our knowledge, not been studied under experimental conditions.

1.2 Research questions

Most studies on sequence learning so far focused on stimulus-guided learning in which the response sequence was generated concurrently with stimulus presentation (Section

1.1.2) or deferred imitation of short sequences (Section 1.1.3). In both of these tasks an attentional selection of a subsequence is not necessary for learning. In contrast, deferred imitation learning of *long* sequences captures the common learning situation in which the movement sequence is too complex for immediate reproduction. When the order of acquisition is not guided by stimuli or a teacher, it is the task of the subject to decide on which part of the movement to concentrate. Therefore, a long sequential memory content has to be acquired in several steps and requires the learner to focus on a specific subsequence in each learning iteration.

Thus, investigating deferred imitation learning of long pointing sequences offers an interesting paradigm for studying an elementary example of how humans acquire sequential long-term memory for rapid learning of complex motor actions achieved through efficient focusing on particular items. These aspects cannot be investigated with the standard learning paradigms such as stimulus-guided learning or deferred imitation of short sequences.

In this thesis, we developed a learning paradigm in which a *long* sequence of spatial positions is learned, where the sequence is too complex for immediate reproduction. Importantly, the order of sequence acquisition is determined by the subject and is not determined by the stimulus presentation or an external teacher as in stimulus-guided learning.

The aim of this thesis is to investigate deferred imitation learning of long sequences and to compare it to stimulus-guided learning. The main general questions addressed are: 1) What are the main characteristic features of deferred imitation learning of long spatial sequences? 2) How are the acquired sequences represented in memory? In order to answer these questions three series of experiments were performed which are presented below in previously published or submitted papers:

(1) The investigation of deferred imitation of long sequences implies the methodological difficulty of assigning a long sequence of reproduced target locations to the stimulus sequence. Learning is instructed with a complex stimulus sequence and the reproduction of the stimulus sequence may be inaccurate and incomplete. A robust method to assign the stimulus reproduction to the original stimulus was not yet available. An assignment algorithm that considers the spatial neighborhood and the order of reproduction was developed for this purpose. This algorithm has been explained and evaluated in the article “A new method to evaluate order and accuracy of inaccurately and incompletely reproduced movement sequences”.

(2) With the newly developed method deferred imitation learning of long sequences was investigated to characterize this particular learning process under various aspects. First the order of sequence-element acquisition was assessed. Then, the question whether the acquired sequence was only temporally acquired or retained for a longer period was assessed with retention tests. Further, the effector dependence of the acquired memory (cf. Section 1.4.2) was assessed by learning in two different learning modes (saccadic eye movements and manual pointing movements) and by transfer tests (eye movements to hand movements and dominant to non-dominant hand). At last, the question whether the positions are stored as absolute positions or a offsets from previous target positions (cf. Section 1.4.4) was investigated.

(3) The three main results reported in the second article showed that 1) subjects acquired the memorized sequence by starting at the first position and by systematical proceeding to subsequent positions, 2) the sequences were stored in long-term memory, and 3) end point control seemed to be more important than amplitude control. These results led us to the further question whether single positions in such spatial sequences can be modified independently. This question was addressed by exchanging two targets of a well known sequence in the deferred imitation learning task. The guiding hypothesis in this experiment was that the exchange of targets does not influence the accuracy and variability of preceding and succeeding targets if the movement sequence is stored as long sequences of independent positions.

Further important aspects of motor memory are related to its dynamics, i.e. the development of the reproduction patterns with repeated sequence reproduction without sequence presentation (cf. Section 1.4.3). In order to evaluate the stability and the drift of the sequence we analyzed the temporal evolution of variable and constant error for reproductions without intermediate stimulus presentation.

1.3 Main features of the new learning paradigm

In order to investigate deferred imitation learning of long spatial sequences we developed a new learning paradigm. In this paradigm a long sequence of 20 spatial positions was presented on a graphic tablet with an integrated display. In order to avoid the possibility that discrete spatial positions were verbally recoded (Isaacs & Vargha-Khadem, 1989) these positions were uniformly distributed on the screen. After the sequence was presented it was reproduced by manual pointing[5] in the absence of any stimuli. The sequence length was chosen so that it could not be reproduced on the first attempt. Subjects learned the sequence by repeated presentation and reproduction.

The learning progress was assessed with three different error measures. In order to evaluate these different error measures the stimulus sequence was assigned to the reproduced target positions with an assignment algorithm. This assignment algorithm was a compromise between purely order based assignment and nearest neighbor assignment. The algorithm was designed in such a way that this compromise could be controlled with a well-defined parameter. The *number of omissions* was defined as the number of targets that were not assigned by the assignment algorithm. This measure is an ordinal measure that quantifies how much sequence content was learned (Ghilardi et al. 2009). The *number of order errors* was defined by the number of transpositions needed to sort the reproduced sequence by a sorting algorithm. The *accuracy error* was defined as the mean distance between target position and assigned reproduction. This continuous error measure quantifies the performance of sequence elements (Ghilardi et al. 2009).

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[5] In a variant of the task the sequence was reproduced by saccadic eye movements.

1.4 Theoretical background

1.4.1 Psychological theories

According to Fitts (1964), learning of new skills proceeds in three stages in which the movement production differs and in which different mechanisms are involved. In the *cognitive stage* one starts to learn the movement, partially by using verbal cues. Movement generation in this stage usually requires a high level of attention. In the second stage, the *associative stage*, a transition from verbal, declarative and conscious control to automatic control of movements occurs. In this stage, actions are 'smoothed out', errors are reduced and actions can be executed faster. The verbal mediation is reduced and actions with many components begin to be grouped into one unified action. In the third stage, the *autonomous* or *automatic stage*, the movement can be executed quickly with little conscious involvement, e.g. skilled typists are able to repeat the spoken words while typing (Shaffer, 1975).

The earliest psychological theory of movement generation was the *response chaining theory* (Washburn, 1916). It states that sensory and proprioceptive consequences of a movement are used as a trigger for the successive movement. Through the association of several movements a complex movement sequence is encoded in memory (see Adams, 1984 for a review). This theory of movement generation does not imply any abstract representation of movement plans and only relies on the well established stimulus-response framework developed in classical and operand conditioning. The importance and ubiquity of abstract movement plans in behavior was emphasized by Lashley (1951) at the Hixon Symposium, which marked a shift from behavioral psychology to cognitive psychology and an emphasis on internal processing mechanism. He rejected chaining theory on the ground that 1) movements can be executed without sensory feedback, 2) the latencies between the production of single sequence elements are too short and 3) specific error patterns suggest the presence of abstract plans for movement generation. Since then, reflex chaining has not been a prominent theory for sequential movements any more and is nowadays generally rejected (Adams, 1984). However, movement generation has been modeled within the framework of recurrent neural networks that do not include an explicit representation of abstract movement plans (Jordan, 1986; Botvinick & Plaut, 2006). These models are sometimes referred to as modern incarnations of the chaining theory (Henson, 2001).

There are further psychological theories that have been proposed in the field of motor learning and control. Adams (1971) proposed the closed-loop theory in which a perceptual trace[6] is stabilized trough feedback derived from knowledge of results. A further component of this theory is a memory trace that corresponds to an abstract motor program and is responsible for the selection and initiation of actions. A further theory on motor learning is Schmidt's schema theory (Schmidt, 1975) in which abstract motor programs are the key idea. With this theory Schmidt emphasizes the generalization of motor actions into abstract motor programs. These motor programs[7] represent a class

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[6] A perceptual trace represents the expected sensory and proprioceptive feedback of a specific movement.

[7] The abstract motor programs are called schemata, following the idea of perceptual schemata which are

of movements that can be parameterized. For example, a basketball player is able to throw a ball from positions that he did not practice. From the view of schema theory he developed a parameterizable schema of the throwing movement. A further notable theory of motor learning is developed from a dynamical systems point of view (Zanone & Kelso, 1992). This theory of motor learning was developed based on the bimanual coordination task (Kelso, 1984) in which movement patterns are characterized by the relative phase of the index fingers. This approach to learning emphasizes the individuality of single subjects, as opposed to classical approaches that characterize learning by a performance curve averaged across a subject population. Learning is interpreted as a qualitative change in the intrinsic dynamics of the subject.

1.4.2 Representation of sequences

Since Lashley's (1951) elaboration on the problem of serial order in behavior, the notion that movement sequences are hierarchically organized is generally accepted. This hierarchical organization is exemplified in natural language production. On the lowest level, speaking is a highly complicated motor act that requires the coordination of the lungs, the glottis, the larynx/tongue and the vocal tract. At a higher level, several movements are grouped into phonemes, which in turn, are grouped into syllables, words and sentences. The hierarchical organization of movement sequences is also evident in writing. Bernstein (1947; cited in Keele, Cohen & Irvy, 1990) investigated the effector-dependence of writing and instructed subjects to write a signature with different effectors, such as the dominant hand, the foot and the teeth (Figure 1.2). Throughout all these movement productions subject-specific characteristics suggest that the signature is represented in an abstract, widely effector-independent manner. However, the signatures differ in legibility when produced with different effectors. Thus, the skill of writing has effector-independent components in addition to effector-specific components that may differ between more or less suitable effectors (e.g. hand and teeth) and because of different amounts of practice (e.g. dominant and non-dominant hand).

Evidence for hierarchical representation has also been found in the error properties of typing (Rosenbaum, Weber, Hazelett & Hindorff, 1986), speech production (Dell, 1986) and finger-tapping (Rosenbaum, 1991). One of the most prominent examples for error patterns indicating hierarchical representation is the finding that speech errors rarely occur across syntactic boundaries (Garett, 1975), e.g. nouns are rarely exchanged with verbs and are rather exchanged with other nouns. Another source of evidence for hierarchical representations is timing. Longer pauses between specific items of a sequence indicate the grouping of items into chunks (Verwey, 1996). Chunking is an ubiquitous phenomenon found in memory research (Miller, 1956), which does not have a formal operational definition. Typically, it describes the grouping of several items in order to increase storage and retrieval capacity. In the 2x10 task (Sakai, Kitaguchi & Hikosaka, 2003) chunking is indicated by longer movement times at chunk beginnings.

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abstractions of percepts (Bartlett, 1932). Schmidt introduced this concept from cognitive psychology into the field of learning. Because of the importance of this concept in this theory, it is named 'schema theory'.

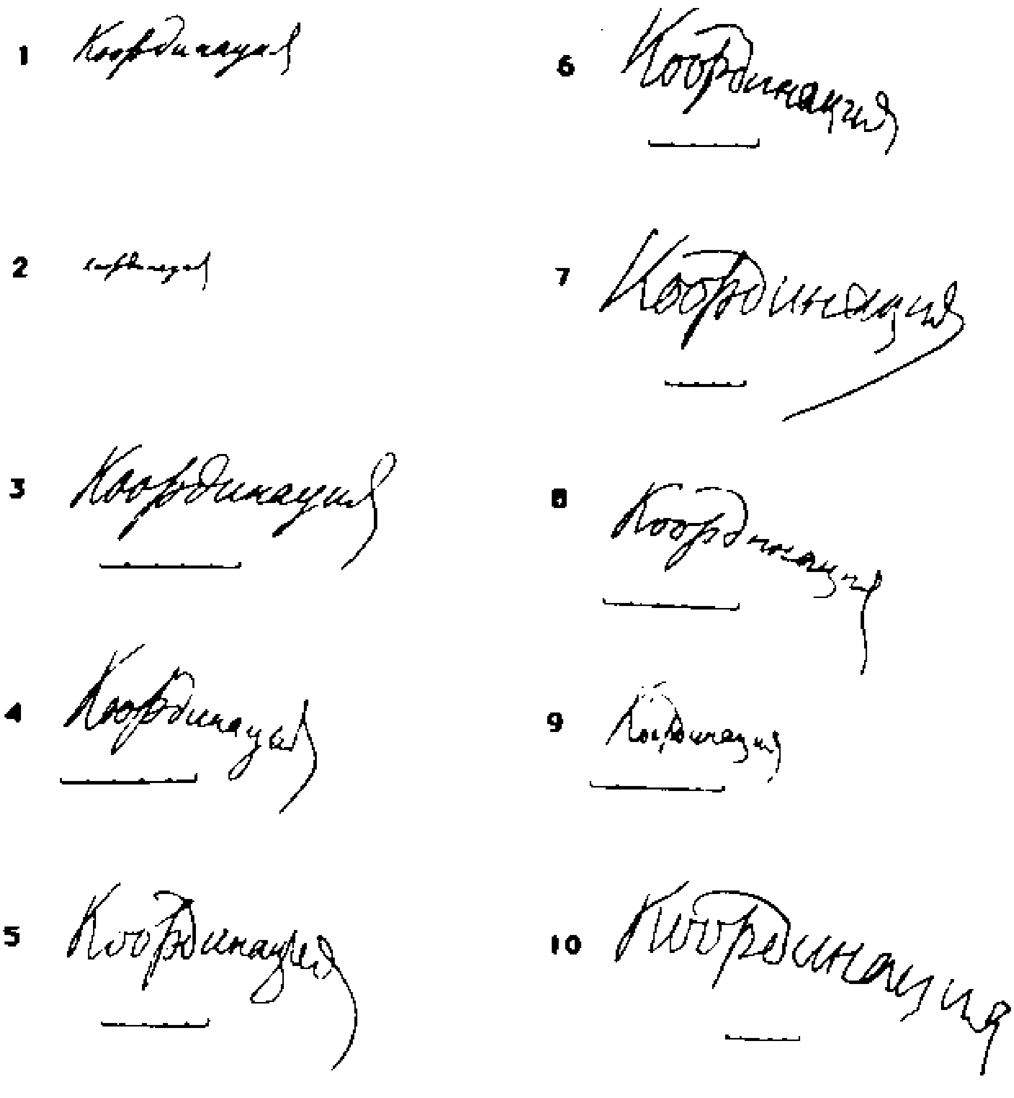

Figure 1.2: Examples of different handwritings with different effectors. The signature was drawn with the dominant hand (1 and 2) in different sizes, with an immobilized hand (3), with the pen attached to the arm (4 and 5) and to the elbow (6), with the right foot (7), teeth (8) left hand (9) and left shoe (10). Source: Keele, Cohen and Irvy 1990.

The behavioral importance of these chunks was shown by testing the performance on shuffled sequences that either preserved or destroyed the chunking structure. When the chunking structure was preserved the performance was superior to the performance with destroyed chunking structure. This finding suggests that each chunk is processed as a single memory unit. Chunking in movement sequences may also be indicated by error propagation (Bock & Arnold, 1993; Ditterich, Eggert & Straube, 1998). If directional errors of single movements can be measured for the produced sequence, correlations between errors of successive items may indicate a grouping of items. Ditterich, Eggert and Straube (1998) found that grouping plays a role in the production of short sequences of saccades.

Hierarchical representations imply that not sequences of concrete motor commands, but abstract nodes are stored for complex movement sequences. These different properties are 1) the metric information that defines the memorized goal position of single actions and 2) the sequential context that defines the order of these actions.[8] In most computational models these two properties are represented in distinct mechanisms (Henson, 2001; Sandamirskaya & Schöner, 2010)[9]. Acquisition of metric information is indicated by a continuous measure of accuracy. The buildup of sequential context is indicated by an ordinal measure that quantifies the number of acquired items, corresponding to the acquisition of an abstract movement plan.

1.4.3 Dynamics of memory representation

Memory representations are not necessarily stable but may change over time. This phenomenon was first investigated by Bartlett (1932) with a serial reproduction protocol. In this protocol a short story and a figure was presented to a subject. The recalled story and figure were presented again as a stimulus for the next reproduction and this process was repeated. At the beginning, both the image and the story showed large changes between reproductions. After several repetitions the changes between successive reproductions became smaller and the reproductions reached a steady state. Nevertheless, both image and story showed small variations. These variations around a steady state were interpreted as a random fluctuation around a stable reference.

The development of memory for spatial configurations was analyzed by Giraudo and Pailhous (1999) by presenting a configuration of 12 dots. The variance and the accuracy of the repeated reproduction were analyzed independently. With repeated production the variability reached a subject-dependent threshold, whereas reproductions tended to converge to patterns which had simple geometric relations. The patterns had a tendency to converge to similar patterns across subjects. This was interpreted as a convergence

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[8] These terms are not clearly defined in the literature and many alternative terms have been introduced for these concepts (Wilde & Shea, 2006).

[9] Whether sequential context and metric information are stored in separate mechanisms or in a distributed fashion is subject to an ongoing theoretical debate (Bowers, Damian & Davids, 2009; Botvinick & Plaut, 2009). A model that is inspired by neurophysiological findings (Rhodes et al., 2004) incorporates the hypothesis that sequential context and metric information are stored separately in the early learning phase and become represented in a distributed fashion in later learning phases.

to figures that follow Gestalt rules. The dynamic aspects of the memory representation of long sequences of pointing movements were investigated in Drever, Straube & Eggert (2011b, chapter 4)

1.4.4 Control strategies for sequence reproductions

Two hypothetical control strategies have been proposed for aimed arm movements. In the first control strategy the desired arm position at the end of the movement is the controlled variable. According to the equilibrium point control hypothesis (Feldman, 1966; Polit & Bizzi, 1979), this end point control strategy is implemented by controlling the length-tension muscle properties of the arm muscles so that the equilibrium point of the arm is moved to the goal position. With the *end point control strategy* errors of sequential arm movements do not accumulate since each end position is controlled independently of the previous movement. In the second control strategy the amplitude of the arm movement is controlled so that the arm moves the desired extent (Schmidt et al., 1979). Evidence for this *amplitude control strategy* was found based on the correlation between errors of successive arm movements (Bock & Eckmiller, 1986). In further studies, Bock and Arnold (1993) showed that both end point and amplitude control contribute to sequences of arm movements.

A similar distinction has been provided by Desmurget et al. (1997) based on the distribution of end point positions of pointing movements. Amplitude controlled movements tend to produce elliptical endpoint distributions, where the axis of highest variance is parallel to the movement direction. In contrast, end point controlled movements produce circular distributions that have no preference for the direction of variability. Desmurget et al. (1997) found that movements constrained by a manipulandum involve control strategies that produce straight path movements with an amplitude control strategy, whereas unconstrained movements that were not programmed to follow a straight line path involve end point control strategies.

There is a close relationship between the control strategy of sequence reproduction and the memory representation of a spatial sequence. The control strategy is defined by a certain error type, i.e. end position error or the error of the amplitude. These errors can only be minimized if the desired value of the control variable (the reference) is represented. Therefore the desired end position has to be represented in memory if the memorized sequence is reproduced under the control of end position, whereas the movement amplitude has to be represented for the amplitude control strategy. The analysis of error accumulation and end point distribution might give valuable insights into the control mechanisms involved in pointing movements and may provide further insight into the representation of spatial positions in long-term memory. This analysis has been performed in Drever, Straube & Eggert (2011a, chapter 3).

1.4.5 Mechanisms of sequence memory

Rhodes et al. (2002a, 2004) have developed the N-STREAMS model, a conceptual model of the mechanisms involved in sequence learning which is related to anatomical structures

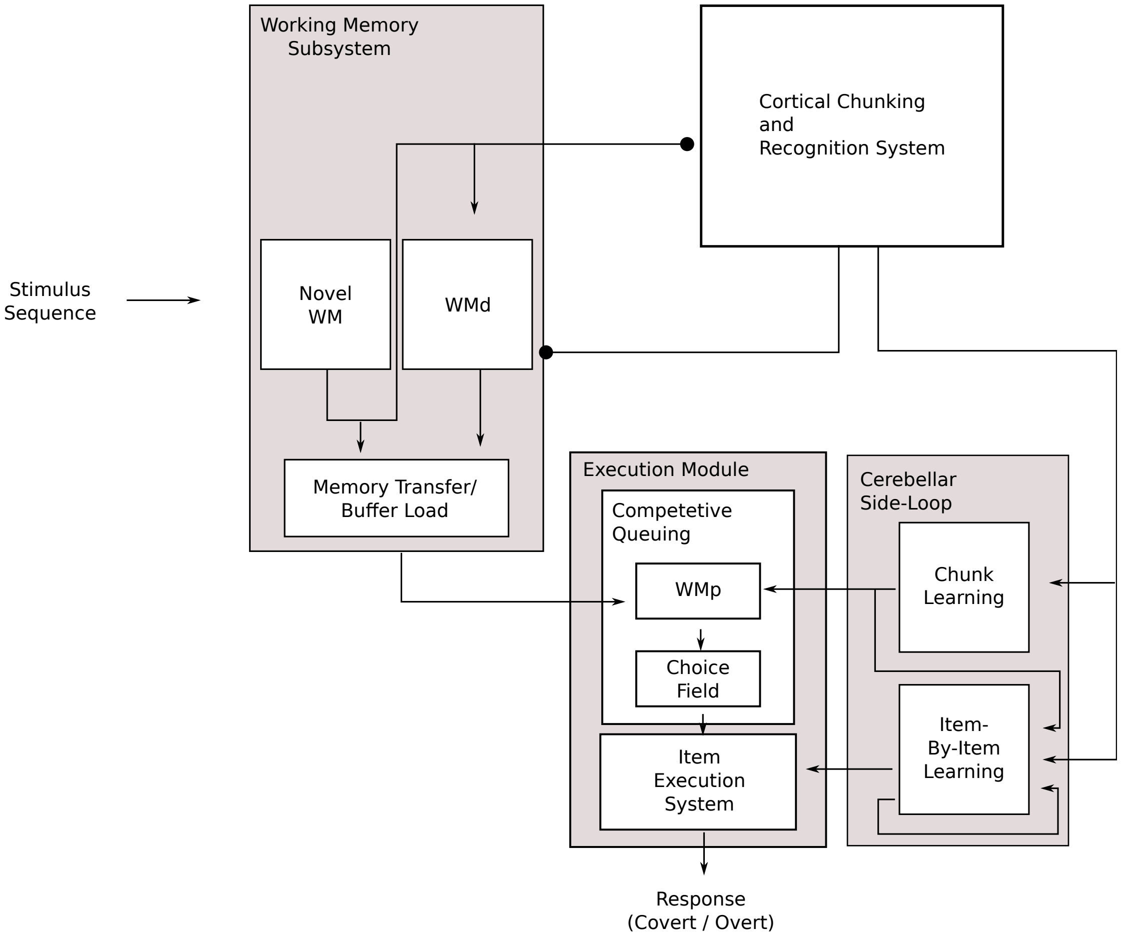

Figure 1.3: The N-STREAMS (adopted from Rhodes et al., 2004). The core of the model is the execution module that executes a movement plan. Movement plans can be provided by the working memory, either directly generated from the stimulus sequence (Novel WM) or recalled from the chunking module (WMd). Further, movement plans can also be provided form the cerebellar side-loop. Connections that are modifiable through learning are indicated with a dot. The connection from WMd to the cortical chunking module is modified to learn the recognition of chunks. The connection from the working memory to the cortical chunking module is modified in order to learn chunk expansions in WMd.

(Figure 1.3). We adopted and extended the N-STREAMS model in order to hypothesize which mechanism might be involved in deferred imitation learning of long spatial sequences. The N-STREAMS model accounts for a large range of effects found in sequence learning studies. The model focuses on the production of short sequences as occur in typing tasks. Learning mechanisms that account for the buildup of a long sequential context, which is the main focus of our learning task, are not addressed. Further, the model addresses stimulus-guided learning and not deferred imitation learning. Therefore we conceptually extended the model with an attentional mechanism and a direct recall pathway from the chunking memory as explained at the end of this chapter. Figure 1.3 shows the essential elements of this model. The extension of this model are eleborated in the general discussion (chapter 5).

Sequence production is performed by the *execution module* based on a movement plan that defines the sequence to be produced. The core of the execution system is the Plan working memory (WMp), a competitive queuing mechanism (Grossberg, 1978) that retains a representation of the movement plan and a choice field that specifies which item is produced next. The chosen movement is executed by the *item execution system.* Prior to execution the movement plan has to be generated, either based on the perceived stimulus sequence or based on memorized sequences. The *working memory subsystem* produces a movement plan of the incoming stimulus sequence for the sequence execution module when the system is in a stimulus-response mode. Unknown stimulus sequences are registered in the Novel WM component and transferred to the execution module for sequence production.

The working memory is also capable of loading previously learned sequences from long-term memory of the *cortical chunking module* into working memory. Previously learned sequences are recognized by the cortical chunking module based on the first few items. The remaining sequence is predicted from these first items and a movement plan is generated in the declarative working memory (WMd) and executed via the execution module. This mechanism can explain anticipated movements in stimulus-guided learning paradigms.

The *cerebellar side loop* learns highly automated sequences in effector specific coordinates during later learning phases. Based on neurophysiological findings (Dum & Strick, 2003) it is divided into two mechanisms. The cerebellar chunking mechanism provides a movement plan that can be loaded directly into the execution module based on a context signal from the cortical chunking mechanism. Thus, when the cortical chunking mechanism recognizes a sequence it not only sends a movement plan to the working memory, but also sends a context signal to the chunking module. Sequence production triggered by the context signal in the cerebellar side loop is faster than the execution of sequences via the cortical working memory component. After learning, sequence chunks can be loaded faster from the cerebellar side loop than from working memory. Further, the cerebellar side loop is, in contrast to the working memory, not subject to the sequence length effect on latency. Thus, the execution of learned sequences from the cerebellar side loop of well learned sequences explains the disappearance of the sequence length effect on latency with extensive training. The item-by-item learning mechanism is capable of learning temporally scalable sequences based on item to item association (Rhodes &

Bullock, 2002b).

2 A new method to evaluate order and accuracy of inaccurately and incompletely reproduced movement sequences

2.1 Abstract

Studying imitation learning of long sequences requires the evaluation of inaccurately and incompletely reproduced movement sequences. In order to evaluate the movement reproduction, it has to be assigned to the original stimulus. We developed an assignment algorithm that considers the Spatial Neighborhood and Order of reproduction (SNOA). To evaluate the features of this analysis it was applied to human performance during learning of long pointing sequences under two conditions: stimulus-guided reproduction with high spatial accuracy and imitation learning with low spatial accuracy. The results were compared with a simple assignment considering Spatial Neighborhood only (SNA) and with a Manual Assignment (MA). In the stimulus-guided reproduction the error measures did not differ between the algorithms. In contrast, with imitation learning, SNOAandMAgenerated higher estimates of order and omission errors than SNA. The results show that SNOA can be used to automatically quantify the similarity of both movement structure and metric information between long target sequences and inaccurate and incomplete movement reproductions.

2.2 Introduction

Human behavior comprises many skills, such as writing, playing the piano or dancing a waltz. All these skills are composed of sequential actions. It is very likely that these complex movement sequences are not learned at the very first attempt, but that a movement plan gradually builds up. Since Lashley's classic work (1951) there has been agreement that the order of movement elements may be independent of the nature of the movement actions. Many paradigms to investigate movement sequences have emerged in the past decades. In these paradigms, subjects are either challenged to reproduce short sequences by saccadic eye movements or button presses (Ditterich, Eggert, & Straube, 1998; Sternberg, Monsell, Knoll, & Wright, 1978), or long sequences that are trained as reactive movements to visible stimuli and become internally generated after learning (Ghilardi, Moisello, Silvestri, Ghez, & Krakauer, 2009; Hikosaka, Rand, Miyachi, & Miyashita, 1995; Wilde & Shea, 2006). These paradigms can be divided into imitation learning, where

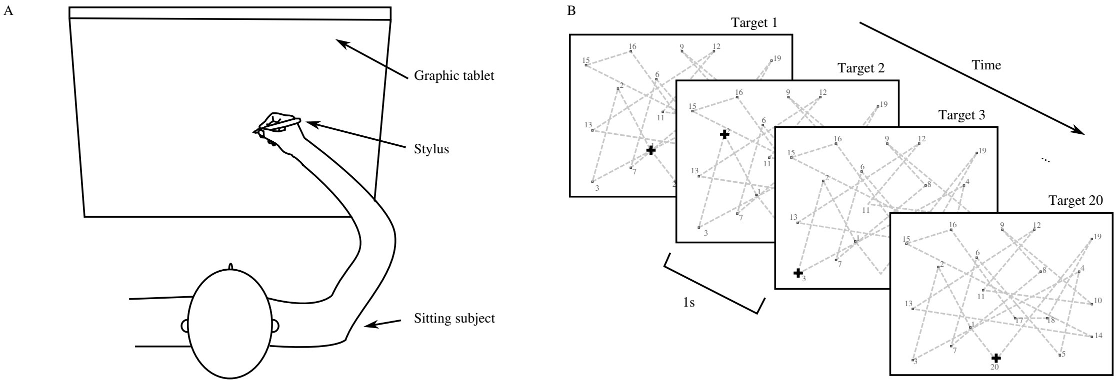

Figure 2.1: Illustration of the learning task. A) The subjects sat in front of a graphic tablet that featured a display for stimulus presentation. The presented target locations were reproduced by pointing with a stylus. B) The training phase of a trial. Twenty target positions were presented one after another with an inter-stimulus interval of 1 s. The disappearance of the last cross was the go-signal for the reproduction

a stimulus is presented and imitated after presentation, and stimulus-guided learning, where the reproduction occurs concurrent with the presentation. Evaluating the reproduction performance in these paradigms requires the assignment of reproduced positions to target positions; a task that differs widely in complexity.

When the stimulus is reproduced by discrete button presses, the assignment of reproductions to targets is trivial (e.g., Hikosaka et al., 1995; Sternberg et al., 1978). Assigning continuous sequence reproduction is more problematic, especially in the presence of order errors and omissions. Consider the task illustrated in Fig. 2.1. In this task a long sequence of stimuli is presented and has to be reproduced in the absence of any stimuli after presentation. In this task the pointing movements have to be assigned to the original locations of the stimulus. For short sequences, this problem can be solved adequately by a simple nearest neighbor assignment (Ditterich et al., 1998). Ambiguous trials that contain order errors or omissions are simply omitted for further analysis.

Most learning paradigms for long sequences are stimulus-guided, thereby allowing an accurate reproduction. With such an accurate reproduction the assignment can be implemented by a nearest neighbor search. In contrast, if the number of reproduced positions is much smaller than the number of target positions, or if the reproduction accuracy is low with respect to the target distances, these methods are not suitable, e.g., during the early phase of imitation learning of long pointing sequences. This is probably one reason why sequence reproduction under these conditions is rarely studied. Inaccurate pointing reproductions are also expected when imitation learning of sequential movements is examined in patients with movement disorders (cerebellar lesions) or memory impairments (hippocampal lesions). Studies focusing on the theoretical issue of how metrical and order information is acquired have focused on stimulus-guided learning (Ghilardi et al., 2009; Wilde & Shea, 2006). Investigating the frequency of order errors during the early phase of imitation learning may give further insight into these theoretical issues.

We investigated imitation sequence learning in a paradigm in which the sequence was internally generated without guiding stimuli. To solve the assignment problem we developed a new algorithm that takes the order of reproduction into account. This Spatial Neighborhood and Order considering Assignment (SNOA) is composed of the longest continuous chunks that minimize the mean distance between targets and assigned reproductions.[1] To illustrate the features of the assignment it was contrasted with the nearest neighborhood assignment, which does not consider the order of reproduction (Spatial Neighborhood considering Assignment, SNA). These two assignments were first compared under a condition in which targets were visible during reproduction and pointing accuracy was high. In this case SNA should achieve a good assignment and SNOA should not deviate from this assignment. In the second condition the targets were reproduced in the absence of any stimuli. In this case inaccurate and incomplete reproductions have to be assigned to the target sequence during learning. We investigated whether the SNOA and SNA assignments deviated under these circumstances and evaluated the plausibility of the assignments by comparison with manual assignments.

2.3 Material and methods

2.3.1 Procedure

Ten healthy subjects participated in the experiments (mean age: 33, range: 28–51 years). They gave informed consent before participating in the study. The study was performed in accordance with the Declaration of Helsinki and was approved by the local ethics committee. The subjects sat in a dark room in front of a graphic tablet that featured an integrated computer display (Fig. 2.1a, WACOM Cintiq21UX, 43.2 × 32.4 cm). The viewing distance between subject and display was about 30 cm. A single experimental trial consisted of a presentation phase and a reproduction phase. During the presentation phase, a long pseudo-random sequence of 20 positions was presented with a white cross (size: 1 × 1 cm) that stepped through the sequence with a fixed inter-target interval of 1 s (Fig. 2.1b). Subjects were instructed to track the target with eye movements, but they were not allowed to perform manual pointing during this presentation phase. After all 20 targets had been presented, the initial position was shown for 1 s, and the cross disappeared. The disappearance of the cross was the go-signal to start the reproduction. Subjects were instructed to reproduce as many target positions as accurately as possible by manual pointing with a stylus on the graphic tablet. They were asked to lift the pen between successive pointing movements. They were instructed to produce the sequence in the correct order, but were allowed to continue production after omissions or order errors occurred. The subjects indicated the end of the reproduction by pressing a button when they could not recall any further target positions. The reproduction was performed under two different conditions. In the first condition all targets were simultaneously visible

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[1] The MATLAB implementation of SNOA can be downloaded at http://www.nefo.med.uni-muenchen.de/~teggert/SNOA/JBRM.tar.gz.

(‘visually guided’; V). As each target was reproduced, its shading changed in order to provide the subject with information about which targets had been already reproduced. In the second condition, the sequence had to be reproduced on a blank screen (‘imitation’; I). All events, target positions, pointing positions (accuracy <1 mm), and the button presses were recorded on a central recording system REX (Hays, Richmond, & Optican, 1982) for later analysis.

The sequence length was chosen in such a way that a complete reproduction on the first attempt was impossible, since the focus of the study was to investigate inaccurate and incomplete sequence reproduction. In one experimental session, 25 trials (alternating presentation and reproduction) were repeated with the same sequence in order to allow subjects to learn the whole sequence.

The target sequences contained only a minimal amount of geometrical regularity since the target positions were chosen randomly from a quadratic area (28× 28 cm). Some constraints were introduced in order to avoid spatial clustering of target positions: The minimal distance between targets was 4 cm. Only one additional position was allowed within a radius of 6 cm around each target. Further interactive inspection assured that target sequences used for training did not contain apparent geometrical features such as three points on a line or four points forming a rectangle. In both conditions subjects learned a new sequence that they had not seen before.

2.3.2 Analysis

The first step of error analysis was the assignment of reproductions to the original target locations for each trial. SNA was performed as follows: for each target the nearest reproduction was found and assigned to the corresponding target. Reproductions that were further away from any target than the minimal distance between targets were not assigned.

SNOA was performed by an algorithm in several steps. The assignment was composed of continuous subsequences of target positions to which reproductions were assigned. These subsequences are called ‘chunks.’ In summary, the algorithm first searched for the longest chunk. This chunk had to minimize assignment costs, as defined later. When this chunk was found, the reproductions and targets belonging to this chunk were removed and the same procedure was applied to the remaining target and reproduction locations until no further assignments were found.

Chunks were found with a linear-order-preserving assignment algorithm (Scott & Nowak, 2006). The algorithm performed an order-preserving assignment of reproductions to target positions by minimizing assignment costs. These costs were defined as the sum of the distances between assigned reproductions and targets and the number of non-assigned targets weighted by a factor ϵ.[2] Thus, in the linearorder- preserving assignment algorithm, a reproduction with a distance larger than ϵ from the nearest target was never assigned.

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[2] ϵ was chosen to be the minimum distance between targets (5.5 cm). Note that ϵ could also be chosen adaptively, e.g. by the asymmetric Hausdorff distance defined by the maximum of minimal target reproduction distances.

To find the longest chunk the linear-order-preserving assignment was applied to all continuous subsequences of targets with a given length. The algorithm started with the full target sequence and proceeded systematically to all shorter subsequences until at least one of these continuous target chunks was completely assigned by the Scott-Nowak algorithm. This assignment defined the longest chunk. If several chunks of the same length were completely assigned, the longest chunk was defined by the matching with the minimal costs.

After the longest chunk was found, the assigned targets and reproductions were removed from the original target sequence and reproduction sequence respectively. Then the algorithm recursively started to search for the next longest chunk. This procedure was repeated until no further assignments were found.

Note that even though this algorithm preserves the order within each of the chunks, it is able to detect any order errors between chunks. This strategy is computationally much more efficient than any combinatorial optimization procedure because of the large number of possibilities to assign reproductions to targets. The linear-ordered assignment algorithm adopted from Scott & Nowak (2006) is a generalization of the efficient dynamic programming algorithm proposed by Levenshtein (1966). Thus, the assignment can be solved with little expenditure of time on a modern computer.

The SNOA assignment was developed to mimic the tendency of human observers to incorporate the order of recall when performing a subjective assignment. To confirm this, the 25th reproduction of the imitation condition (I) of eight subjects was manually assigned by four human evaluators (Manual Assignment: MA). The evaluators were familiar with the experiment but had no extensive training on assignment. All evaluators were told that the subjects had three different error possibilities: number of omissions, accuracy error and order errors. The target sequence and reproduction sequence were illustrated by static line drawings with numbered vertices, superimposed on a computer monitor. Each reproduction vertex either had to be classified as an outlier or had to be assigned to a target vertex in a bijective manner.

Based on SNA, SNOA or MA, three different error measures were defined. The omission error was defined by the number of non-assigned targets. The accuracy error was defined by the mean distance between assigned targets and reproductions. The order error was defined by the number of transpositions that was needed to sort the reproductions into a linear ascending list with a shell sort algorithm. The shell sort algorithm achieves sorting with a very small number of pairwise exchanges (Pratt, 1972). To simplify references to an error based on a specific assignment method, its name will hereafter be attached as a prefix to the error name, e.g., SNA accuracy error is the accuracy error evaluated based on SNA.

2.4 Results

2.4.1 General observations

Generally, no subject was able to reproduce the sequence after the first trial, either in the visually guided or in the imitation condition. Most subjects started with the reproduction

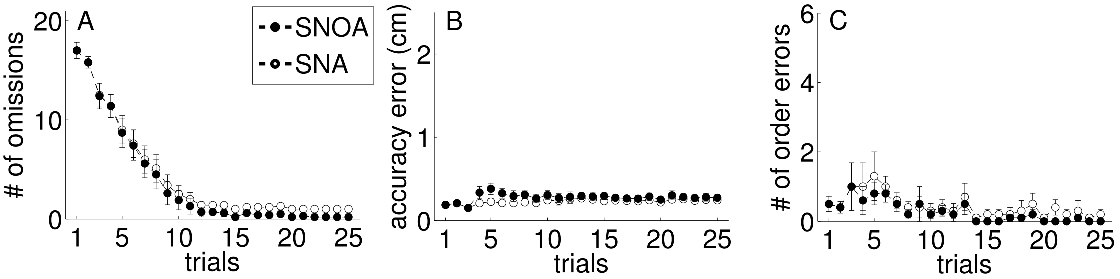

Figure 2.2: Serial position curves illustrating the learning process. The recall probability of target positions as a function of serial position. The first trials are indicated by light gray and later trials by darker gray. (A) Subjects started in the beginning to recall early target positions and advanced to later target positions. Learning occurred from the beginning to the end of the sequence. (B) After re-exposition to the learned sequence subjects were able to recall most of the positions of the sequence in the first trials. Omission occurred mostly at the end of the sequence.

of only few targets, which in general were at the beginning of the sequence and increased the number of reproductions after each learning trial. In this way the sequence was learned from the beginning to the end. The time until subjects were able to reproduce the whole sequence varied from subject to subject and was much shorter in the visually guided condition. Note that the accuracy errors and order errors at the beginning of learning would have been much higher if subjects had been forced to reproduce the whole sequence.

2.4.2 Subject performance during visually guided reproduction

The resulting number of omissions, the accuracy error and the number of order errors under visually guided reproduction conditions (V) are shown in Fig. 2.2. Under this condition the error evaluation based on SNA and on SNOA did not differ substantially. In this paragraph, the reported subject performance is based on SNOA, and differences between SNA and SNOA are reported in the next paragraph. The main learning progress was reflected in the number of omissions. Subjects started with 16 omissions on average, and the performance saturated at a few omissions after 11 trials (0.2 ± 0.4 omissions). Thus, subjects were able to reproduce the whole sequence after the 11th trial. Pointing to the visible target locations was very accurate throughout the whole experiment (0.3 ± 0.1 cm). Before the tenth trial about one order error occurred on average. After the tenth trial, order errors occurred very rarely (0.5 ± 0.5 omissions).

2.4.3 Differences between SNA and SNOA

Before that tenth trial, the number of omissions did not differ between the measures. After the tenth trial, SNOA indicated slightly fewer omissions than SNA (Fig. 2.2a).

The average number of omissions after the tenth trial was 1.2 ± 0.4 (SNA) and 0.5 ± 0.4 (SNOA). The accuracy of pointing did not change over time when evaluated with the SNA algorithm (Fig. 2.2b). The SNOA algorithm indicated a small temporary decrease of the accuracy during trials 5-6. The number of order errors was low throughout the whole experiment and was only slightly lower for SNOA in trials 5-6. Otherwise, the number of order errors did not differ between SNA and SNOA (Fig. 2.2c), which was expected for the visually guided condition.

2.4.4 An illustrative example of the differences between SNA and SNOA

The differences between SNA and SNOA are illustrated with an example in Fig. 2.3. It shows a detail of the reproduction and assignment of the 6th trial of one subject. In this sequence, target 14 is close to target 5. The subject reproduced the sequence 4-5-6 correctly, but accidentally the reproduction of target 5 is spatially closer to target 14 than to target 5. SNA assigns reproduction 5 to the spatially closer target 14, whereas SNOA correctly assigns reproduction 5 to target 5. Thus, SNOA judges reproduction 5 as an inaccurate reproduction of target 5 rather than an accurate reproduction of target 14. In contrast, SNA judges the reproduction as a confusion of target 14 with target 5. The frequency with which SNOA judged three consecutive reproductions as a continuous sequence and SNA did not was 2.09 times per trial on average.

2.4.5 Subject performance during imitation

The number of omissions, the accuracy error and the number of order errors when subjects reproduced the sequence on the blank screen (condition I) are shown in Fig. 2.4. In this paragraph, the reported subject performance is based on SNOA. The differences between SNA and SNOA are reported in the next paragraph. The main learning progress was reflected in the number of omissions. Subjects started with 16 omissions on average, and the performance saturated at about 2 omissions after 15 trials. In condition I the number of trials needed to reproduce the whole sequence was larger and when learning saturated the number of omissions was higher than in condition V [number of omissions in the last trial: 1.5 ± 1.6 (I), 0.2 ± 0.4 (V), Fig. 2.4a]. The accuracy error was constant at about 2 cm throughout the whole experiment. Pointing was much more inaccurate than in condition V (Fig. 2.4b). On average, the number of order errors started below one, increased to two and finally decreased again to below one order error (Fig. 2.4c).

2.4.6 Differences between SNA and SNOA

The number of omissions was higher when the analysis was based on SNA. The final performance saturated at five omissions as opposed to the two omissions indicated by the SNOA-based analysis. The accuracy error was almost constant with both assignments, but was lower for the SNA-based analysis. The number of order errors started similarly to the SNOA-based order errors, but instead of a final decrease, the SNA assignment indicated that the number of order errors increased and reached a final value of more than two.

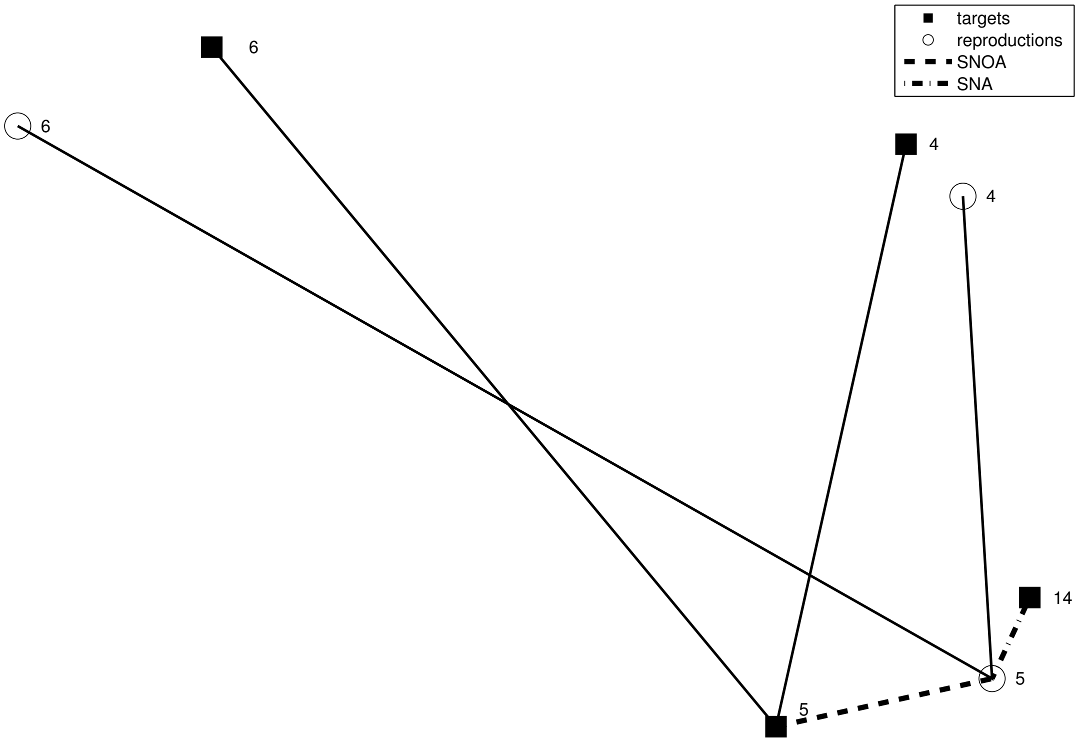

Figure 2.3: Illustration of the assignment problem with inaccurate and incomplete reproductions. Targets 5 and 14 are spatially close. The reproduction of target 5 is closer to target 14 than to target 5. In this case SNA produces a false order error, whereas SNOA favors correct order at the expense of the accuracy error that becomes only slightly larger.

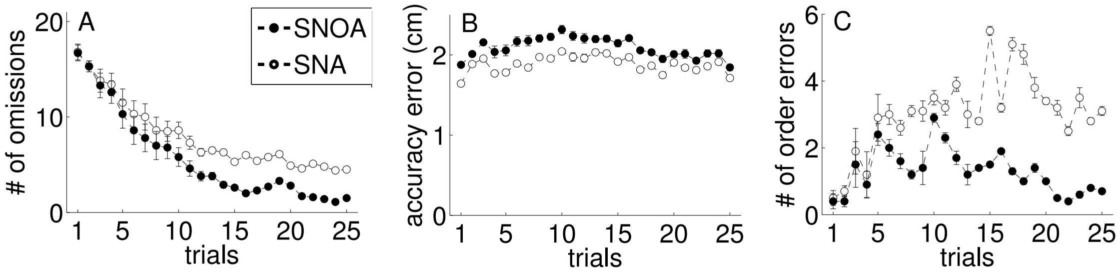

Figure 2.4: SNA produced higher estimates of omissions and order errors than SNOA. Time courses of the mean error measures (±SE) in the imitation learning condition (condition I), pooled across ten subjects. The analysis is either based on SNOA (*filled circles*) or SNA (*circles*)

2.4.7 Comparison of manual assignment, SNA and SNOA

The comparison between the manual assignment SNA and SNOA is presented in Fig. 2.5 for eight individual subjects. Compared to MA and SNOA, SNA produces more order and omission errors in each of the eight subjects. For all subjects the SNA number of omissions was higher than MA and SNOA omissions. In four subjects the number of omissions did not differ between SNOA and MA, and in four subjects it was higher in SNOA than in MA. The mean number of omissions across the eight subjects was 0.7 ± 0.3 (MA), 4.5 ± 1.8 (SNA) and 1.5 ± 1.6 (SNOA).

The SNA number of order errors was much higher than MA for six subjects and did not differ for the other two subjects. The SNOA number of order errors differed from MA omissions in only two subjects. The mean number of order errors across the eight subjects was 0.3 ± 0.3 (MA), 3.1 ± 2.5 (SNA) and 0.7 ± 0.1 (SNOA).

The accuracy error was nearly identical for all assignments [mean accuracy error across subjects and evaluators: 2.0 ± 0.1 (MA), 1.7 ± 0.2 (SNA), 1.8 ± 0.3 (SNOA)]. In summary, SNOA mimicked MA more closely than SNA. The strongest differences between SNA and MA emerged in the overestimate of the number of order and omission errors when the evaluation was based on SNA (black and gray bars in Fig. 2.5, MA-SNA).

2.5 Discussion

The new order considering assignment algorithm (SNOA) was successfully applied to a learning paradigm that required subjects to learn and produce a long sequence of continuous target positions. The algorithm was compared under two conditions to the nearest neighbor assignment (SNA) that does not take reproduction order into account. In the condition with visually guided reproduction (condition V), pointing accuracy was high. The error measures obtained from SNOA and SNA showed no qualitative difference. In contrast, during imitation learning (condition I) with low spatial accuracy, SNA generated a higher number of omissions and order errors than the manual assignment MA and SNOA.

2.5.1 Features of the assignment algorithm

The assignment of reproductions to target positions is the crucial step in the analysis of the reproduction performance. The difficulty in this task is to differentiate among inaccurate reproductions, order errors and pointing movements that cannot be assigned to any target. In general, the decision whether an incorrect reproduction is classified as an accuracy error with correct order or as an order error with high spatial accuracy can only be solved by a heuristic assignment strategy. The simplest solution to this assignment problem is the nearest neighbor assignment (SNA). This assignment induces a high number of order errors that increase over trials without guiding stimuli (Fig. 2.4c). Studies in repeated serial recall of word lists showed that order errors tend to decrease during learning (Klein, Addis, & Kahana, 2005). This suggests that the increasing number of

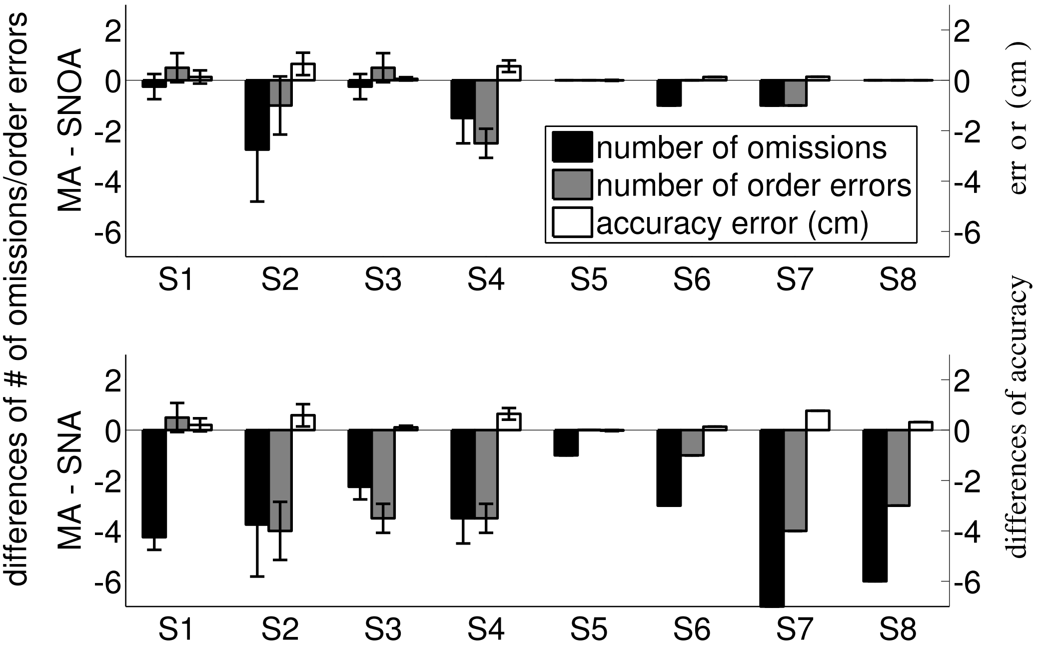

Figure 2.5: Differences between manual assignment (MA) and assignment considering spatial neighborhood and order (SNOA) and assignment considering spatial neighborhood only (SNA). The differences in number of omissions, number of order errors and accuracy error are shown for eight individual subjects. Whiskers indicate the standard deviation across the four manual assignments. For the last four subjects all evaluators agreed in their MA. The number of order and omission errors were clearly overestimated by SNA compared to MA

order errors quantified by SNA is rather an artifact of the assignment than a feature of the learning process.

Another commonly used alternative to evaluate reproduced movements with respect to the original is the so called "average path error," which is defined by the mean accuracy error resulting from purely order-based assignment (e.g., Basdogan, Kiraz, Bukusoglu, Varol, & Doğanay, 2007; Schwager, Anderson, Butler, & Rus, 2007). With this method, a reproduction skipping one or several targets and all subsequent reproductions will be inappropriately assigned and will lead to an inappropriate increase of accuracy error. Thus, this method is, in contrast to SNA, not suitable to evaluate discontinuous reproductions that are subject to omission errors.

SNOA can be considered as a compromise between SNA and purely order-based assignment since SNOA takes the order of reproduction into account by favoring longer continuous chunks reproduced with slightly lower accuracy over isolated assignments with high accuracy. This preference can easily be strengthened by increasing the parameter ϵ (see Methods). This strategy is reasonable under the assumption that spatial information is stored as order preserving chunks rather than as isolated positions. It is important to note that this assignment is able to detect any sort of order error, since the linear ordered assignment could detect the reproduction of a target chunk in any location within the reproduction sequence. Moreover, for the same reason, it also works well independently of whether omissions occur at the beginning, the end or anywhere in the target sequence. It can also handle "explorative" reproductions that are not related to any memorized target location. The algorithm does not assign reproductions that are too far away from the nearest target (threshold ϵ) or reproductions for which all targets within this ϵ-neighborhood are parts of longer chunks. These non-assigned reproductions were classified as explorative reproductions.

It is important to note that the SNOA cannot be considered as an objective standard for evaluating any type of sequential movement reproduction because there is no direct knowledge of the intended movements. However, the SNOA allows inaccurate and ordered reproduction to be favored over accurate and incorrectly ordered reproduction in a well-defined way (by modifying the parameter ϵ). This feature is essential for evaluating inaccurate and incomplete reproductions, since lack of this feature under such circumstances must lead to systematic overestimation of pointing accuracy simultaneously with an inadequately increase of apparent "order errors" (see Fig. 2.3).

The comparison to the manual assignment showed that SNOA performs a more reasonable assignment than SNA when pointing is inaccurate. When targets are visible and SNA is very likely to assign the correct target, the SNOA assignment is nearly identical to SNA (Fig. 2.2). Small differences can be found in early trials in the accuracy error. These differences are related to inaccurate reproductions that are accidentally close to targets with large order distances. These targets are assigned by SNA, ignoring the large order distance. SNOA detects the structural similarity between the target and reproduction subsequences and leads to a more plausible assignment.

2.5.2 Features of the error measures

Many theories in motor learning suggest that the structure of a movement sequence is determined independently of the metrical features of the movement (see Shea & Wulf, 2005 for a review). The acquisition of movement structure is quantified with a categorical measure, and the metrical features are quantified by a continuous measure. With our assignment algorithm the number of omissions can be used to characterize structural similarity between target and reproduction, and the accuracy error can be used to characterize the metrics of the movements. This interpretation is justified under the condition that ordered reproductions of movements are more likely to occur than non-ordered reproduction. In this case, and if the assignment is problematic, an assignment that considers the order, such as SNOA, will always give better results than order-ignoring assignments like SNA. Consequently, the time course of accuracy error and the number of omissions can also be used to quantify the learning progress of metrical features and movement structure, respectively. Additionally, it is possible to quantify whether errors occur in the acquired movement structure by the number of order errors.

The error measures are not fully determined by the assignment. The number of omissions can be defined as a strictly positional, relative order or lenient scoring (Addis & Kahana, 2004). The strictly positional scoring only counts target positions that are recalled in the correct order. The relative order scoring also includes target positions that have the correct predecessor. The lenient scoring counts all target positions that were assigned. In the approach tested here the number of omissions was chosen to be a lenient scoring, because SNOA allowed simultaneous quantification of order errors. The same alternatives (strictly positional, relative or lenient) also exist for the selection of the targets contributing to accuracy error. The problem with the lenient selection applied here is that accuracy measures evaluated on erroneously assigned target reproduction pairs lead to a systematic overestimate of the accuracy. In the SNOA assignment it is less likely that a reproduction is assigned erroneously to nearby targets than in SNA. Therefore, the lenient selection including the non-ordered assignments in the accuracy measure is less error prone than with SNA.

2.5.3 Specificity of the algorithm to imitation learning of long position sequences

Learning and memory of movement sequences have been subject to investigation in several studies. The task presented in this article has the unique feature that a long sequence of unconstrained pointing movements is learned with a delayed reproduction. Generally the application of SNOA is only favorable in tasks that require the assignment of inaccurate and incomplete pointing sequences. This section discusses the application of SNOA to other tasks.

The buildup of the structure and metric information of movement sequences has been quantified simultaneously by Ghilardi et al. (2009) in a stimulus-guided learning paradigm. In stimulus-guided paradigms learning is observed as a shift from stimulus-driven to internally-driven responses. Under these conditions the movements are always directed to the correct target, and pointing accuracy is very high. Thus, the assignment problem does not occur, and a nearest neighbor assignment is sufficient. It has been shown that delayed reproduction resulted in superior acquisition than concurrent reproduction in imitation learning (Weeks, Hall, & Anderson, 1996). This result suggests that different mechanisms and processes might be involved in delayed imitation learning. In order to study these potential differences the acquisition of long movement sequences has to be studied without guiding stimuli. Our assignment algorithm allows the investigation of order errors in imitation learning for long movement sequences.

Visual spatial learning has been assessed in clinical research and diagnosis using the Corsi block-tapping task (Berch, Krikorian, & Huha, 1998). The assessment in this task concentrates on the immediate recall memory span of visual-spatial items. In this task the stimuli, physical objects or locations on a computer screen are visible during reproduction, and the assignment is achieved either by direct physical contact with the object or by simple SNA. With SNOA the assessment can be extended to delayed imitation learning of long sequences. This assessment might reveal typical error patterns in the acquisition of metric and sequential information in patients. These error patterns may further characterize deficits and play a role in clinical diagnosis.

Imitation learning has been studied with sequences of connected pen strokes (Agam, Galperin, Gold, & Sekuler, 2007; Sekuler, Siddiqui, Goyal, & Rajan, 2003). Most likely this task involves different control strategies than our pen-up pointing task (Desmurget, Jordan, Prablanc, & Jeannerod, 1997). Moreover, since previous studies focused on short pen-stroke sequences, order errors were not expected to play a significant role and were not analyzed (Agam et al., 2007). Instead, the assignment was implemented by fitting of local metric deformations of the reproduction in order to match the stimulus sequence. Such pattern-matching techniques (e.g., Burr, 1981) become problematic with inaccurately and incompletely reproduced movement sequences, especially when the number of targets is much higher than the number of reproductions (Chui & Rangarajan, 2003). In contrast, considering the reproduction order makes the assignment robust with respect to outliers (Scott & Nowak, 2006). Thus, even though SNOA is not expected to provide major advantages for the existing pen-stroke tasks, it may become suitable for evaluating inaccurate and incomplete reproduction of long pen-stroke sequences.

Since pattern-matching algorithms fit local deformations, they further assume that the distances between the targets and the corresponding reproductions are linked to the spatial position of the targets. Such systematic deformations may play an important role when the reproduction of the motor sequence is mediated by mechanical devices to which subjects are not fully adapted (mouse pointer, mechanical levers, etc.). However, such systematical spatial deformations probably play a minor role when pointing is performed with the hand in a highly trained working space, as in our paradigm. Even though the SNOA presented here does not consider such deformations, a combination of order considering assignment and fitting of local deformations may be a useful strategy to extend the current approach.

2.6 Conclusion

With the new assignment method presented in this article the investigation of movement sequences could be extended to experimental conditions with inaccurately and incompletely reproduced movement sequences. The comparison to a simple nearest neighbor assignment showed that such an approach is necessary to evaluate these movement sequences under these conditions. The investigation of learning in such situations might induce new theoretical insights into differences between the acquisition of movement structure and the acquisition of metric information. Further, it may reveal learning deficits of patients with movement disorders or memory impairments.

3 Learning deferred imitation of long spatial sequences

3.1 Abstract

Sequence learning has been the subject of research in various paradigms but has not been investigated for learning deferred imitation of long spatial sequences. In this task no guiding stimuli support the sequence reproduction and all sequence information has to be recalled from memory. We investigate this kind of imitation learning with a task in which a long sequence of spatial positions has to be reproduced without guiding stimuli, either by manual pointing or by ocular fixations. Sequences consisting of 20 positions were acquired after only 25 training trials. The persistence of learned sequences over several days showed that the sequence was retained in long-term memory. A transfer test revealed that the learned sequence was independent of the effector. A detailed analysis of the error distributions of pointing and ocular fixations was performed to characterize the guiding control signal. The independence of the variable position errors from the movement directions as well as the lack of error propagation between successive targets suggest that the reproduction in this learning task was guided by sequential positions rather than sequential displacements.

3.2 Introduction

Humans are able to acquire complex movement sequences in a short time. For example, tying a knot can be learned in 10 min and the skill is retained for a long time. We investigate sequence learning in a task where a long sequence of spatial locations has to be reproduced. Since the seminal work of Lashley (1951), the acquisition of sequential actions has attracted a lot of attention in research. It has been investigated in tasks like the Corsi block tapping task (Berch, Krikorian & Huha, 1998), the 2×5 task (Hikosaka et al., 1995), the serial reaction time task (Nissen & Bullemer, 1987) and serial reaching tasks (Ghilardi et al., 2009, Wilde & Schea 2006, Verwery 1996, see Rhodes et al., (2004) for a review). Many of these studies (Verwey, 1996, Rhodes et al., 2004) suggest that generating effector-specific cerebellar chunks which are successively loaded into a motor execution buffer is an essential mechanism for reproducing motor sequences. This theory was supported by Hikosaka et al. (1998) showing that unilateral inactivation of the cerebellar dentate nucleus affected the reproduction of well-learned motor sequences when they were executed with the hand ipsilateral to the inactivation and if this hand was the same used to learn the sequence. In addition, Hikosaka et al. (1998) also observed that the same cerebellar inactivation had no effect on the reproduction with the contralateral hand. This is clear indication for a sequence memory that is not purely effector specific.

It is also known (Hikosaka et al., 1998) that cortical areas (SMA, pre-SMA) are functionally important especially for the acquisition of new motor sequences rather than for reproducing learned sequences. Different parts of the basal ganglia (Miyachi et al. 1997, Hikosaka et al. 1999) are essential for learning or for reproduction of movement sequences. These findings have led to the notion that sequence learning occurs in parallel starting from stimulus anticipation in sensory coordinates and proceeding to effector-specific sequence generation after longer training. The learning tasks of the mentioned studies share the common feature that the movement goal was present during reproduction. Thus, in these learning tasks anticipation is probably achieved by a learning process which associates the next target position with the previous or a few recent target positions (Nakahara, Doya & Hikosaka, 2001). Therefore, this learning approach, hereafter called "stimulus anticipation", offers the possibility to generate long sequences by successive completion of short sensory chunks identified on the basis of the available visual stimuli. In this way long sequences could be generated by completion of only few chunks without need for generating a long sequential context. A series of studies investigated theses "cortical chunking and sequence recognition systems" (Verwey 2001, Rhodes et al., 2004). However, stimulus anticipation and chunking may be less efficient learning mechanisms in the deferred imitation learning task. In this task the stimulus sequence is first presented and reproduced only after presentation (McDonough et al., 1995). In contrast to stimulus anticipation learning, deferred imitation of pointing sequences challenges the buildup of sequential context, especially if the presented sequence is not clearly structured by spatial or temporal grouping. In the past little experimental data has been collected with this type of learning task, especially with long sequences, since the evaluation of inaccurately and incompletely reproduced sequences is difficult.

To solve these problems we have developed a method for error quantification for such experimental tasks (Drever, Straube & Eggert, 2010). In the current study, we will use this method to further investigate imitation learning of long pointing sequences.

This will allow to gain further experimental knowledge concerning a differentiation between different aspects of learning, namely the differentiation between the acquisition of sequential context and the acquisition of metric information (Ghilardi et al., 2009). Until now it is not known whether order errors occur more frequently while learning deferred imitation of pointing sequences. It is also not known whether the acquisition order of sequential context differs from the acquisition order in stimulus anticipation paradigms. Possibly, in deferred imitation, recency and primacy effects, as known from word list learning (Kahana, 1996), may affect the acquisition of both metric information and sequential context. Our previously presented method (Drever, Straube & Eggert, 2010), which is able to simultaneously quantify both of theses aspects, was especially developed for these questions.

A further question addressed by the present study is whether deferred imitation learning concerns an effector-specific or a more general spatial memory (Hikosaka et al., 1999). To that aim transfer experiments in which sequences are learned in two motor modalities were conducted. In one the sequence is reproduced by manual pointing and in the other it is reproduced by saccadic eye movements. Transfer tests from the non-dominant hand to the dominant hand and a transfer test from saccadic eye movements to manual pointing movements were conducted in order to investigate the effector specificity of this learning.

The final question of this study concerns the mechanisms used to store the sequence. It may be represented as a sequence of absolute positions or as a sequence of sequential displacements. If the target positions are coded as relative displacements, the control strategy for the reproduction of the sequence would be expected to optimize the straightness of the movements. We adopted the analysis of Desmurget et al. (1997) which allows trajectory controlled movements to be differentiated from endpoint controlled movements. Further, Bock & Arnold (1993) proposed that absolute and displacement coding strategies for the control of sequential pointing movements can be distinguished by the positive correlation of successive movement errors. A positive correlation between successive errors, hereafter called “error propagation”, indicates that displacement coding strategies are involved in movement control.

A lack of error propagation hints at a control of end position. We analyzed the error propagation in both eye and hand reproductions to further clarify the coding of spatial sequences in the present task.

3.3 Methods

3.3.1 Experiment I: Pointing movements

3.3.1.1 Subjects and apparatus

Eight healthy subjects participated in the experiments (mean age: 28.88 years, range: 23–48 years). One subject was not able to perform the task and was excluded from analysis. The handedness of subjects was assessed with the Oldfield handedness test (Oldfield, 1971). Five of the seven subjects were right-handed, two were left-handed. The subjects gave informed consent before participating in the study. The study was performed in accordance with the Declaration of Helsinki and was approved by the local ethics committee.

The target positions were presented on an LCD-screen with an integrated writing tablet (Fig. 3.1A WACOM Cintiq 21UX, width×height: 43.2cm×32.4cm= 35.75° ×28.36°). Subjects sat in a dark room at about 60cm in front of the graphic tablet which was in a comfortable writing position, pitched out from the frontoparallel plane by 30°. Target positions were indicated by a white cross (width = height = 1 cm; bar width: 2 pixel). The target positions were reproduced by pointing on the blank screen with a stylus. The end of the reproduction was indicated by a button press. All events, target positions, pointing positions (accuracy<1mm), and the button presses were recorded on a central recording system REX (Hays, 1982) for later analysis.

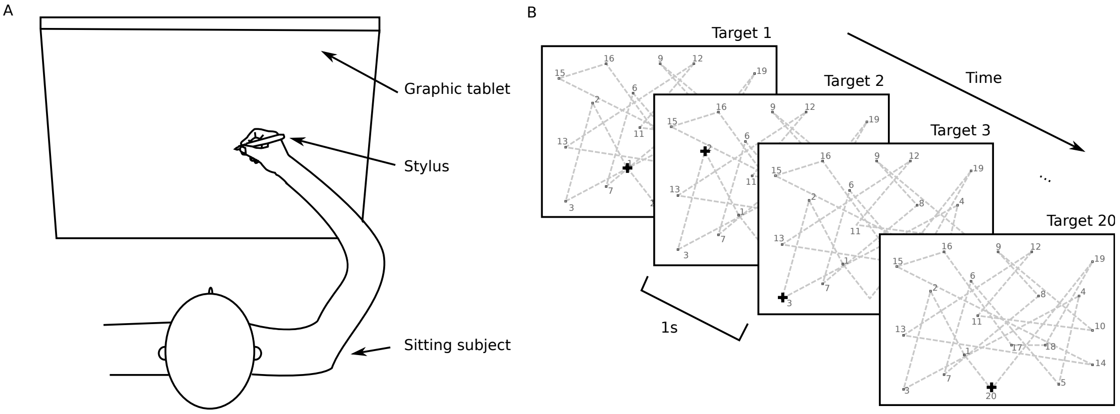

Figure 3.1: Illustration of the manual pointing sequence learning paradigm. (A) The subjects sat in front of a computer screen that featured an integrated graphic table. (B) The task was to learn a sequence of 20 target positions. During presentation only a single target position was shown at a time. All target positions were presented consecutively with an inter-target interval of 1 s. After presentation the reproduction phase started. Subjects were instructed to reproduce as many target positions as accurately as possible in the correct order. Targets were reproduced by manual pointing in Experiment I and ocular fixations in Experiment II.

3.3.1.2 Task

The task was to reproduce a sequence of 20 target positions by manual pointing. Each trial consisted of a presentation phase and a deferred reproduction phase. During the presentation phase, the sequence was presented with a white cross (size: 1cm×1 cm). The target positions were presented one after another with a fixed inter-target interval of 1 s (Fig. 3.1B). The subjects were instructed to track the target with eye movements, but they were not allowed to perform manual pointing during this presentation phase. After all 20 target positions had been presented the initial target was shown for 1 s and disappeared. The disappearance of the target was the go-signal to start the reproduction on the blank screen. The subjects were instructed to reproduce as many target positions as accurately as possible. They were asked to lift the pen between successive pointing movements and to produce the sequence in the correct order, but were allowed to continue production after omissions or order errors occurred. The subjects indicated the end of the reproduction by pressing a button when they could not recall any further target positions or thought that they reproduced the whole sequence. In one experimental session, 25 trials (alternating presentation and reproduction phases) were repeated with the same target sequence.

The sequence length was chosen in such a way that a complete reproduction was impossible on the first attempt. The sequences were generated off-line before the experiment as follows. The target sequences contained only a minimal amount of geometrical regularity since the target positions were chosen randomly from a uniform distribution on a quadratic area (28cm×28cm= 26.26° ×26.26°). Some constraints were introduced in order to avoid spatial clustering of target positions. The minimal distance between target positions was 4 cm. Only one additional target position was allowed within a radius of 6 cm around each target position. Further interactive inspection assured that sequences did not contain apparent geometrical features such as three target points on a line or four target points forming a rectangle. After having been selected in this way the sequence was stored on a hard disk and used for all subjects participating in the same experimental session.

3.3.1.3 Experimental protocol

Sequence learning, retention and effector transfer were investigated in five different experimental sessions performed on five different days. In the first session (Day1) subjects performed the sequence learning task with Sequence 1. In the second session (Day2, 24 h later) learning was continued with the same sequence, allowing retention to be tested. In the third session (Day3, 24 h later) anewsequence (Sequence 2) was learned in order to differentiate effects of general skill learning from learning of a specific sequence. In the fourth session (Day9, 7 days later) the learning procedure was again performed with Sequence 1 in order to assess long-term retention. In the fifth session (Day14, 5 days later) the effector was changed from the dominant hand to the non-dominant hand while learning was continued with Sequence 1.

3.3.1.4 Analysis

Algorithm and error measures. The assignment of reproductions to target positions was performed by an algorithm that takes the order of reproduction into account. This algorithm is described in detail in Drever, Straube & Eggert (2010). Briefly, the algorithm assigned the longest continuous sub-sequences that minimized a cost measure. The cost measure was defined as the sum of the distances between target positions and reproductions. Non-assigned target positions were added to the cost measure with a weight ϵ. This omission cost was set to 6 cm, i.e., the minimal radius of a circle in which two target positions were allowed during sequence generation (see Section 2.2.2). Based on this assignment three error measures were defined. The number of omissions was defined as the number of targets to which no reproduction was assigned. The accuracy error was defined as the mean distance between assigned targets and reproductions. The accuracy error was measured in degree. The order error was defined as the number of transpositions that were needed to sort the reproductions into a linear ascending list with a shell sort algorithm. The recall probability of target positions was estimated by counting the number of times a target position was assigned to a reproduction across subjects. It was normalized by dividing by the number of subjects. The recall probability is plotted as a function of trials in a serial position curve.

Analysis of experiments. The median and the interquartile range (IQR) are reported for all error measures. Plots show the median and error bars according to Velleman and Hoaglin (1981). The time course of the number of omissions was fitted with a piecewise linear function. The learning progress was divided into an initial learning phase and a final phase in which no further learning occurred. The initial learning phase was fitted with a linear function $f(x) = \alpha \cdot x + \beta$, where x denotes the trial number, α the initial slope, and β the start value. The final phase was fitted with a constant function $f(x) = \gamma$, where γ is the final performance. The three free parameters were determined by minimizing the sum of the squared error between fit and data for each subject. The accuracy error and the order error were fitted with a single linear function. Differences in conditions were analyzed with a Friedman ANOVA with *condition* as repeated measure factor, applied separately on the fitted parameters start value and initial slope. Differences between *start value* and *final performance* were analyzed with a Mann–Whitney U-test. Post hoc tests for the Friedman ANOVA were performed using the statistics package R (Galili, 2011).

Direction of variance in reproductions. For each subject, all reproductions assigned to a specific target form a reproduction distribution. The reproduction distributions are analyzed from the experimental sessions on Day1 and Day2. The dependence of the main direction of variance on the previous target position is analyzed with a principal component analysis as in previous studies (Gordon, Ghilardi & Ghez, 1994). The first principal component indicates the main direction of variance, whereas the eigenvalue of the first principal component is proportional to the variance in the main direction. The proportion of the first and second principal component characterizes the ellipticity of the distribution. Based on this proportion we defined an *ellipticity index* $i = 1 - \frac{PC2}{PC1}$, where $PC1$ is the eigenvalue of first principal component and $PC2$ is the eigenvalue of the second principal component. The ellipticity index equals zero for circular homogeneous distributions and one for maximally elliptic distributions. The main directions of variance were compared for each reproduction distribution with respect to the direction of straight displacement to the target starting from the last target (displacement direction). In order to compare different reproduction distributions they were each rotated to a new coordinate system that was aligned with the straight displacement direction. After the transformation the *deviation of the main direction of variance* is defined by an angle ϕ that ranges from $-90°$ to $90°$, where $0°$ indicates that the main direction of variance is identical to the displacement direction. The sphericity of pointing distributions was tested with Mauchley's sphericity test. Only those pointing positions whose preceding pointing position was also assigned to the preceding target were submitted to this analysis. From the 3500 total available (seven subjects×20 targets 25 trials) pointing positions, 2022 and 2824 could be used from Day1 and Day2, respectively. The distribution of angles ϕ within this sample was tested for uniformity with a Kolmogorov–Smirnov goodness-of-fit test.

Error propagation. To analyze the error propagation the correlation coefficient between the error vectors of two successive pointing movements assigned to two successive targets was calculated. The Pearson's correlation coefficient was calculated separately for each of the two dimensions (horizontal and vertical). An overall measure quantifying the amount of error propagation between successive errors was calculated by the root mean square (RMS) of the two correlation coefficients. This measure is hereafter called RMS correlation. The significance of the RMS-correlation coefficient was evaluated according to the Bonferroni correction. It was considered to be significant at a level of 0.05 if at least one of the two p-values of the horizontal and vertical correlations was significant at a significance level of 0.025. The significance of Pearson's correlation (r) was evaluated by a two-tailed T-test on the test statistic $t = N{-}2/1{-}r^2$.

3.3.2 Experiment II: Eye movements

3.3.2.1 Subjects and apparatus

Four healthy subjects participated in the experiments (mean age: 35 years, range: 28–47 years). The experiment was performed in a dark room. Subjects sat in front of a 40 cm×30cm (width×height) CRT-screen (Conrac, Mars 9320) at a viewing distance of 68.5 cm. The head was supported by a chin-rest. The screen had a resolution of 1280 pixel×1024 pixel and a vertical frame rate of 85 Hz. The target was a white, horizontally and vertically symmetrical cross (width = height = 0.55°; bar width: 2 pixel).

The two-dimensional eye position was recorded using a custom-made monocular video-based eye tracker (Schneider et al., 2006) at a sampling frequency of 100 Hz. The resolution of this system was below 0.1°, and total accuracy was below 0.5°. Details of the 2D calibration of this tracker are described in (Ladda et al., 2007). Eye movement data and the stimulus timing signals were recorded on a central recording system (Hays, 1982).

After learning, subjects reproduced the pointing sequences learned with eye movements on a writing tablet by manual pointing. In contrast to Experiment I, the writing tablet (WACOM SD310E) was not integrated with the visual display but was located on a separate table. The pointing area on the writing tablet was constrained to 28cm×21cm and was viewed from a distance of about 80 cm. Thus, the viewing angle on the writing tablet was smaller than the viewing angle of the corresponding position on the CRT-screen by a factor of 0.61.

3.3.2.2 Task

In this task subjects were required to perform the deferred imitation task from Experiment I in a different motor modality. The reproduction occurred in this case with ocular fixation instead of manual pointing movements. The experiment consisted of 38 trials. After the learning session, in which subjects learned to reproduce the sequence of fixations in the absence of visual targets, they were asked to perform a sequence of pointing movements with a stylus on the writing tablet in the same way as in Experiment I. They repeated this task five times without any feedback. The stylus did not produce any drawings on the writing surface.

3.3.2.3 Experimental protocol

In the first session subjects learned to reproduce a sequence of target locations by ocular fixations on a blank screen (Day1-E). Immediately after the first session subjects were instructed to reproduce the learned sequence on the writing tablet (Transfer). In a second session 24 h later, the same sequence was presented again (Day2-E). In this session the sequence was again reproduced by a sequence of ocular fixations.

3.3.2.4 Analysis

Saccade detection. The 2D eye velocity was computed by differentiating the horizontally and vertically calibrated eye position and filtering with a symmetrical Gaussian low-pass (cut-off frequency of 33 Hz; transmission gain of 0.1 at 85 Hz). Saccades were detected when the 2D eye velocity increased above 30 °/s. Searching forward and backward from the time of peak velocity, the beginning and the end of the saccade were defined as the first time at which the 2D eye velocity vector deviated more than 90° from the eye velocity at peak velocity. All intervals between the saccades were considered fixations. From these fixation intervals only those with durations longer than 200ms were used for further analysis.

Assignment. The assignment was performed with the same assignment algorithm as in Experiment I. Saccadic eye movements are more likely to be initiated by involuntary control processes than manual pointing movements. To account better for such involuntary explorative saccades the weighting factor ϵ was adjusted for each subject and trial, rather than keeping this factor constant as in Experiment I. It was adjusted to be the maximum of all minimal distances between targets and reproductions, that is the asymmetric Hausdorff distance.

Analysis of experiments. The same error measures (number of omissions, accuracy error and number of order errors) as in Experiment I were used for eye movements. As in Experiment I, the number of omissions was fitted with a piecewise linear function and the other two error measures with a linear function.

In the Transfer condition the sequence of target positions learned on the CRT-screen had to be reproduced on a proportionally scaled writing area. Therefore, a scaling factor, a horizontal translation, and a vertical translation were applied to the pointing positions as recorded from the writing tablet before submitting them to the assignment algorithm. These three parameters were fitted to each pointing sequence by minimizing the cost measure of the assignment algorithm.

Direction of variance and error propagation. The direction of variance and the error propagation were analyzed for Day1-E with the same methods as in Experiment I.

Only those pointing positions whose preceding pointing position was also assigned to the preceding target were submitted to this analysis. From the 3040 total available (4 subjects×20 targets 38 trials) pointing positions, 1044 could be used from Day1-E. Qualitative differences between error propagation in eye and hand movements were tested with a Mann–Whitney U-test on the RMS-correlation coefficients of eye and hand movements.

3.4 Results

3.4.1 Experiment I

3.4.1.1 General observations

All subjects were able to learn the sequence during the first session of the experiment. In the first trial subjects were able to recall 1–5 target positions. They started to recall the target positions at the beginning of the sequence and advanced to later target positions (Fig. 3.2A). In this way subjects learned the sequence from the beginning to the end by appending the next target positions to the learned sequence in each trial. After 16 trials subjects were mostly able to recall all target positions. The mean inter-pointing interval between two successive movements was 1.14 s±0.18 s (mean ±SD), which is close to the timing of the stimulus presentation (1 s). When subjects were re-exposed to a familiar sequence after retention time (24 h) they were able to recall most target positions even in the first trial (Fig. 3.2B). Some omissions of target positions occurred at the end of the sequence (Fig. 3.2B, trial 1–5). Thus, the modification of memory content seemed to be mainly focused on the end of the actually stored sequence, even though this particular learning strategy was not imposed either by the stimulus presentation or by the learning instruction.

3.4.1.2 Learning progress of omission errors and differences between conditions

The number of omissions showed a large learning progress for unknown sequences (Fig. 3.3; Day1, Day3). In these conditions, subjects initially showed 15 omissions on average (median β), a mean decrease of 10 omissions per trial (median γ), and a final value of only one omission (median α). The start value of omissions (β) differed significantly across different conditions, as shown by the Friedmann ANOVA ($p < 0.01$). The four omissions on average which were seen during the first re-exposition with a familiar sequence (Day2, Day9, Day14), were significant less than 15 initial omissions on Day1 and Day3 (post hoc: $p < 0.01$). The same high number of omissions when learning a new sequence on Day1 and Day3 (post hoc: $p < 1$) showed that learning was related to a specific sequence and not to a general skill to perform this task.

The start value on Day2 did not differ from the final number of omissions on Day1 ($p < 0.4$). Thus, the learned sequence on Day1 was still present on the following day. Subjects were able to learn the sequence in the short time of 25 trials (˜30 min) and were able to retain it for at least 24 h.

The final number of omissions (γ) was smaller on Day2 than the start value (β) on Day9 ($p < 0.01$), indicating that some knowledge about sequence 1 had been forgotten

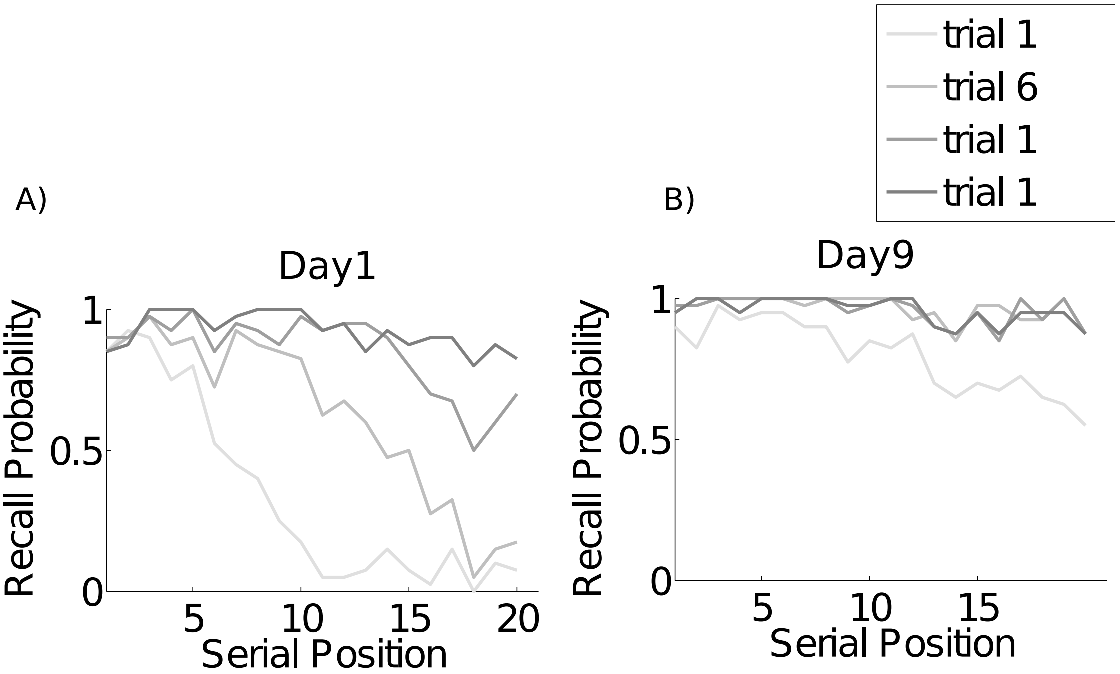

Figure 3.2: Serial position curves illustrating the learning process. The recall probability of target positions as a function of serial position. The first trials are indicated by light gray and later trials by darker gray. (A) Subjects started in the beginning to recall early target positions and advance ed to later target positions. Learning occurred from the beginning to the end of the sequence. (B) After re-exposition to the learned sequence subjects were able to recall most of the positions of the sequence in the first trials. Omission occurred mostly at the end of the sequence.

at the beginning of Day9 either because of the long time after the last practice with this sequence on Day2, or because of retroactive interference caused by learning the new sequence on Day3. However, the sequence was not completely forgotten, since the start value on Day9 was significantly smaller than on Day1 (difference of median Day9–Day1: -6.9, post hoc $p < 0.01$).

Changing the effector from the dominant hand on Day9 to the non-dominant hand on Day14 did not affect the number of omissions, as shown by a Mann–Whitney U-test ($p < 0.1$) comparing the final offset of omissions on Day9 (median [IQR]: 0.76 [1.7]) with the start value of omissions on Day14 (median [IQR]: 0.94 [3.6]). The final number of omissions did not differ between conditions ($p < 0.4$).

3.4.1.3 Accuracy and order error

The accuracy error showed no overall learning progress. Fig. 3.4 shows the linear fits of the accuracy time courses of all subjects observed on Day1. There was a small negative tendency for the slopes (α, median [IQR]: -0.01 [0.02]) that did not differ significantly from zero (Mann–Whitney U-test, $p < 0.08$). The initial slope did not differ between conditions (Fig. 3.5A, $p < 0.3$). Neither did the offset (Fig. 3.5B, $p < 0.2$). Note that the accuracy was also not affected by the effector transfer to the non-dominant hand on Day5 (Fig. 3.5B, Day9/Day14).

Order errors occurred very rarely (median [IQR]: 0.09 [1.0]) errors across subjects, trials and conditions) and did not show a significant improvement. This was confirmed by a Mann–Whitney U-test showing that the average slope across subjects on Day1 (median [IQR]: -0.01 [0.05]) did not significantly differ from zero ($p < 0.3$). This was similar for the other days since neither the slope ($p < 0.9$), nor the offset of the number of order errors differed between conditions ($p < 0.3$).

3.4.1.4 Directions of variance in reproductions

Nearly half of all analyzed pointing distributions (49 of 132 at Day1; 59 of 128 at Day2) showed, according to Mauchley's test, significant deviations from sphericity (Fig. 3.6). A dependence of the pointing error on the displacement direction from the previous target position would have been indicated by a peak in the distribution of the main variance direction of these elliptical pointing distributions around 0°. However, the main directions of variances for significant spherical reproductions were distributed uniformly in Day1 and Day2 (Kolmogorov–Smirnov: $p < 0.4$). This result suggests that the pointing error did not depend on the displacement direction from the previous target position.

3.4.1.5 Error propagation

Error propagation from one pointing position to the next did not occur consistently. Across subjects and targets, only 39 of 140 (7×20) target transitions showed a significant RMS coefficient (see Section 2). The number of significant RMS coefficients per subject ranged from 4 to 8). The mean RMS-correlation coefficient was 0.37 ± 0.17 (mean $\pm$SD, $N= 132$) across all target transitions and subjects. The mean of the significant RMS

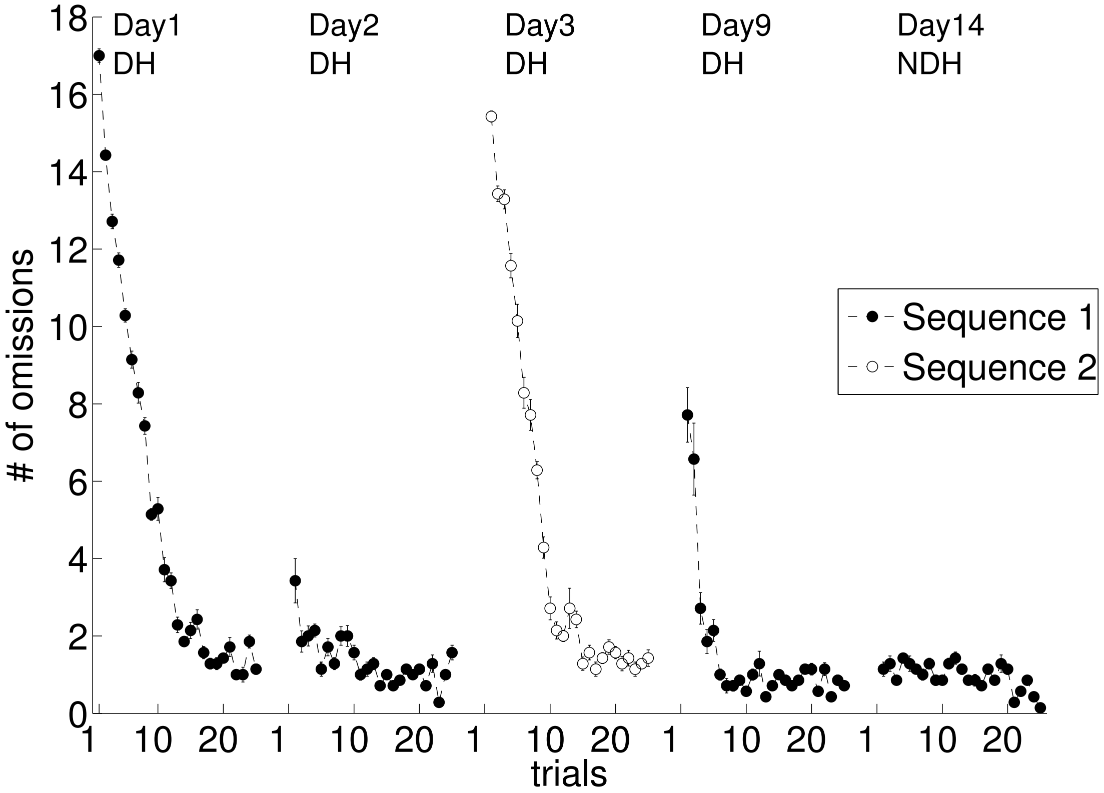

Figure 3.3: Learning progress quantified by the number of omissions (median±error bars, seven subjects). Day1: On the first day the number of omissions decreased until performance plateaued after 15 trials. Day2: On the second day subjects were able to reproduce the sequence from the first trial onwards and performance increased gradually. Day3: Performance on the new sequence 2 did not differ from performance on the first day (first learning day of sequence 1). Day9: Fewer omission errors than on Day1 indicate that part of the sequence was still remembered after a longer retention time and the intermediate learning of sequence 2. Day14: The sequence was learned robustly and the effector transfer did not affect performance.

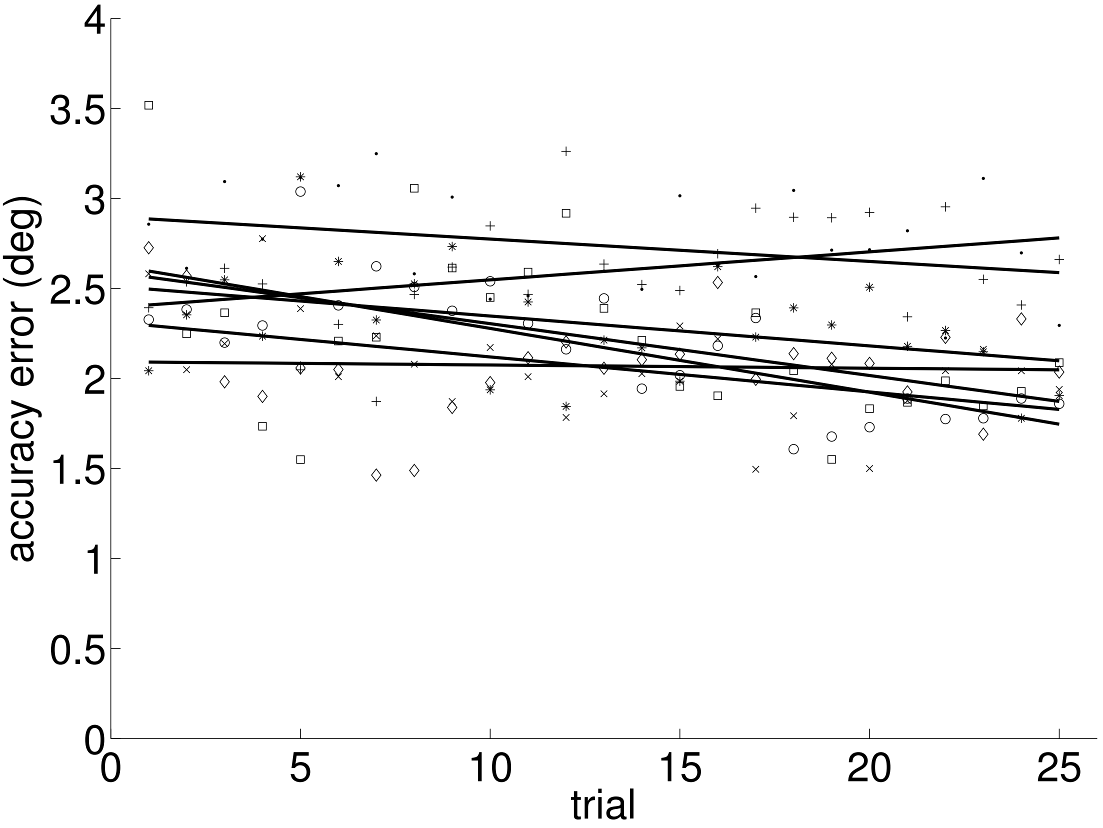

Figure 3.4: Accuracy error analysis for all subjects on Day1. The accuracy error is plotted for single subjects together with a linear fit (symbols for subjects 1–7: plus sign, circle, asterisk, point, cross, square, diamond). All slopes except one were negative but did not differ from zero significantly (Mann–Whitney U-test, $p < 0.08$).

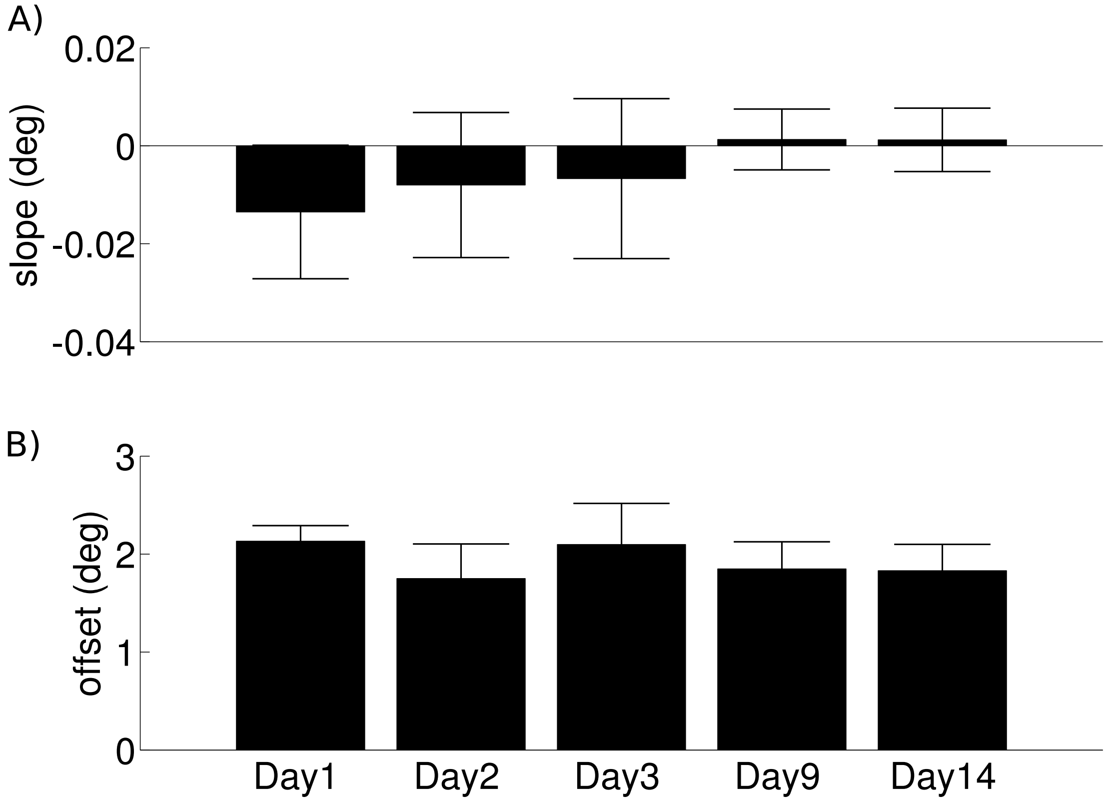

Figure 3.5: Comparison of accuracy errors across conditions. (A) The slopes of the fitted accuracy error (median±error bars, seven subjects). Slopes did not differ between conditions and did not differ significantly from zero. Subjects showed no learning progress concerning the accuracy of pointing movements. (B) The offset of fitted accuracy errors did not differ between conditions. The accuracy did not differ between conditions, even when the sequence was reproduced with the non-dominant hand (Seq1-ND).

coefficients of correlation was 0.56±0.10 (mean±SD,N= 39). The few significant correlations and the low value of the correlation coefficient showed that there was no systematic error propagation between successive pointing positions toward successive targets.

3.4.2 Experiment II

3.4.2.1 General observations

Subjects were able to reproduce the whole sequence after the first learning session (Day1-E). Compared to the reproduction in Experiment I, subjects produced more fixations than pointing positions from the very first trial (Fig. 3.7). The number of fixations increased faster, compared to the number of pointing positions. Some of the fixations were explorative since, on average, 28 fixations were performed for only 20 target positions. The inter-fixation intervals were 0.72 s±0.35 s (mean ±SD) on average across subjects and trials.

3.4.2.2 Learning progress of omission errors and differences between conditions

The number of omissions showed a large learning progress when the sequence was first presented (Fig. 3.8, Day1-E). At the beginning of the experiment subjects showed 11 omission errors on average (β), which was not significantly smaller than in Experiment I ($p < 0.2$). The learned sequence was initially prolonged by two targets per trial (α). Thus, the learning speed tended to be faster with ocular fixations than with hand pointing. However, this tendency did not reach significance ($p < 0.4$). The final value of the number of omissions (median [IQR]: 2.5 [2.1]) did not differ between ocular fixations and hand pointing ($p < 0.9$).

In the Transfer condition subjects were able to reproduce the sequence manually on the graphic tablet after learning with eye movements. The scaling parameters obtained by the fitting procedure showed that the viewing angles of the reproduced pointing positions on the writing tablet were smaller than the reproduced fixations on the CRT-screen by a factor of 0.55. This scale factor is close to the relation of the extension of the drawing areas between writing tablet and screen (0.61, see Section 2). The fitted horizontal and vertical translations corresponded approximately to the center of the writing tablet.

The start value of the number of omissions differed significantly between the three conditions ($p < 0.04$). The start value in the on Day2-E was significantly smaller than on Day1-E (post hoc: $p < 0.05$).

There was no difference in the final number of omissions across conditions ($p < 0.4$). The final number of omissions on Day1-E did not differ from the initial number of omissions in the Transfer condition ($p < 0.2$).

3.4.2.3 Accuracy and order error

The average slope of the accuracy across subjects (median [IQR]: 0.0 [0.01]) on Day1-E did not differ significantly from zero ($p < 0.2$). Also during pointing reproductions (Transfer condition) and during the learning session on Day2-E there was no progress

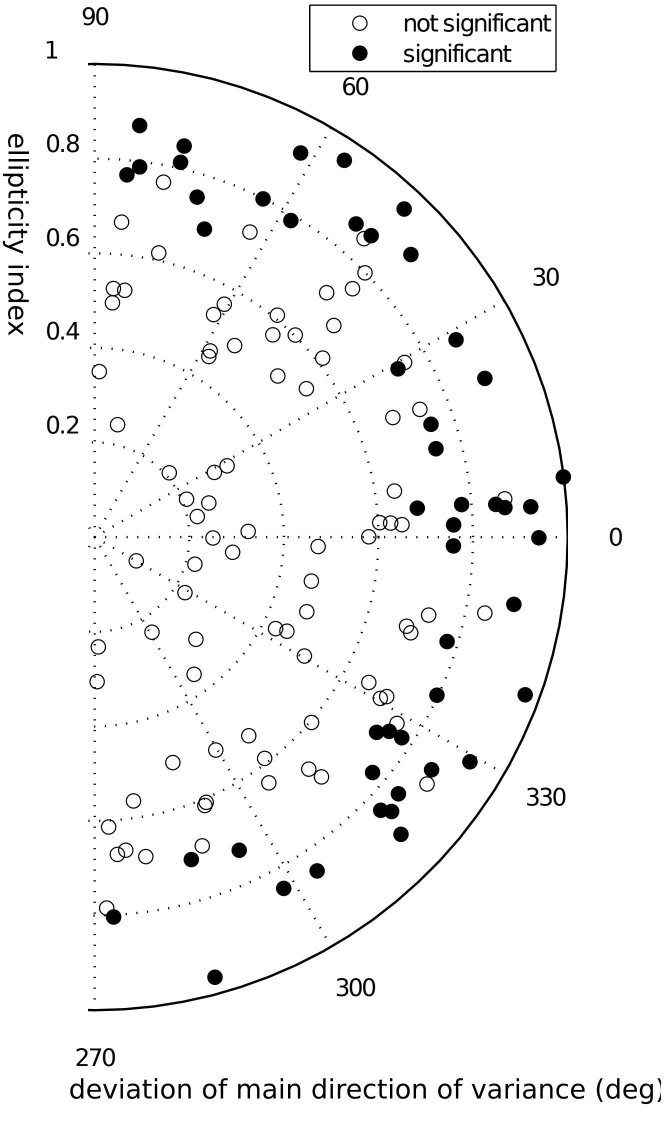

Figure 3.6: The deviation from the main directions of variance for reproduction distributions on Day1. Main directions were pooled over 10 subjects and 20 target positions (N= 132). The uniform distribution of angles of main directions of variance (dots: not significantly spheric, filled dots: significantly spheric) shows that the distribution of pointing movements did not depend on the preceding target position.

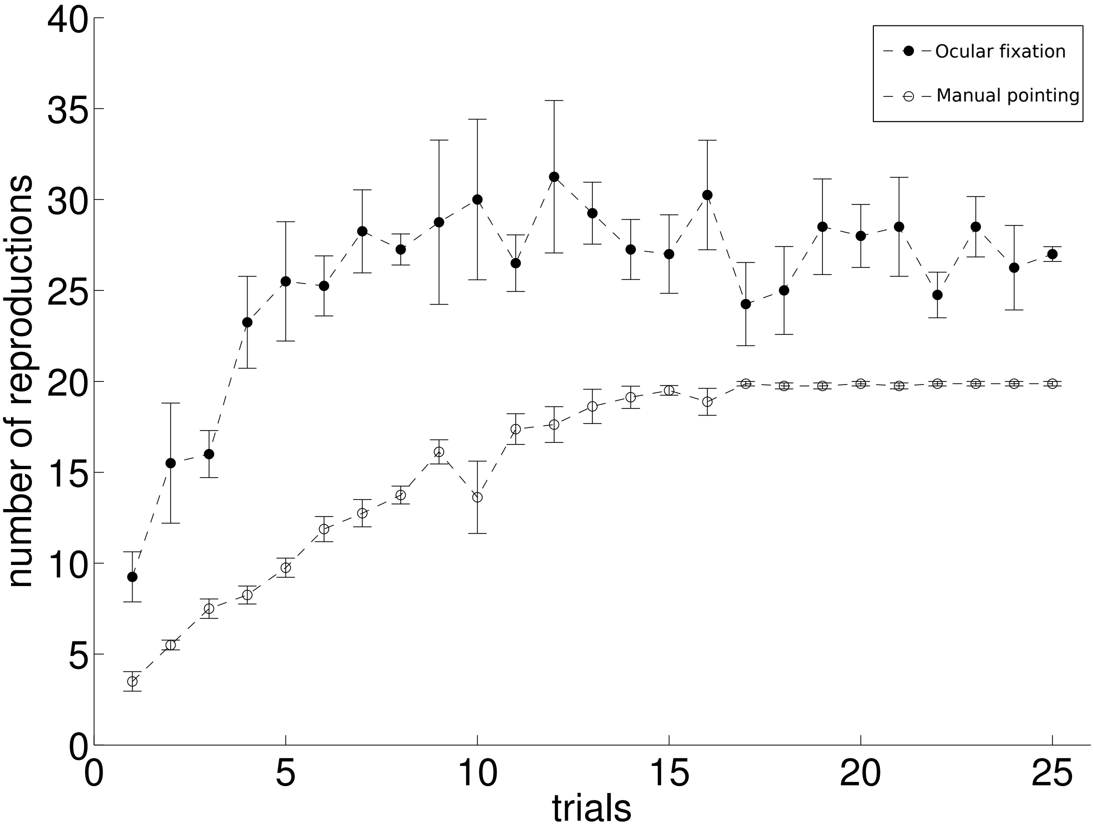

Figure 3.7: The number of reproductions for pointing movements (Day1, seven subjects median±error bars) and ocular fixations (Day1-E, four subjects median±error bars). Initially there were more ocular fixations than manual pointing movements. The number of ocular fixations increased faster than the number of pointing movements.

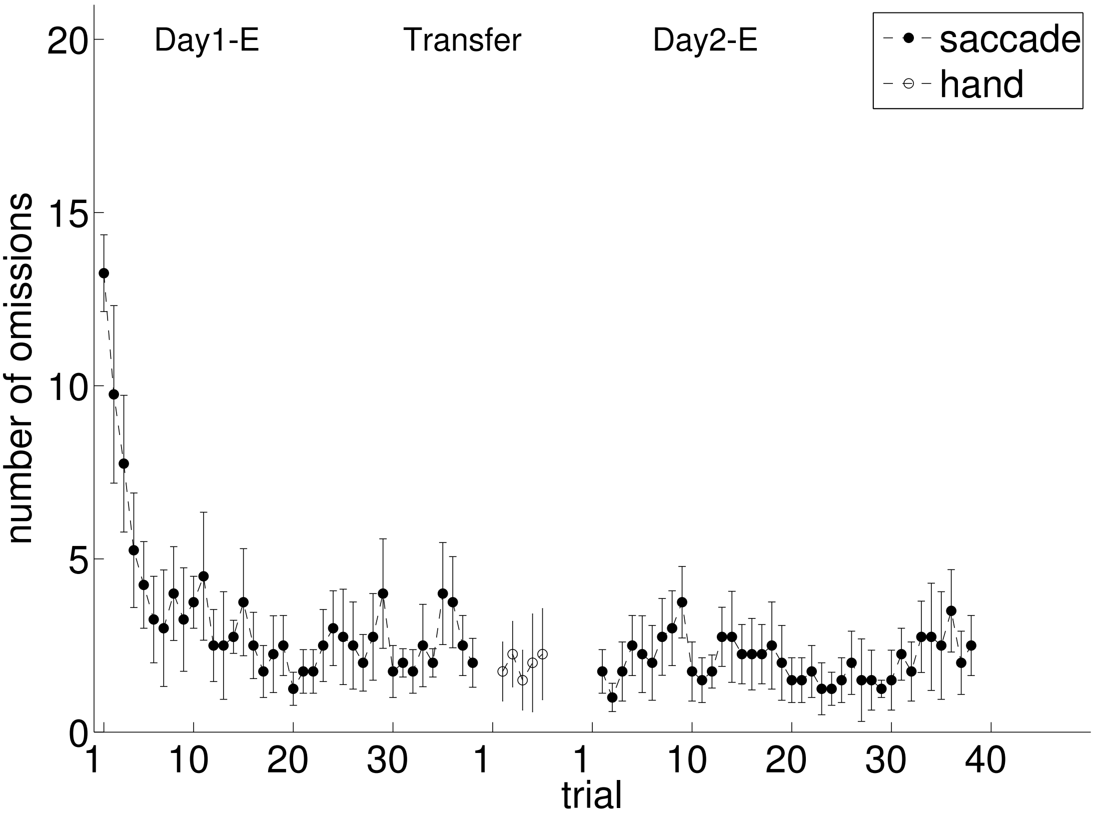

Figure 3.8: The number of omissions for Experiment II (median±error bars, four subjects). Sequence learning with ocular fixations did not qualitatively differ from learning with manual pointing movements. All subjects were able to recall the sequence in the Transfer condition on a graphic tablet immediately after the first session. After a retention of 24 h (Day2-E) subjects were able to recall the complete sequence in the first trial.

in the accuracy since there was no significant main effect of condition on the accuracy slope ($p < 1$). The accuracy offset differed between conditions ($p < 0.04$). The offset was larger (post hoc: $p < 0.04$) on Day1-E (median [IQR]: 1.79 [0.21]) than in the Transfer condition (median [IQR]: 1.17 [0.20]). Thus, accuracy seemed to be slightly better in manual pointing than in fixations.

As for reproductions by manual pointing, there was no systematic improvement of the order errors during the sessions since the average slope fitted to the time course of order errors did not differ significantly from zero in ($p < 0.12$). There was a significant difference between conditions, as indicated by a main effect on the fitted error offsets ($p < 0.01$). The number of order errors was smaller (post hoc: $p < 0.05$) in the Transfer condition (median [IQR]: 0.00 [0.15]) than in Day1-E (median [IQR]: 6.58 [4.31]).

3.4.2.4 Directions of variance in reproductions

With fixations fewer reproduction distributions were elliptical than with pointing. On Day1-E 14 of 72 reproductions were significantly elliptical and on Day2-E only 3 of 66 reproductions were significantly elliptical. As for pointing positions, the distribution of the main direction of variance of significantly elliptical distributed fixation positions was uniform ($p < 0.8$).

3.4.2.5 Error propagation

As in the pointing movement experiment, error propagation from one target to later targets did not occur consistently. Per subject a minimum of 1 and a maximum of 4 (out of 19 possible target transitions) RMS correlations were significant (see Section 2). The mean of the significant RMS correlations across subjects and transitions was 0.56 ± 0.17 (mean ±SD; N= 11). The size of the significant RMS correlations did not differ between eye and hand movements (rank sum test Day1-E versus Day1: $p < 0.9$). Thus, no qualitative difference concerning error propagation occurred between sequence reproduction with ocular fixations and with pointing movements.

3.5 Discussion

The experiments presented here shed light on some characteristics of deferred imitation learning of long spatial sequences. In this task, long spatial sequences were learned in a relatively short time not depending on whether they were reproduced by manual pointing or ocular fixations. The buildup of sequential context was quantified by the number of omissions, whereas the metrics of the reproduced sequence were quantified by the accuracy error. Learning was focused on the prolongation of the sequential context by new positions rather than on a gradual improvement of the metrics. The sequence was learned starting from the target positions that occurred early within the sequence and advancing systematically to later target positions. Retention tests showed that learning was not only a temporary effect but learned sequences were retained for several days. Reproduction performance was almost independent of the effector. The learned sequence could successfully be transferred from the dominant to the non-dominant hand and from ocular fixations to pointing movements. The qualitative characteristics of the learning process were similar for eye and hand. Detailed analysis of the pointing and fixation distributions showed that distributions of pointing and fixation errors were circular, homogeneous and not related to the movement direction leading to the actual pointing or fixation, suggesting endpoint controlled movements. Significant propagation of position errors between successive pointing positions, that would have been expected if a displacement coding played a major role, occurred only rarely.

3.5.1 Buildup of sequential context in deferred imitation

Learning of sequential context is considered as a special aspect of sequential learning and has been distinguished from the learning of metric information. These two aspects have been described as structural and metrical characteristics (Kelso, 1981), essential and nonessential characteristics (Schmidt, 1975), movement sequence structure and articulatory activities (Wilde & Shea, 2006), and implicit and explicit components (Ghilardi et al., 2009). In stimulus anticipation paradigms, the acquisition of sequential context cannot be fully investigated because the occurrence of sequential errors is limited by the experimental condition. In these tasks, performing an anticipatory movement to a wrong location can easily be avoided by waiting for the next stimulus to be presented. The unconstrained and non-stimulus guided reproduction in the present study allowed the buildup of sequential context to be investigated. Subjects were not constrained by the task instructions to acquire target positions in a certain order. The finding that sequence acquisition started at the beginning of the sequence shows that this acquisition order does not only occur when acquisition order is constrained by the task, e.g., in the 2×5 task (Hikosaka et al., 1995). Nevertheless, systematic prolongation of the memorized sequence is not the ubiquitous mode for sequential learning, e.g., in a serial reaching task (Moisello et al., 2009) the acquisition did not start with the first targets but with elements occurring at arbitrary locations in the sequence. This suggests that the acquisition order starting at the beginning is specific to deferred imitation learning task.

The improvement in accuracy was not significant, whereas the number of omissions showed a distinct improvement. The lack of accuracy improvement might be related to a missing incentive or a threshold phenomenon. In studies with deferred imitation of short sequences (Agam et al., 2007) an improvement in accuracy was observed. The learning mode elicited by this study differs from the learning mode in our task with respect to the buildup of sequential context. In deferred imitation of long sequences the buildup of sequential context was the main aspect of the learning progress, whereas it played only a minor role with short sequences.

Sequences of spatial positions are not only retained in short-term memory, but can be recalled after a longer period of time. Long-term retention was observed for learning with manual pointing movements and ocular fixations. The long-term retention of sequences is an important feature of this task. The fact that the number of omissions at the end of the first session was equal to that at the beginning the second session (Pointing movements:

Fig. 3.3, ocular fixations: Fig. 3.8) suggests that in all subjects the retention at the beginning of the second day can be inferred from the number of omissions at the end of the first day. There were no clear indications of essential consolidations during the retention interval. Thus, the large learning progress on the first day may be a good indicator for successful transfer of the sequential context into long-term memory. This may offer a useful tool for clinical diagnosis of deficits in consolidation processes in long-term memory.

3.5.2 Effector-independent learning of spatial sequences

Long sequences of spatial positions were learned with manual pointing movements and ocular fixations. It is important to discuss whether the differences in performance between these effectors reflect differences in the underlying learning mechanisms or is based on differences in the motor execution. With eye movements more fixations were produced than in manual pointing movements (Fig. 3.8). This difference is probably related to the motor execution since involuntary explorative saccades are difficult to suppress whereas comparable involuntary explorative hand movements are very unusual.

The slightly higher accuracy in the manual reproduction after learning with ocular fixations is somewhat surprising since previous studies have shown that in visually guided (Gorbert & Sergio, 2009) and memory guided, combined eye–hand movements the variable error of the hand is larger than that of the eye (Sailer et al., 2000). The apparent higher precision of the manual pointing presented here may reflect an artifact due to the additional scaling parameter that had to be fitted to the manual reproductions in Experiment II. However, differences of the overall average of a performance measure between the effectors can easily be attributed to the motor execution (independent of its direction) and do not imply differences in a learning mechanism.

In contrast, differences in the time course of a performance measure during learning may indicate effector-specific learning mechanisms. A possible candidate for such a difference is the finding that the initial number of omissions was smaller, and the prolongation of the reproduced fixation sequence tended to be faster with ocular fixations (Experiment II) than with hand movements (Experiment I). Since the slope differences did not reach significance across the population,we do not consider this as strong support for effector-specific learning mechanisms.

Besides these differences, the qualitative characteristics, especially the dominance of sequence prolongation compared to metric improvements, were similar for both motor modalities. In summary, this similarity suggests that the underlying learning mechanism was not effector-specific. This is further supported by the result that ocular fixations and hand pointing showed similar retention performance. Similar long-term retention between eye and hand learning tasks stronger argument for effector independent memory than effector transfer after short-term learning since the latter may also be explained by immediate coupling of two motor systems. In contrast, the similar long-term retention suggests that the memory used in both tasks is the same.

The hypothesis of an effector-independent spatial representation of a sequence may also be of interest for eye–hand coordination studies. On the one hand coupling between eye and hand can be interpreted as an indicator for the coupling between two motor systems (Johansson et al., 2001). On the other hand it is known that highly coordinated and even predictive eye movements can be performed together with the hand movements of another subject without involvement of hand movements of the observer (Flanagan & Johansson, 2003). These two observations, even though they may appear contradictory on a first glance, could be related to an effector-independent action plan which can be used by both motor systems.

Recent research on sequence learning led to the theory that learning of movement sequences occurs concurrently on two levels of representation (Verwey, 1996; Hikosaka et al., 1999; Nakahara, Doya & Hikosaka, 2001; Kovacs et al., 2010). These studies showed that a fast learning process can acquire a representation in effector independent visual coordinates, whereas effector-specific learning occurs on a much slower time scale. The acquisition of the effector independent sequence was reflected by an increase in the number of reproduced items in the 2×5 task (Hikosaka et al., 1995) and in serial reaching tasks (Ghilardi et al., 2009). The acquisition of motor representation was reflected by an increase in reproduction speed (2×5 task) or accuracy (serial reaching task (Ghilardi et al., 2009). In the task of the current study the prolongation of the memorized sequence was achieved within 20 min and was effector independent. Therefore it seems likely that the fast visual learning process proposed by Hikosaka et al. (1999) is also involved.

3.5.3 Sequential position memory versus sequential displacement memory

Desmurget et al. (1997) found that pointing distributions were spherical for unconstrained pointing movements in which the subjects hand touched an external surface only at the start and at the end of the movement. The distributions of movement end positions were elliptical when the movement was constrained by a surface during its entire duration. These results lead to the hypothesis that unconstrained movements are endpoint controlled movements, whereas constrained movements are controlled to follow a straight line path in task space. In our experiment, pointing was not constrained, and subjects lifted the stylus between successive pointing positions. Consistently with the results of Desmurget et al. (1997) most reproduction distributions were spherical. This finding suggests that endpoint rather than connected straight line movements are controlled in our task.

A further criterion for the involvement of position signals in the control of sequential pointing movements was developed by Bock and Arnold (1993). They analyzed the error propagation and found larger error propagation (indicated by higher correlation coefficients between successive pointing positions) after direction changes with acute compared to blunt angles. Thus, the absence of strong correlations in the current experiment is probably due to the feature that the vast majority of all direction changes were larger than 90°. This is an important difference to the study of Ditterich, Eggert & Straube (1998) who observed larger correlations (up to 0.55) between successive fixation errors. The very small average correlation coefficients reported in the current study (0.37) were as small as the correlation coefficients (0.37) observed by Bock & Arnold (1993). Only 28% of the correlation coefficients differed significantly from zero. This suggests that error propagation was nearly absent and, following the argument of Bock, Bélanger & Steinbach (1995), supports the view that the movement controller was responsive to position signals.

In contrast to most previous experiments investigating control strategies based on precision and error propagation of pointing movements (Desmurget et al., 1997, Bock & Arnold, 1993), position signals in the present experiment were retrieved from a sequential spatial memory and were not guided by visual input. Therefore, the evidence for end-point position control suggests that memory of consecutive positions rather than memory of consecutive displacements is involved in learning deferred imitation of geometrically irregular spatial sequences.

4 Organization and re-organization of long sequences of pointing movements

4.1 Abstract

In the deferred imitation sequence learning task a long sequence of pointing movements is learned without guiding stimuli during pointing. This task implies a gradual buildup of the sequence in memory. In the present study we investigate whether the sequence is prolongated by appending chunks of items or single items (organization), how an initially learned sequence changes during reproduction without further feedback (consolidation), and how a local modification of a learned sequence affects reproductions of target positions near the sequence modification (re-organization). Changes of the number of pointing movements as well as their constant and variable error were assessed. The sequential buildup proceeded almost linearly from the beginning to the end of the sequence indicating a sequence prolongation by appending single target positions. The variable error did not change whereas subject specific constant errors developed in the absence of feedback. Subjects were able to appropriately reorganize the learned sequence, but constant and variable errors of pointing movements near the sequence modification did not change. Larger inter-response intervals before and after local modification suggest that the exchanged targets were learned as single chunks. These results show that it is possible to locally modify a learned sequence of pointing movements without affecting their neighbors in the sequence.

4.2 Introduction

Complex motor actions performed by humans are of a sequential nature (Lashley, 1951). Everyday tasks such as lacing a shoe, brewing a coffee or driving a car require a series of movements to be performed in the correct order. More specialized activities such as playing the piano or playing sports are also examples of such motor sequences. Learning new motor sequences is a process in which the actions and their sequential order have to be remembered correctly.

How sequences are generated and learned has been the subject of extensive research for a long time (see Adams (1984) for a review). To quantify the learning progress different measures that focus on performance aspects were used. Timing is quantified by the time to initiate a sequence (Verwey, 1996), sequence execution speed (Sternberg et al., 1978), and reaction time in the serial reaction time task (Nissen & Bullemer, 1987). The metric accuracy of the sequence items has been quantified with movement precision (Ghilardi et al., 2009) smoothness of sequence production (Wilde & Shea, 2006) and a measure of angular deviations (Sekuler et al., 2003). Hikosaka et al. (1999) have further focused on the number of trials needed to learn a new sequence. This aspect concerns the buildup of a new motor program and differs essentially from the aspects of reaction time and metric accuracy which are related to the gradual modification of an existing motor program. In a previous study (Drever, Straube & Eggert, 2011) we observed that the aspect of sequential buildup is especially important for deferred imitation learning of long sequences of pointing movements. Furthermore the sequential memory which is build up in this learning task is a general spatial memory rather than a motor memory since it transferred easily between motor modalities (eye and pointing movements).

The process of sequential buildup can be seen as the prolongation of a sequence of abstract motor actions which are organized in hierarchies. Since the influential work of Lashley (Lashley, 1951) the hierarchical organization of abstract movement plans has been emphasized. Hierarchical accounts of sequence representation and productions are supported by a large body of experimental findings from the fields of finger tapping (Rosenbaum et al., 1986), speech production (Dell, 1986) and typewriting (Rosenbaum, 1991). A central finding is that recall improves when a large number of items can be subdivided into groups corresponding to a coding schema that is already known. E.g., the sequence “FBI, CIA, KGB, TWA” is much easier to remember than the sequence “FB, ICI, AKG, BTW, A” (Bower et al. 1969) because each of the three-letter chunks corresponds, in contrast to the unfamiliar grouping, to a known item on a higher hierarchical level. For movement sequences, the hierarchical organization into chunks is reflected in timing patterns. The item at the beginning of the chunk shows a longer inter-response interval than items within the chunk (Verwey, 1996; Ditterich, Eggert & Straube, 1998; Sakai, Kitaguchi & Hikosaka, 2003). This kind of hierarchical coding suggests that the packaging of several items into chunks plays a major role in sequence production and memorization. However, in deferred imitation learning of long sequences of pointing movements (Drever, Straube & Eggert 2011) it is less well known at which hierarchical level the sequential buildup takes place.

One possibility is that the prolongation of the sequence takes place at the level of chunks consisting of multiple target positions. This is indicated by error propagation between successive fixations in saccadic sequences (Ditterich, Eggert & Straube, 1998). The error propagation suggests that chunks are retrieved from memory and executed as a single unit. In a previous study on learning of long spatial sequences we did not find significant error propagation between items (Drever, Straube & Eggert, 2011). This result might indicate that, during the early learning phase of the acquisition of long spatial sequences, the prolongation of the sequence takes place on the level of single target positions. If the sequence were not prolonged by single target locations but by appending chunks we would expect that positions within the chunks would not be stored independently and that a reorganization of one position would effect other positions in the chunk.

Therefore we performed an experiment in which a recently learned sequence was locally modified by replacing two target locations. If learning occurs at the level of chunks and not at the level of single target positions in our task, we expect that the replacement of targets affects the accuracy and the variability of the reproductions of neighboring target positions.

Further important aspects of motor memory are related to its dynamics (Zanone & Kelso, 1992). Stability and drift of memory were investigated in order to describe these dynamics. In particular, the relaxation of a learned pattern towards stable fixpoints in the absence of feedback may reveal features of intrinsic attractors interacting with recently acquired patterns (Giraudo & Pailhous, 1999). To evaluate stability and drift of sequence memory in our task, the time course of variable and constant error was assessed in the absence of feedback (Experiment II).

4.3 Methods

4.3.1 Subjects and apparatus

Nine healthy subjects participated in the experiments (mean age 32 years, range: 25 – 50). Two subjects were not able to reproduce the whole sequence after the first experiment and were excluded from analysis. Subjects gave informed consent before participation in the study. The study was performed in accordance to the Declaration of Helsinki and was approved by the local ethics committee.

The stimulus sequence consisted of 21 target locations, in which the first target location was the same as the starting location. The sequence length was chosen in such a way that a reproduction of the whole sequence in the first trial is virtually impossible. Target locations were chosen randomly to avoid regularities or geometric figures in the sequence with the constraints that the minimal distance between two target locations was 4 cm and that not more than two target locations occurred within a radius of 6 cm. The average distance between successive targets was 11 cm.

4.3.2 Task and protocol

Subjects learned a long sequence of pointing movements following the paradigm described in (Drever, Straube & Eggert 2010). They were seated in a dark room in front of a computer screen with an integrated graphic tablet (WACOM Cintiq 21UX, 43.2 x 32.4 cm, viewing distance 30 cm). The sequence of 21 target locations was presented with a white cross on the screen (width=height=1 cm; bar width: 2 pixel) while subjects only looked but did not point at the targets. Targets were presented one after another with an inter-target interval of 1 sec. The disappearance of the last target location served as a go signal for sequence reproduction. The subjects were asked to reproduce the target sequence after presentation using a pen to point to the memorized target locations on the blank screen. In between the reproductions of the single target positions the pen was lifted from the tablet surface. Subjects were instructed to reproduce the target locations as accurately as possible. No particular incentive for completeness of the reproduction was given. Subject were instructed not to interrupt or to perform corrective movements when noticing an order error. They were asked to stop the reproduction and to indicate this by pressing a button when no further target positions could be remembered. All events, target locations, pen position (accuracy < 1 mm), pen pressure on the tablet, and the button presses were recorded on a central recording system REX (Hays 1982) for later analysis.

4.3.2.1 Experiment I

In the first experiment subjects performed 25 trials. In each trial the same sequence was presented and subjects were instructed to reproduce as many target locations as they could remember. The purpose of this experiment was to investigate the sequential buildup in the same learning paradigm as already used in a previous study on deferred imitation learning (Drever, Straube & Eggert 2011), and to quantify whether learning increments in this task consist of single items or groups of multiple items forming chunks.

4.3.2.2 Experiment II

In the second experiment, starting only a few minutes after the end of Experiment I, the time course of the reproduced pattern and its variability was tested in the absence of any feedback. The experiment started with 3 trials with alternating presentation and reproduction of the same sequence used in Experiment I. After that subjects reproduced the learned sequence 60 times without an intermediate presentation of the sequence.

4.3.2.3 Experiment III

Experiment III was performed one day after Experiments I and II and tested the reorganization of the memorized sequence when the target sequence learned in Experiment I was modified by replacing two target locations (5 and 15) with new target locations. The new target locations were displaced by an average of 14 cm, inducing a noticeable difference in the sequence structure. Before the experiment subjects performed three practice trials with the target sequence from Experiment I. During these practice trials subjects were made aware of which targets would be modified in the following experiment. In pilot studies, this instruction turned out to be necessary, because otherwise subjects tended to interrupt the sequence reproduction after a sudden replacement of a target. Thus, this instruction was necessary to investigate the effect of an isolated replacement on neighboring items.

Experiment III consisted of 6 blocks of 13 trials. In the first three trials of a block the modified target sequence was presented and reproduced. In preliminary studies we determined that this time span suffices to learn the modified target sequence. In the following 10 trials subjects reproduced the modified sequence without intermediate presentation. Thus, each of the six blocks consisted of 3 learning trials and 10 reproduction trials.

4.3.3 Analysis

For each pointing movement the first maximum pen pressure was used to define the pointing time. The reproduced position was defined by the pen position at pointing time. The inter-response interval was defined by the time interval between successive pointing times, with the *n-th inter-response interval* denoting the interval between the reproduction of target n and the reproduction of the next target. The inter-response interval is the sum of the time subjects remain on the previous reproduction and the movement time.

The analysis of the sequence reproduction required the assignment of reproduced positions to target locations. The assignment was performed with the algorithm described and evaluated in (Drever, Straube & Eggert 2010). The algorithm is a compromise between nearest neighbor assignment and ordered assignment. It searched for the longest continuous sub-sequences that minimized a cost measure. The cost measure was defined as the sum of distances between target locations and reproductions. Non-assigned target locations were added to the cost measure and weighted by a factor ϵ (=30cm). Targets that were not part of the first assigned subsequence were assigned with the same procedure to the remaining reproductions. This procedure was repeated until no further assignment was found.

Based on this assignment several error measures were defined.

4.3.3.1 Experiment I

The learning progress in Experiment I was quantified by the *number of reproduced target locations.* The *accuracy* of the reproduction was quantified by the mean distance between reproductions and target locations per trial.

4.3.3.2 Experiment II

The time course of the drift was quantified by the *drift vectors* defined as the vector difference of the reproduction between the current trial and the first trial, specifically for each target. The *direction of the drifts* was defined for each target and subject by the slopes of the linear regressions of the horizontal and vertical components of the drift vector over trials. A drift was considered significant when the T-tests on either the horizontal or vertical regression slopes were significant at a level of 0.025 (i.e., Bonferroni corrected). To answer the question whether subjects drifted towards a common or towards different configurations an overall measure of the dissimilarity of the reproduced sequences across subjects was computed as follows. The inter-subject reproduction distance was defined for each target and for each of the possible 21 (7 choose 2) subject pairs as the distance of the corresponding target reproductions between the subjects. The inter-subject reproduction dissimilarity was defined as the median of the inter-subject reproduction distance across all targets and subject pairs. The difference of the *inter-subject reproduction dissimilarity* between the last and the 4th trial (i.e. the first without preceding target presentation) provides a measure of inter-subject drift diversity. Whether this measure was positive was tested with a Mann-Whitney U test. An overall measure of the drift time course across all targets was defined by the average of the length of the drift vector across all targets. This measure was smoothed by a moving average with a window size of 3 trials to yield the measure we call *mean absolute drift distance.* The mean absolute drift distance was parameterized by fitting an exponential function $f(t) = a \cdot (1 - \exp -c \cdot t)$ in which t denotes the trial number, a is the saturation level, $a \cdot c$ is the initial slope and

c is the inverse of a time constant which is expressed in terms of the trial number.

The drift vector and the mean absolute drift distance defined above reflect the constant error of the reproduction. In order to evaluate the variable error of the reproduction the variance was estimated in a time window of 3 trials for each subject and the x- and y-component. The *RMS variance* was defined as the root mean square of the variances in the x- and y-component.

4.3.3.3 Experiment III

In Experiment III only the reproductions towards the exchanged target positions (5, 15), the neighboring target positions preceding the target exchange (4, 14) and those succeeding the target exchange (6, 16) were included in the analysis. To analyze the mean time course of sequence reorganization across the six blocks a *normalized reproduction error* was computed by means of a coordinate transformation. The reproduction positions were rotated into coordinates aligned with the direction of the target exchange specifically for targets 5 and 15 and specifically for each block. This allowed a comparison of the effects of the exchange on neighboring reproductions across the two targets (5, 15) and across blocks. All reproduced pointing positions (and the corresponding targets) were translated by a shift (o) that mapped the old target position on the origin of the coordinate system. An additional rotation (D) and a homogeneous scaling (s) were applied in such a way that the difference vector between the old and new target were mapped on the x-axis at the position $\begin{bmatrix} 1 \\ 0 \end{bmatrix}$. Thus, the complete transformation (x) was defined by

$$\underline{\tilde{x}} = s \cdot \mathbf{D} \cdot (\underline{x} - \underline{o})$$

$$\mathbf{D} = \begin{bmatrix} \cos(\phi) & -\sin(\phi) \\ \sin(\phi) & \cos(\phi) \end{bmatrix}$$

$$\phi = -\tan^{-1}\left(\frac{t'_{ny} - t_{ny}}{t'_{nx} - t_{nx}}\right)$$

in which $\underline{t}_n = \begin{bmatrix} t_{nx} \\ t_{ny} \end{bmatrix}$ and $\underline{t}'_n = \begin{bmatrix} t'_{nx} \\ t'_{ny} \end{bmatrix}$ denote the positions of the target being modified (n= 5, 15) before and after the modification. The scaling factor was defined by:

$$\begin{bmatrix} 1/s \\ 0 \end{bmatrix} = \mathbf{D} \cdot (\underline{t}'_n - \underline{t_n})$$

According to the range of modifications applied across blocks the median scaling factors (s) was 0.053 cm^{-1} (IQR: 0.088 cm^{-1}). By this normalization a shift of the reproduction error in the direction of the target exchange is indicated by a change of normalized reproduction error exclusively in the direction of the x-axis. The normalized transformation allowed us to average the time course of the reproduction errors across experimental blocks despite differences in the actual exchange direction between the blocks. Moreover it allowed us to relate the change in the reproduction error directly to the changes of the neighbors in the sequence. All average time courses across blocks were computed in a window starting three trials before the target exchange (labeled -2 to 0) and ending 10 trials later (the three trials performed after presentation of the sequence with the exchanged target are labeled 1 to 3).

The systematic changes of the mean reproduction were assessed by the *mean normalized reproduction error* averaged across blocks. The inter-trial variability of reproductions was assessed by an estimate of the within-subject and within-trial variance of target reproductions from the repetitions across blocks. This estimate was computed in the same translated and rotated coordinates used to define the normalized reproduction error. However, since the inter-trial variability did not depend on the size of the target change, variance was expressed in units of cm^2 and not scaled with respect to the size of the target replacement. The within-subject residual variance was computed as the variance of the reproduction position across blocks specifically for each subject and each trial after subtracting the expected within-subject mean derived from normalized reproduction error. Then the final estimate of the within-subject and within-trial variance was defined by the average of the within-subject residual variance across subjects. For the sake of brevity this measure will be called *residual variance* hereafter.

Statistics on the effects on the mean *normalized reproduction error* and the *residual variance* were performed with repeated measures ANOVA with the factors *component* (2 levels: x/y), *trial* (13 levels: trials per block), and *target* (2 levels: first/second exchange).

To further assess whether the reproductions neighboring the exchanged target belong to a common chunk or form independent memory items the inter-response interval was compared between movements towards the exchanged (5, 15), the neighboring (4, 6, 14, 16), and the remaining targets. Differences of the inter-response interval were analyzed with a Friedman-ANOVA with the factor target group and levels *neighbors*, *exchanged targets* and *remaining targets*. Alpha-errors with a probability of less than 0.05 were considered significant. Posthoc tests were performed using the Scheffé test.

4.4 Results

4.4.1 Experiment I

In the first experiment subjects learned the sequence of 21 target positions within 25 trials. The same learning process as described in detail in (Drever, Straube & Eggert 2011) was observed. A typical time course of learning is illustrated in Figure 4.1. Subjects started to reproduce the first items of the sequence in the correct order. In each trial more target positions were acquired in serial order. Omissions dropped almost linearly from 16 omissions in the first trial to 1 omission in the 15th trial on average across subjects. Thus, one target per trial was acquired on average. The fastest learning subject needed 8 trials, the slowest learning subject needed 21 trials to acquire the sequence (first reproduction without omissions). Two subjects who took more than 25 trials to achieve complete reproduction were excluded from further analysis. Figure 4.1 also shows that the most frequent sequence prolongation per trial was 1 which is very close to the average prolongation speed. This was also true for 5 of the 7 subjects indicating that the

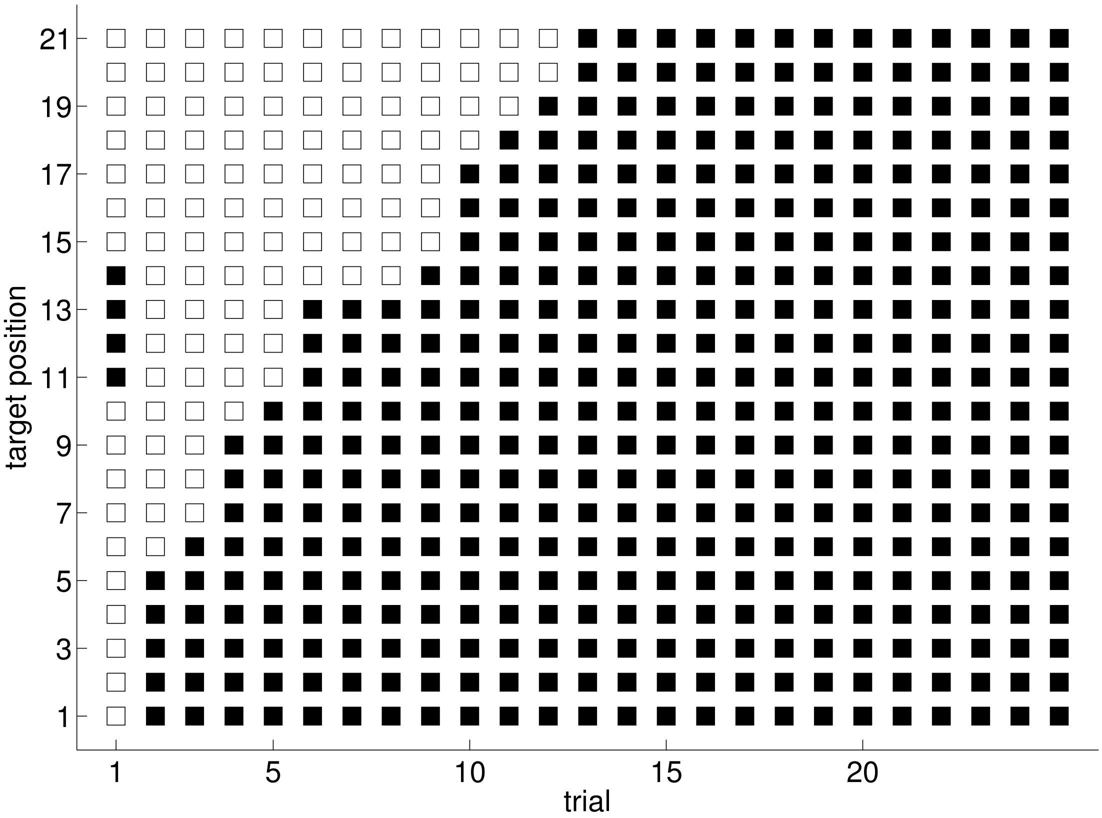

Figure 4.1: Assignment map for a single subject. Filled squares indicate assigned targets and white squares indicate non-assigned targets. This map illustrates the basic features found in the sequence learning task. Learning starts from targets at the beginning of the sequence and advances to later targets. Memorized targets are stable and not forgotten when new targets are added to the sequence. The most common sequence prolongation is one target per trial.

sequential buildup proceeded almost linearly. The accuracy of reproduction was 2.87+/-1.65 cm on average across subjects. The slope of the linear regression to the accuracy error did not differ from zero (T(6)=-1.90, p<0.2). Thus, the accuracy of reproduction did not change in the early learning phase.

4.4.2 Experiment II

The regression analysis on the components of the drift vector revealed that about two thirds of all reproductions drifted (91 out 147) as confirmed by T-tests on the individually estimated regression parameters. In 91 cases either the horizontal or the vertical regression slope differed significantly from zero at an alpha-level of p<0.025. These tests were performed for each subject and target location. Figure 4.2 shows that the directions of the total drift vector, defined as the drift vector of the last trial, were very

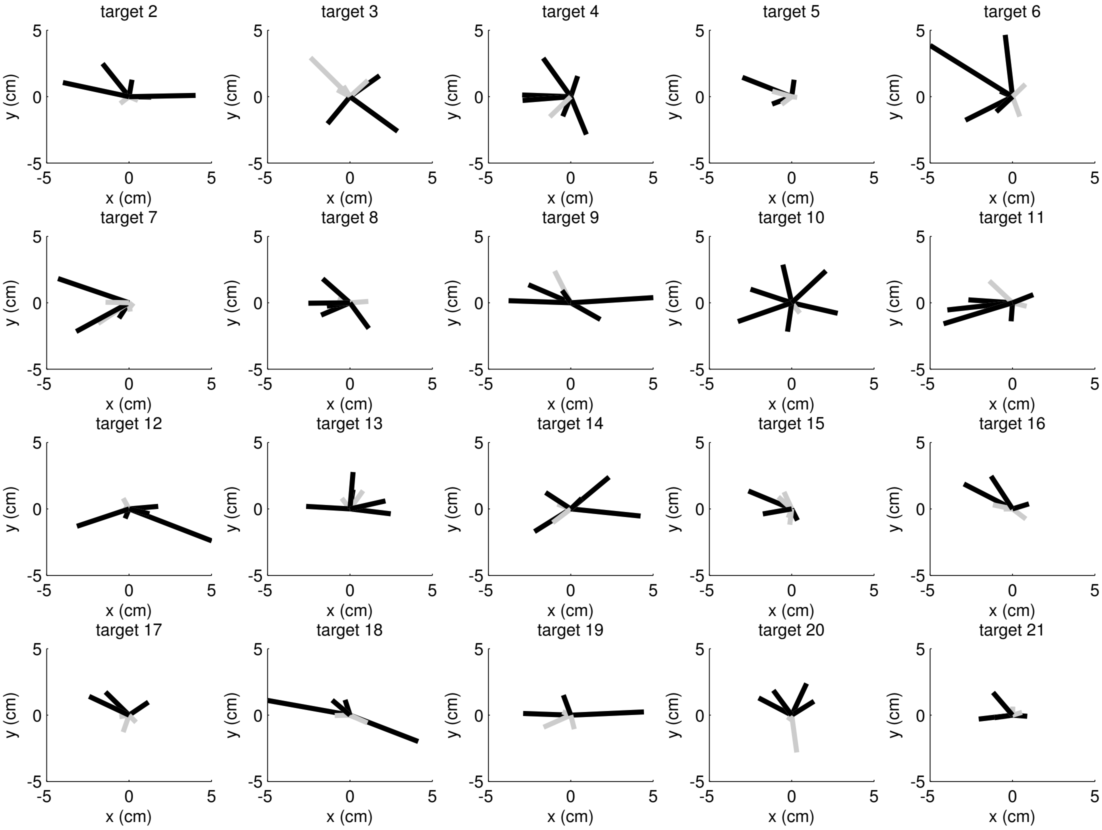

Figure 4.2: Total drift vectors for each subject and each target. Significantly drifting vectors are plotted in light gray, whereas non-drifting vectors are plotted in black. There was no apparent common drift direction between subjects for all targets. The wide distribution of total drift vectors indicates that reproductions did not drift to a common pattern across subjects.

inhomogeneous across subjects. Different directions of the total drift vectors do not necessarily imply that subjects ended up at different reproduction patterns because the initial reproduction patterns were not identical between subjects. However, the median inter-subject reproduction dissimilarity (see Methods) was significantly (Mann-Whitney U test: $p<0.01$) larger in the last trial (median/ IQR: 4.61/4.76 cm) than in the 4th trial (median/ IQR: 3.4/3.22 cm) indicating that the inter-subject drift diversity increased during the experiment.

More detailed results about the time course of the drift (independent of the different directions) were obtained by the mean absolute drift distance (Figure 4.3A). The time constant of the mean absolute drift distance was $1/c=5.46+/-3.37$ trials (averaged across subjects, $N=7$). The mean absolute drift distance saturated at 2.63+/-0.39 cm and differed significantly from zero ($T(6)=17.92$, $p<0.01$). The RMS variance of reproductions did not change over trials (Fig. 4.3B).The slopes of the linear regressions of RMS variance were 0.01+/-1.32 cm/trial and did not differ from zero (T-Test on slopes of linear regressions, T(6)=0.76, p< 0.5). Thus, the memorized sequences did not drift towards a common pattern across subjects, but converged towards individual patterns.

4.4.3 Experiment III

4.4.3.1 Systematic changes of the mean reproduction position

All subjects were able to perform the task and to learn the modified target sequence during the 3 training trials. The mean time courses of the normalized reproduction errors across blocks and subjects of the exchanged target locations (5 and 15) and their neighboring target locations (4, 6, 14 and 16) are shown in Figure 4.4.

The interrelations of the systematic reproduction errors across blocks were analyzed with an ANOVA on the *mean normalized reproduction error* with the three factors *component* (2 levels: x/y), *trial* (16 levels: trials per block), and *target* (2 levels: first/second exchange within the sequence). Three of these ANOVA were performed separately, one for each of the three target pairs (4, 14, 5, 15, 6,16). For the target pairs 4, 14 and 6, 16 there was a significant main effect of the factor *component* (4, 14: F(1, 6)=19.80, p<0.01; 6-16: F(1, 6)=10.28, p<0.05). This effect occurred specifically for the reproductions to target 6 (x:-0.04+/-0.16, y:0.15+/-0.09]) but not for that of target 16 (x: -0.02+/-0.07, y: 0.01+/-0.09) as indicated by the interaction between the factors *component* and *target* (F(1,6)=6.15, p<0.05). This interaction occurred similarly for the reproductions on the target pairs 4, 14 (F(1,6)=5.94, p<0.06) and reflects the fact that directions of the small errors of reproductions neighboring the largely modified reproductions (5, 15) were not related to the direction of the target exchange. In contrast, the normalized reproduction errors of the modified reproductions were both dominated by a clear component in the x-direction (towards the new target), as indicated by the highly significant main effect of the factor component (F(1,6)=769.17, p<0.001) without a *component-target* interaction.

The time course of the reorganization of the sequence was analyzed by the effects and interactions of the factor trial in the ANOVA of the *mean normalized reproduction errors* applied for the targets 5 and 15. There was a highly significant main effect (F(1,6)=86.77, p<0.001) and an interaction with the factor *component* (F(15, 90)=29.46, p<0.001) related to the fast change of the reproduced position in the direction of the target exchange (Fig. 4.4A, solid, trial 1). The reproduction change occurred immediately after the target exchange as confirmed by the posthoc test showing that the x-component of the mean normalized reproduction errors did not differ within the trials -2 to 0 (0.06+/-0.12) and also not within the trials 1 to 13 (0.96+/-0.09). In contrast, the reproductions in all trials 1 to 13 after the target exchange differed significantly from those before (trials -2 to 0). The direction of reproduction change corresponded exactly to the direction of the reproduction since the y-component (overall mean: -0.01+/-0.15) did not differ between in any trial (posthoc p <0.9).

In contrast to this strong and fast change of the reproduction of the exchanged targets (5 and 15) the neighboring reproductions in the sequence (4, 14, 6, 16) did not change (Fig. 4.4A, dashed, dashed-dotted). The ANOVA on these neighboring reproductions

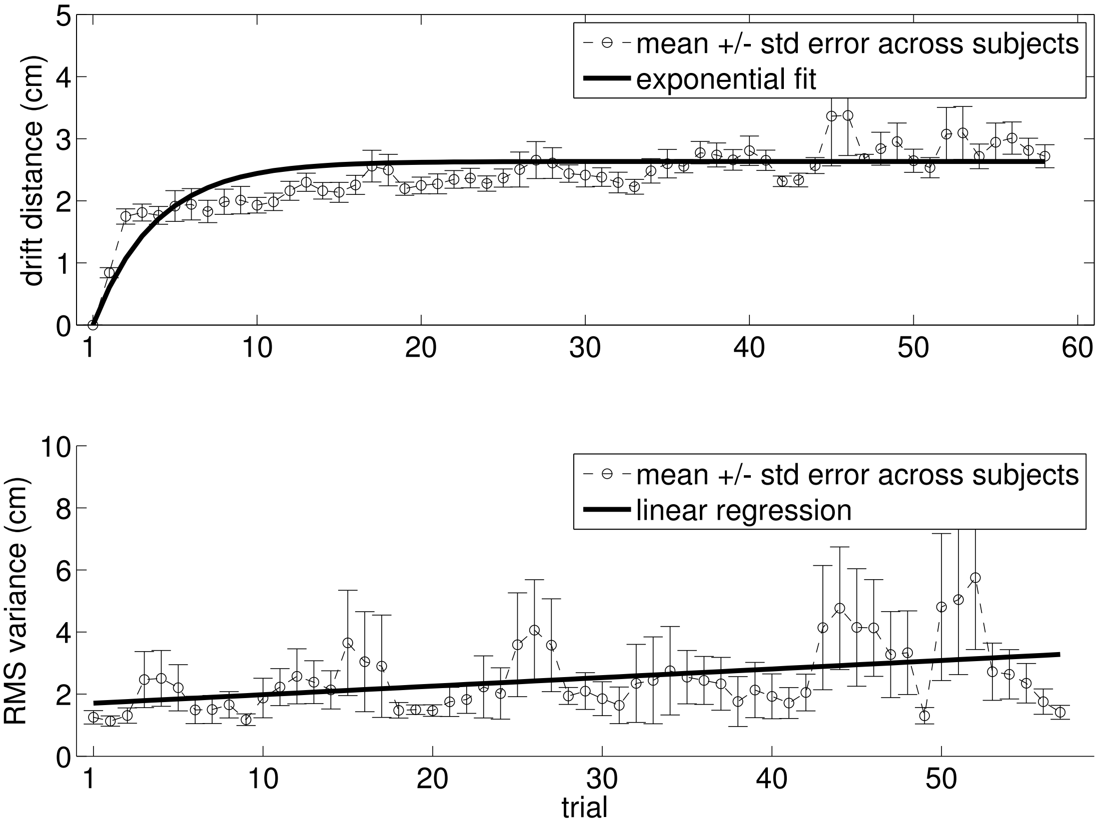

Figure 4.3: Analysis of the stability of the memorized sequence in the absence of feedback (Experiment II). A) The mean and the standard error of the mean absolute drift distance across 7 subjects (dotted line). The mean exponential fit was obtained from the mean of the fitted parameters across subjects (thick black line). Reproductions drifted from the initial reproduction location and the drift saturated with a time constant of 5 trials. B) The mean and standard error of the RMS variance (dotted line). The mean linear regression was obtained from the mean fitted parameters across subjects (thick black line).The RMS variance of reproductions did not increase over trials.

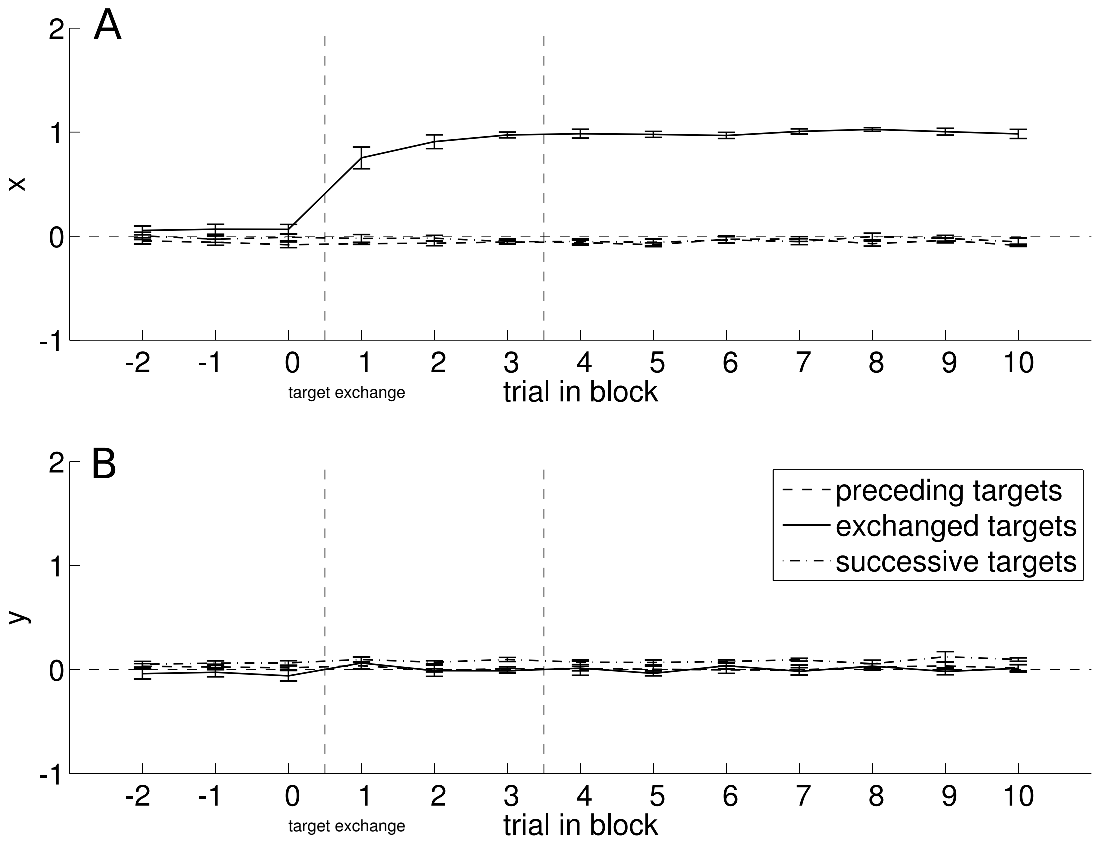

Figure 4.4: The x- and y-components of the normalized reproductions to the preceding target (4 and 14, dashed), the exchanged target (5 and 15, solid) and the successive target (6 and 16, dash-dotted). The plot shows the average across 6 blocks and 7 subjects. The target position was exchanged in the first trial of the block (labeled trial 1 on the x-axis). Reproductions to persistent target positions were transformed to the origin and reproductions to exchanged target position were transformed to (1, 0). The trials before the target exchange are the last 3 trials of the previous block. The exchanged target position was correctly reproduced in the first trial. Neighboring target positions were not affected by the sequence modification.

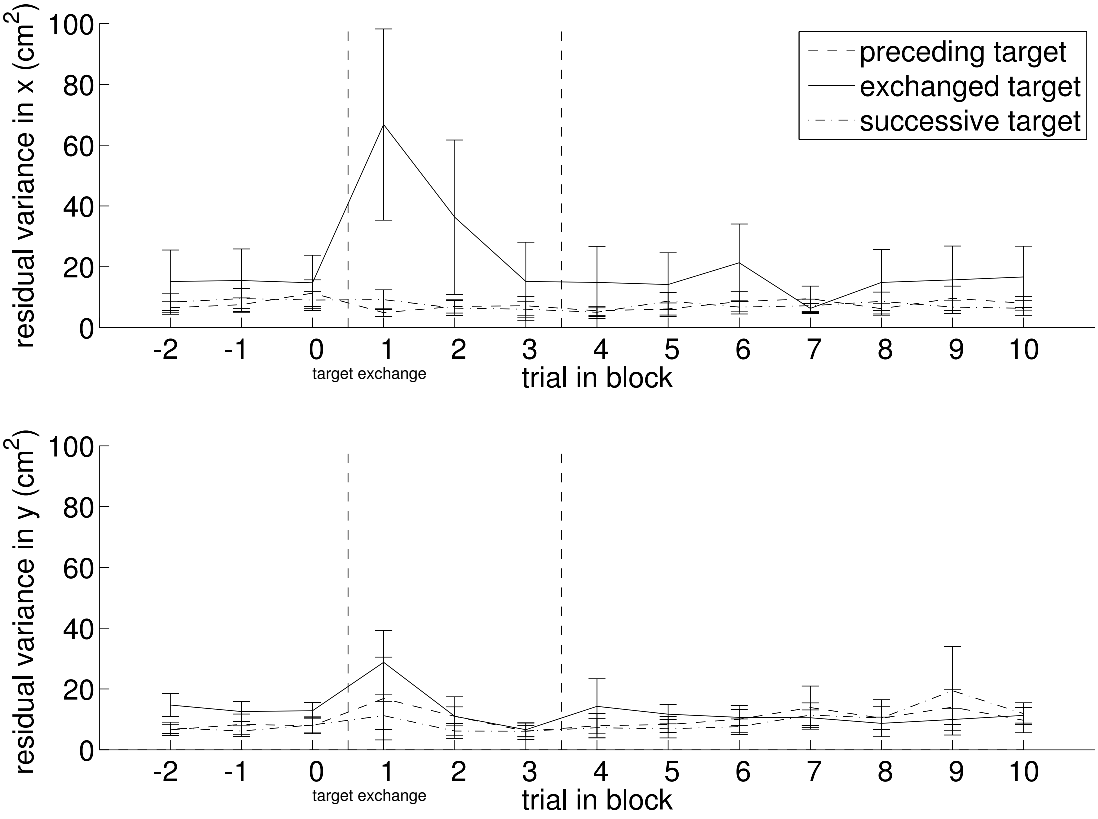

Figure 4.5: The mean residual variance in the horizontal and vertical component across 6 blocks and 7 subjects (+/- standard error). The residual variance temporally increased for reproductions to the exchanged target positions (dashed) after the target exchange in trial 1. The residual variance did not change for reproductions to preceding (dashed) and succeeding target positions (dash-dotted).

did not show any significant main effect or interaction of the factor trial.

4.4.3.2 Residual variance of the reproduction

The residual variance of reproductions, shown in Figure 4.5, was analyzed using an ANOVA with the same factors (*target*, *component* and *trial*) that were used in the analysis of the mean normalized reproduction error. No main effects or interactions of the factor trial were observed for targets preceding the target exchange (4, 14) and for targets succeeding the target exchange (6, 16). Thus, the residual variance for reproductions to neighboring target positions was not affected by the target exchange (Fig. 4.5A/B, dashed, dashed-dotted).

The residual variance of reproductions to exchanged target positions (5,15, Fig. 4.5A/B, solid) showed clear changes across trials (Main effect *trial*: F(12,72)=4.26, p<0.01) which differed between the direction of the target change and its orthogonal direction (Interaction *trial x component* F(12,72)=2.26, $p<0.05$). The Scheffé posthoc test on this interaction showed that the residual variance in the x-component was higher ($p < 0.05$) for trial 1 (66.80+/-83.19 cm^2) than for all remaining trials (16.72+/-30.20 cm^2). The residual variance in the y-component did not change over trials (posthoc, $p < 0.9$). Thus,the residual variance increased specifically in the direction of the target exchange, and not in the orthogonal direction during the reorganization of the reproduced sequence.

4.4.3.3 Inter-response intervals

There was a significant difference in the inter-response intervals between the three target groups (Friedman-ANOVA, $p < 0.01$). The inter-response intervals before the modified reproductions (5,15, median +/- IQR: 0.92 +/- 0.08 s) were larger (post-hoc, $p < 0.01$) than those before their neighbors (4, 14, 6,16: median +/- IQR: 0.83+/- 0.07 s), and these in turn were larger (post-hoc, $p<0.01$) than the inter-response intervals before the remaining reproductions (median +/- IQR: 0.70+/- 0.09 s). These differences can point to differences in recall time or simply be related to differences in movement duration. However, the signs of the differences in the inter-response interval did not correspond to the differences in movement amplitudes that were largest for the remaining targets (16.93 +/-3.49 cm), intermediate for the exchanged targets (14.73+/-5.82 cm), and smallest for the neighboring targets (12.00+/-11.07 cm). Thus, assuming similar movement speed, the differences in the inter-response interval seem to be related to the recall time.

4.5 Discussion

The three experiments revealed several main results. Subjects learned to point with a pencil to a sequence of 21 target positions, which were presented on a writing tablet, until they gained a stable representation of the sequence. Almost all subjects were able to reliably reproduce this pointing sequence from memory after 25 presentation and reproduction trials. The assignment map for a representative subject (Fig. 4.1) illustrates how the sequence is acquired in the early learning phase. The sequential buildup proceeded almost linearly from the beginning to the end of the sequence whereas accuracy did not improve in the early learning phase. These features seen in a typical individual subject (Fig. 4.1) are very similar to the group behavior in the same task as it was shown in a previous paper (Drever, Straube & Eggert, 2011a). In the absence of any further feedback (Experiment II) the pointing sequence acquired in this setup drifted with repeated reproduction towards a stable pattern. However, each individual subject developed an individual drift. In contrast to the constant error indicating drift, the variance of the reproduction did not change across trials. When two isolated target positions of the sequence were suddenly modified (Experiment III) subjects were able to perform an appropriate reorganization of the learned sequence within 1 to 3 trials. Neither mean position nor variance of reproductions to neighboring target positions were affected during this reorganization of the sequence. The latencies of reproductions to exchanged and neighboring targets were longer than those to the remaining targets.

4.5.1 Variability and drift of the reproductions of spatial configurations

Variability and drift were extensively investigated for experimental tasks in which spatial configurations had to be reproduced not sequentially as in the current study but in parallel as in the study of Giraudo & Pailhous (1999). Under these conditions neither variability nor drift showed significant time courses after complete learning. Drifts of the memory content in the absence of feedback occurred only after very short initial training. In contrast, in our sequence learning experiment significant drifts occurred even after a considerable number of training trials when learning of the sequence had already reached a certain level of saturation (see Fig. 4.1). It should be noted that saturation in the parallel configuration learning is related to the learning progress in accuracy. Saturation in our experiment is related to sequential build up. Experiment I showed that progress in accuracy was minimal under sequence learning. Thus, the occurrence of drifts in the mean reproduced position in our sequential task may be related to a lower degree of consolidation in the learning of spatial accuracy. This is also supported by the observation that the accuracy error in Experiment I (2.87 cm) was larger in our sequential reproduction task than in the parallel configuration task of Giraudo & Pailhous (1999) (accuracy: 1 cm).

Drifts in the parallel configuration learning task were attributed to common principles of shape recognition (Todorović 2007). However, the increasing inter-subject reproduction dissimilarity during Experiment II showed that the drifts occurring in the absence of feedback in our experiment did not converge toward a common pattern.

All these differences between the sequential and the parallel conditions may point to a fundamental difference between these two memory tasks in the type of progress that is achieved. In the parallel configuration learning task the spatial relations between all targets are simultaneously available whereas in the sequential learning task spatial relations between targets have to be indirectly derived from memory. Therefore learning of position information of single item may dominate pattern learning in the sequence learning task.

4.5.2 Modifications of sequence items and effects on neighboring items

The sequence modification did not lead to a breakdown of the whole sequence, but subjects were able to recall the modified sequence one or two trials after the modification. This result is in line with other experiments showing that local modification of a memory sequence can be performed without reorganization of the whole sequence, especially in the early learning phase. Wilde & Shea (2006) have shown with transfer tests that local changes in a 16-element movement sequence did not impair performance. In contrast, global changes such as shuffling intact subsequences (Sakai, Kitaguchi & Hikosaka 2003) or reversal of the whole sequence (Rand et al. 1998) in late learning phases profoundly affected the performance and lead to an increase in the number of errors. The results suggest that the memorized sequence can be locally modified after learning, whereas global changes of the sequence lead to the acquisition of a new sequence.

The local changes in the target sequence only had a local effect. The mean reproduction position of the exchanged target position, but not that of neighboring target positions, changed after sequence reorganization. This result shows that the position information of the changed item can be selectively modified independently of the position information of its neighbors. The possibility to change the position information of single targets without changing neighboring items suggests that the target locations were encoded independently of each other for each item. The question whether the item and order information of sequences are coded independently of each other or in a distributed fashion has been addressed from a modeling perspective with parallel distributed processing models (PDP) in which items are encoded in a context depended manner, i.e., item information is not independent from order information (Jordan 1986, Cleeremans & McClelland 1991, Botvinick & Plaut 2006, Nakahara et al. 2001). In contrast, most models of short term memory implement an independent encoding of item and order information (Burgess & Hitch 1999, Page & Norris 1998). Long term memory is also modeled with an independent encoding of item and order information (Sandamirkaya & Schöner, 2011). The possibility to selectively modify single target positions without effecting neighboring target positions favors an independent encoding of item and order information during the early phase of deferred imitation learning of long spatial sequences.

The high selectivity of the estimate of the within-subject residual variance obtained in Experiment III also points in the same direction. The residual variance increased temporally during the reorganization specifically in the direction of mean change and only for reproductions to the actually modified target positions (5, 15), but not for the reproductions to neighboring target positions in the sequence. Notably this effect cannot be explained by effects on the variance estimates induced by mean changes during the estimation interval because the mean residual variance used in our analysis is an unbiased within-subject, and within-trial estimator. Thus, this observation reflects an effect of sequence reorganization on the variable error and is not a pure byproduct of the selective change of the constant error on our variance estimate.

Increased variable error of movement production is characteristic at the beginning of the early phase of motor learning (Müller & Sternard 2004). Large motor variance may reflect processes related to the reorganization of a motor response such as exploration of the space of possible movements (Cohen & Sternard 2009). Therefore, the selective increase in residual variance during sequence reorganization suggest that in our experiment not only target information was stored specifically for a single item, but also the relearning mechanisms were operating in a specific way on the different pointing movements. It seems that the reorganization of the movements that had to be modified could be selectively facilitated without interacting with the consolidation state achieved for the single movements neighboring in the sequence.

In that respect reorganization of the movement sequences investigated in this study differs fundamentally from the reorganization of periodical movements as described by the dynamical system approach for the learning of movement patterns (Zanone & Kelso 1992). Reorganization of such movements is typically reflected in changes of a global movement parameter (such as the relative phase in bi-manual coordination) involving all parts of the movement. These changes are not restricted to a temporal segment of the whole period. Nevertheless, increased variability of the global movement parameter is a characteristic of ongoing reorganization of the system in the generation of periodical movements as well.

The observed specificity of the changes in mean and variance of reproduced position for the exchanged items may point to a general organization principle of movement sequences. However, it is important to stress that the presented results do not allow a generalization to other experiments. In our experiment the sequence order of the replaced items (5, 15) was identical in each block. Moreover these positions in the sequence were preselected by the instructions during the practice trials that made subjects aware of which targets were exchanged in the upcoming experiment. These features of our experimental conditions may have induced a segmentation of the sequence that prevented these particular items around the modified one from being incorporated into a chunk. This is supported by our observation that the longer inter-response intervals before reproductions to the exchanged target were larger.

5 Discussion

We introduced a new paradigm in order to investigate the learning process in deferred imitation learning of long spatial sequences. In this paradigm a long sequence of 20 target positions was presented on a screen and then reproduced in the absence of stimuli after presentation. The key feature of this paradigm is that sequences are too complex to be learned at once and are reproduced incompletely and inaccurately during learning. First, we developed an assignment algorithm as a method to analyze incompletely and inaccurately reproduced sequences of pointing movements (Drever, Straube, & Eggert, 2010). Based on the sequence assignment the error measures *number of omissions*, *order error* and *accuracy error* were evaluated. We were able to show that these error measures were appropriate to analyze the buildup of sequential context and the improvement in accuracy simultaneously for incompletely and inaccurately reproduced sequences because 1) the estimate of order errors based on the assignment algorithm was more accurate than the estimate of order errors based on a nearest neighbor assignment and 2) a comparison of errors based on a manual assignment showed that the assignment was very similar to judgments by human operators.

The characterization of the learning process (Drever, Straube & Eggert, 2011a) during the acquisition of long sequences of pointing movements and saccadic eye movements showed that long sequences could be acquired in a rather short time of about 20 minutes. The learning process was focused on the prolongation of the sequence, whereas the improvement of accuracy of single items did not occur in this early learning phase. The sequence was acquired by focusing on a subsets of items in each trial. Subjects started learning with the first 1-5 target positions at the beginning of the sequence advancing with one target per trial to later target position in the order of the sequence. Retention tests have shown, that the sequence learning was not a temporary effect but that the sequence was retained for at least two weeks. Subjects were able to acquire the sequence with different effectors, either with manual pointing movements or with saccadic eye movements. The reproduction performance was not dependent on the effector used for sequence production and the learning processes were qualitatively similar between eye and hand. Further, the sequence could be transferred between different effectors. Sequences learned with the dominant hand could be reproduced with the non-dominant hand and sequence learned with eye movements could be reproduced by manual pointing.

The error distributions of single target positions were analyzed, in order to find indicators for the memory representation of spatial sequences (cf. Section 1.4.4). The detailed analysis of the reproduction distributions showed that the pointing positions did not depend on the direction of the previous target position. This result suggests that the end point of the movement rather than the displacement from the previous target position is controlled. Further, an analysis of the error propagation showed that directional errors between successive pointing movements were rarely correlated. This result further supports the view that end point positions were controlled and represented.

When the sequence was reproduced repeatedly in the absence of any feedback, e.g. the sequence was not presented between successive reproductions, the representation of the memorized sequence drifted towards a stable pattern. The sequence representation did not drift towards similar patterns between subjects, as observed in spatial configuration reproductions (Giraudo & Pailhous, 1999), but drifted to subject specific patterns. Further, the variance of reproduction did not change over trials. These results suggest that the representation of sequences stabilize to subject specific patterns in deferred imitation learning of long spatial sequences.

In further experiments the sequence was modified by replacing two target positions with new target positions. Subjects were able to learn the modified sequence within only 2 to 3 trials. This local replacement did not disturb the performance for the rest of the sequence. Further, the replacement did neither affect the position nor the variance of reproductions to the preceding and succeeding (i.e. neighboring) target positions, supporting the view that single target positions are represented in memory independently of each other. However, the longer intervals between reproductions to exchanged and neighboring targets opposed to the rest of the target positions may indicate that these particular target positions were reproduced or stored in a specific way. Thus, from our experiments it is not known whether the independence we observed holds for all items or whether it was related to that specific memory or recall mode.

5.1 Comparison with previous experiments

We investigated for the first time deferred imitation learning of long sequences. The assignment algorithm, which was specifically developed to analyze deferred imitation learning of long sequences is unique and allows the assignment of incompletely and inaccurately reproduced sequences. Other approaches to analyze long memory-guided sequences which are not guided by visual stimuli are not known to the author. Assignment methods based on local deformations which were developed to analyze short sequences (Sekuler et al., 2003), were not suitable for the analysis of longs sequences (Drever, Straube & Eggert, 2010). Because of the missing methodological tools, it has previously not been shown that these long sequences can be acquired in such a short time. Importantly, previous studies could not show which strategy is applied to determine the order of acquisition, either because the acquisition order was determined by the stimulus or task instruction (Hikosaka et al., 1995), or because the sequence was short enough to be learned in a single shot (Sekuler et al., 2003).

The feature of our task that sequences are acquired in a relatively short time of 20 minutes is important because it shows that long spatial sequences can be quickly acquired. Most clinical test batteries for memory loss focus on immediate serial recall to probe spatial memory. In such tests, such as the working memory index (WMI) in the Wechsler Adult Intelligence scale (WAIS, Kaufman AS & Lichtenberger, 2006), the evaluation of sequential visual memory is not included. The fast acquisition of sequences found in deferred imitation learning of long spatial sequences and the retention in long term memory after this short learning period may provide a clinical tool for the assessment of deficits in visual long term sequence memory.

The fast acquisition of sequences is a general feature that is found in sequence learning. For example, learning progress in our paradigm and the 2x10 task was quite similar. Sequences were acquired in 10-15 trials in our learning paradigm (Drever, Straube & Eggert, 2011) and in the 2x10 task (Sakai et al, 1998; Sakai, Kitaguchi & Hikosaka, 2003). Further, in the serial reaction time task sequences were acquired in 80 trials and in 16 trials in the serial reaching task (Wilde & Shea, 2006). Thus, the short learning time in deferred imitation learning is comparable to the learning time in stimulus-guided learning. Our results show that fast acquisition of long sequences is also possible in deferred imitation learning of long sequences.

The qualitatively similar learning progress with eye and hand movement suggests that an effector independent representation is learned. The effector independence of sequence representation found in our task has been also demonstrated in other studies for the exchange from the dominant to the non-dominant hand (Rand et al., 1998, Park & Shea, 2002). According to Hikosaka and colleagues (1999) sequences are acquired concurrently in visual and motor coordinates. The representation in visual coordinates is effector independent and can be quickly acquired, whereas the representation in motor coordinates is effector dependent, acquired more slowly and requires less cognitive resources for execution. Our findings suggest that the long sequences of manual pointing and saccadic eye movements are represented in visual coordinates. An automated representation in motor coordinates does not seem to develop over a short time period of two weeks.

The error propagation between target reproductions in long sequences has not been analyzed before. This phenomenon has been investigated for short sequences of memory saccades (Ditterich, Eggert, Straube, 1998), where a large part of the directional saccadic error was correlated. A possible explanation of this result was that some saccades can be executed as groups, or chunks. Therefore, we argue that the missing of error propagation in our data indicates that the target positions of the sequence are stored as independent targets, rather than chunks. In the literature (Verwey, 1996; Sakai, Kitaguchi & Hikosaka, 2003), chunking in sequences plays an important role. Typically the timing between single items is used as an indicator for chunking. Our detailed analysis on the error propagation and the reproduction distribution offers an alternative approach to analyze chunking in movement sequences. This analysis provides a new indicator for chunking in long sequences of pointing movements, which follows the arguments from Bock and Arnold (1993) and Ditterich, Eggert and Straube (1998).

The drift of sequences was not analyzed before in the literature for long term memory, but only for spatial patterns by Giraudo & Pailhous (1999). These authors proposed that memorized spatial patterns drift (in the absence of feedback) towards Gestalt-like figures. In contrast to this observation, we found subject specific drifts towards individual patterns. The differences in the findings may be related to the fundamental differences between both tasks. Spatial patterns allow to use the relations between target positions for memory encoding, whereas relations between targets are only explicitly available for succeeding target positions during stimulus presentation. Thus, spatial patterns may be better memorized as Gestalt-like subject-independent patterns than long spatial sequences.

The effect of the local sequence modifications has been explored previously by Wilde and Shea (2006) with locally distorted sequence transfer. In this task a sequence non-proportionally scaled after learning in a transfer condition. They found that the local change did not impair performance in the early phase (1 day of learning) and conclude that the sequence can be flexibly modulated during this learning phase. The fast reorganization of the sequence in our task and the selective effect on the exchanged target positions support the view that sequences are represented in a visual representation that is still very flexible during the early learning phase.

5.2 Characterization of deferred imitation learning of long spatial sequences

The first main question of this thesis concerned the main characteristic features of deferred imitation learning of long sequences. Specifically the learning speed, the retention time, the acquisition order, and the learning content were investigated. Sequences were acquired in a rather short time (about 20 minutes) and were retained for at least two weeks. The long term retention is an important feature of the learning process in this task because the large learning progress on the first day may be a good indicator for the successful transfer of sequential context into long term memory. In stimulus-guided learning paradigms it could not be shown explicitly whether a long sequential context is acquired because stimuli could have been used as recall cues in stimulus guided learning. We were able to show that a long sequential context can be quickly acquired in deferred imitation learning.

We could show that the order of sequence acquisition occurred in the order of sequence presentation through the analysis of the serial position curves (Drever, Straube & Eggert, 2011: Figure 3.2). This specific order of sequence acquisition has also been found in the 2x10 learning task (Sakai et al., 1998). The 2x10 task is very similar to the deferred imitation learning task. Both tasks require the learning of 20 spatial positions. The differences are that 1) the stimuli were present during reproduction, 2) the order of acquisition was defined by the task instruction and 3) the spatial positions were constrained to a grid of 16 discrete target positions in the 2x10 task. These features of the 2x10 task favor a very efficient memory representation consisting of a sequence of categorical (symbolic) items while the learning progress is experimentally restricted to successive prolongation of this sequence by chunks that do not exceed two items. In contrast, in the current task categorical representation of the items is more difficult to develop because the number of possible target positions is not known from the beginning. Also, the order of acquisition was not constrained by the task instruction. Therefore, the current experiment showed that successive prolongation is a natural strategy to learn long sequences that is automatically chosen by all subjects. This systematic prolongation shows that subjects selected only the positions that follow immediately the last positions they had already stored from the complete sequence presentation. This selection is probably achieved by an attentional mechanism.

How such an attentional mechanism might operate during sequence learning is demonstrated with a conceptual extension of the N-STREAMS model (Figure 5.1). In this model, sequences are learned in the cortical chunking and recognition systems by repeated exposure. The connections between the chunking module and the working memory are modified such, that known sequences are recognized and anticipatorily executed. This mechanism explains sequence learning in the serial reaction time task in which no active, attentive selection of a currently trained subsequence is necessary. In order to account for the active selection of sub sequences we introduced an attentional mechanism. This mechanism gates the information by selecting the current set of target locations that are learned in the cortical chunking module. The cortical chunking module monitors which target locations are already learned and informs the attentional module which part of the sequence will be learned in the next trial. Our findings show that the this selections starts with the first items of the sequence and advances to later target positions. These findings suggest that an attentional mechanism has to be included in models of deferred imitation learning of long sequences.

Attentional selection seems to play an important role in many natural learning tasks in which subject have to focus on certain aspects of the stimulus. This attentional selection is probably not limited to item selection demonstrated in the current experiments, but may also concern selection of certain stimulus dimensions such as posture, rhythm and timing, or the step order. Such selections may be necessary to prevent working memory overflow. Our experiments focus the item selection occurring while learning long sequences. Other attentive selections were not investigated.

The systematic prolongation is not a general feature of sequence leaning. In serial reaction tasks all sequence elements were concurrently acquired (Boyer, Destrebecqz, Cleeremans, 1998). Also in serial reaching tasks (e.g. Ghilardi et al., 2009) sequence elements were not acquired in a systematic order. These findings suggests that systematic selection of sequence items during learning is important especially in tasks in which reproduction from memory cannot be replaced by stimulus guided reproduction.

During the 25 learning trials, the accuracy of reproduction did not improve in the present study. Thus, in the early learning phase the learning progress was dominated by the buildup of the sequential context and the improvement of metric accuracy played only a minor role. In contrast to this finding in our studies, other studies on deferred imitation of short sequences (Agam et al., 2007) and serial reaching tasks (Ghilardi et al., 2009) showed an improvement of accuracy. This difference in reproduction performance suggests that learning progress in our task differs with respect to the acquisition order (successive versus parallel improvement across items), and with respect to the information that is actually stored in memory. Since there is no need to store long sequential context in repeated immediate recall or in serial reaction time tasks it is plausible to assume that memory resources can primarily be used for learning of metric accuracy. In contrast, the completion of the total sequence seems to be the primary goal in deferred imitation learning of long sequences. This primary goal seems to be more relevant than improvements in accuracy. Besides these two extremes of learning processes acting either in parallel or successive across the sequence items, intermediate forms may also exist. In a

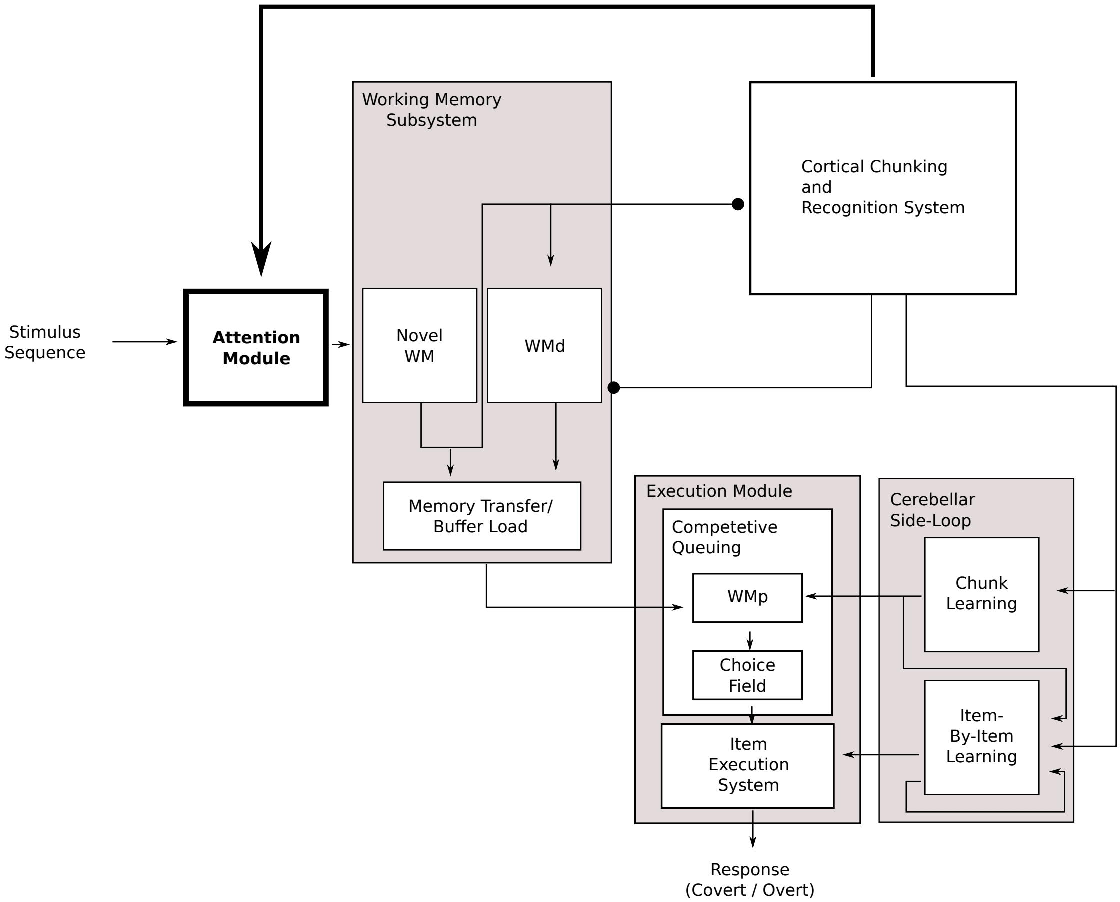

Figure 5.1: The modified conceptual N-STREAMS model. The additional attention module is denotd by thick black lines.

preliminary (unpublished) series of pilot experiments we modified our learning paradigm by providing metric feedback after each pointing movement, but only for positions reproduced from memory. In this experiment we observed the same successive improvement across sequence items but significant accuracy improvement in contrast to our standard setup. Thus, this condition was an example for an intermediate learning mode between that of the serial reaction time task and that of deferred imitation learning.

5.3 Memory representation in early deferred sequence learning

The second question concerned the memory representation of long sequences in deferred imitation learning. Considering that learning may occur at different levels, e.g. effector specific motor programs or more abstract goal representations, it is interesting at which level deferred imitation of long sequences operates (cf. Section 1.4.2). The general effector independence in our learning task suggests that learning proceeds on a higher, abstract level. This acquired representation does not seem to generalize across sequences, since the learning of a new sequence was not facilitated by a previous sequence acquisition. Thus, a generalization of an abstract motor program, as proposed in schema theory, did not occur in our experiment. The acquired memory resembles rather to rote learning or a recording on a tape than condensation of stimuli into a schema.

The single items of seem to be represented independently from each other, as suggested by the missing error propagation between memorized target positions, the almost circular error distributions and the restricted effect of a local sequence modification. These independent representations differ fundamentally from a fluent movement representation that is acquired in the automated stage in motor learning (Hikosaka et al., 1999).

5.4 Conclusion

With deferred imitation learning of long sequences we successfully introduced a new learning task that allows to investigate complex sequential motor learning which require attentional focus on specific aspects. We were able to show that an attentional mechanism guides the learning process and proceeds sequentially from the first to the last item in the sequence. This mechanism enables the learning of complex movement sequences and optimizes the learning speed. Furthermore, the results showed that early learning phase was dominated by the acquisition of new sequence elements rather than by accuracy improvements. Together with the findings of effector-independence these results suggest that abstract movement plans play an important role in early sequence learning. The analysis of memory representation suggests that target positions are stored independently from each other in this specific learning task. This was further confirmed by local sequence modification that did not affect memorized positions of adjacent targets. These results suggest that chunking may not play such an important role in deferred imitation of long spatial sequences as it does in other sequence learning tasks.

6 Zusammenfassung

Um komplexe Bewegungssequenzen zu erlernen, ist es notwendig, eine aktive, aufmerksamkeitsgesteuerte Selektion des gelernten Inhalts vorzunehmen. Der dazu notwendige Selektionsmechanismus kann nicht in klassischen, stimulusgetriebenen Sequenzlernparadigmen untersucht werden, da er erst bei Bewegungsausführungen, die nicht durch externe Stimuli angeregt werden, notwendig ist. Im *verzögerten Imitationslernen* wird die gesamte Sequenz präsentiert und die Reproduktion wird erst nach Beendigung der Präsentation durchgeführt. Um zu untersuchen wie die Selektion in natürlichen Lernsituationen abläuft und welche Einflussparameter es hierbei gibt, haben wir ein neues Lernparadigma entwickelt, in dem lange Sequenzen durch verzögertes Imitationslernen erlernt werden. In dieser Lernaufgabe wird eine lange Stimulussequenz auf einem Grafiktablett präsentiert und nach dem Ende der Präsentation durch manuelle Zeigebewegungen reproduziert. Da die Sequenz die Kapazität des Kurzzeitgedächtnisses durch ihre Länge überschreitet muss sie in mehreren Versuchen reproduziert werden. Damit muss eine aufmerksamkeitsgesteuerte Selektion beim Lernen stattfinden.

In der ersten Studie wurde eine Methode für die Evaluierung der Reproduktion in der neuen Lernaufgabe entwickelt. Die Zuweisungen der Reproduktionen zu den Zielpositionen birgt eine große methodische Schwierigkeit. Dieses Problem wurde durch einen Zuweisungsalgorithmus, der die Reihenfolge der Reproduktion mit in Betracht zieht, gelöst. Der Algorithmus wurde erklärt, mit einem Nächster-Nachbar-Algorithmus verglichen und durch einen Vergleich mit einer manuellen Zuweisung validiert. Die Ergebnisse zeigen, dass der Zuweisungsalgorithmus eine angemessene Methode für die Analyse von langen Zeigebewegungssequenzen ist und dass er für die Evaluierung der Reproduktion und des Lernprozesses im verzögerten Imitationslernen von langen Sequenzen geeignet ist.

In der zweiten Studie haben wir weiter untersucht, wie sich die Versuchspersonen lange Zeigesequenzen aneignen. Die Studien der Langzeiterinnerung haben gezeigt, dass die Sequenzen für mindestens zwei Wochen im Langzeitgedächtnis behalten werden. Eine Untersuchung zum Effektortransfer hat belegt, dass die Sequenzen in einer effektorunabhängigen Repräsentation behalten wurden. Die Verteilung der Zeigepositionen wurde detailliert analysiert, um das Kontrollsignal bei den Zeigebewegungen zu charakterisieren. Die Analyse zeigt, dass die Positionsfehler unabhängig von der Bewegungsrichtung waren und dass es keine Fehlerfortpflanzung zwischen sukzessiven Zeigebewegungen gab. Diese Ergebnisse weisen darauf hin, dass in dieser Lernaufgabe eher Endpunkte als Bewegungstrajektorien repräsentiert werden.

In der dritten Studie wurde die Organisation und Umordnung der Sequenzrepräsentation im Gedächtnis evaluiert. Änderungen in Sequenzreproduktionen, zwischen denen die Sequenz nicht noch einmal präsentiert wurde, haben gezeigt, dass die erinnerten Zielpositionen in den ersten Durchgängen von der initialen Repräsentation abtreiben, wobei sich diese Veränderung nach fünf Durchgängen stabilisiert. Die Analyse der Abweichungen der einzelnen Zielpositionen macht deutlich, dass es keine systematische Veränderung für einzelne Versuchspersonen gab, und dass die Repräsentation nicht zu ähnlichen, sondern zu verschiedenen Mustern zwischen Versuchspersonen abgewichen ist. Um zu untersuchen, ob die Sequenz unterteilt in Teilsequenzen (engl. chunks) abgespeichert wird, haben wir ein Experiment durchgeführt, in dem zwei Zielpositionen einer wohlbekannten Sequenz verändert wurden. Dieser Austausch hat weder die Position, noch die Varianz von benachbarten Zielpositionen beeinflusst. Diese Resultate unterstützen den Standpunkt, dass eher einzelne Zielpositionen als Teilsequenzen gelernt werden.

Folglich legen unsere Studien nahe, dass das Erlernen von komplexen Bewegungssequenzen durch einen aktiven Selektionsprozess geführt wird, der es ermöglicht, sich schnell abstrakte Handlungspläne anzueignen. Unsere Ergebnisse unterstützen des Weiteren die Ansicht, dass diese Handlungspläne als Folge von unabhängigen, absoluten Zielpositionen repräsentiert werden.

7 Summary

Learning complex movement sequences requires an active, attentional selection of the content that is learned. The selection mechanism can not be investigated in classical stimulus-guided sequence learning paradigms because it requires a movement sequence production that is not triggered by external stimuli. In *deferred imitation learning* the whole stimulus sequence is presented and reproduction is started only after the presentation has ended. In order to investigate how the selective control of the learning process proceeds in natural learning situations and to investigate all influencing parameters we developed a new paradigm in which long sequences were learned by deferred imitation learning. In this task a long sequence of stimuli was presented on a graphic tablet and reproduced by manual pointing after the stimulus presentation was finished. Since the sequence exceeded the capacity of working memory because of its length it had to be reproduced and learned in several trials. Therefore, an attentional selection was required during learning.

In our first study a method for evaluating reproduction performance in the new learning paradigm was developed. The assignment of reproductions to target positions posed a major methodological difficulty. This problem was solved by introducing an assignment algorithm that takes the order of reproduction into account. The algorithm was explained, it was further compared to an algorithm that performs a nearest neighbor assignment and finally validated by a comparison to a human operator assignment. The results showed that the assignment algorithm is an appropriate method for analyzing long sequences of pointing movements and is suitable for evaluating reproduction performance and learning progress in deferred imitation learning of long sequences.

In the second study we investigated further how long sequences of pointing movements are acquired. Long-term retention tests showed that the sequences were retained for at least two weeks in long-term memory. A transfer test showed that the sequences were represented in an effector independent representation. The distributions of pointing positions were analyzed in detail in order to characterize the control signal of the pointing movements. The analysis showed that position errors to successive target positions were not dependent on the movement direction and further, that directional error did not propagate to reproductions of successive target positions. These results suggest that end points rather than movement trajectories are memorized in this learning task.

Our third study evaluated the organization and reorganization of the sequence representation in memory. The change in sequence reproduction without intermediate presentations showed that the remembered target positions drifted away from the initial representation, where the target drift saturated after about 5 trials. The analysis of the drift direction of representations of single target positions showed that there was no systematic drift direction for single subjects. Further it indicated that the representation did not drift to similar, but to different patterns across subjects. In order to investigate whether sequences are encoded in chunks or as single target positions we performed an experiment in which two target positions in a well learned sequence were exchanged. We analyzed the effect of the target exchange on target positions neighboring the exchanged target position. The target exchange effected neither the position nor the variance of neighboring memorized target positions. These results support the view that single target positions rather than chunks of target positions are memorized.

Thus our study suggests that the sequence acquisition is guided by an active selection process which is able to quickly acquire abstract movement plans. Our findings further support the view that these movement plans are represented as strings of independent, absolute target positions.

8 Publications

1. Drever J, Straube A, & Eggert T (2010). A new method to evaluate order and accuracy of inaccurately and incompletely reproduced movement sequences. Behav Res Methods, 43(1), 269-277.
2. Drever J, Straube A, & Eggert T (2011a). Learning deferred imitation of long spatial sequences. Behav Brain Res, 220(1), 74-82.
3. Drever J, Straube A, & Eggert T. (2011b).Organization and re-organization of long sequences of pointing movements. Submitted to Behav Brain Res.

9 Abstracts

1. Drever J, Eggert T & Straube A. Buildup of sequences in procedural memory. 19. Okulumotoriktreffen München-Tübigen-Zürich. 07.02.2009, Tübingen.
2. Drever J, Eggert T & Straube A. Kopplung von Ordnung und Inhalt beim sensomotorischem Sequenzlernen. 53. Jahrestagung der Deutschen Gesellschaft für Klinische Neurophysiologie und Funktionelle Bildgebung mit Richard-Jung-Kolleg München, 26.03-28.03.2009
3. Drever J, Eggert T & Straube A. Selective and nonselective memory buildup in the acquisition of long pointing sequences. Computational principles of sensorimotor learning. September 13.09-15.09 2009, Kloster Irsee, Germany.
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6. Drever J, Eggert T & Straube A. Sequence assignment considering spatial neighborhood and order: a new method to evaluate inaccurately and incompletely reproduced movement sequences. Interdisciplinary College 2010. 12.03-19.03.2010, Günne at lake Möhn, Germany.
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