The influence of eye movements on sequence learning

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Matthias Massing

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Dean:

Univ.- Prof. Dr. rer. nat. Cornelius König

Saarland University, Germany

Principal Advisor:

Univ.- Prof. Dr. phil. Stefan Panzer

Saarland University, Germany

Second Advisor:

Prof. Charles H. Shea, PhD

Texas A&M University, USA

"Wer aufhört besser zu werden, hat aufgehört, gut zu sein."

-Philip Rosenthal

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Abstract (English)

The aim of the dissertation is the systematic investigation of the role of eye movements in motor sequence learning. The literature offers contradictory findings on the question of whether eye movements are necessary for learning a motor sequence. For a closer look, three experiments were performed using two different movement sequences: a 16-element movement sequence, one-dimensionally presented on a horizontal plane (Experiment 1) and a simple motor sequence task, presented in two dimensions on a horizontal and vertical plane (Experiment 2 & 3). All sequences were performed via an extension and flexion motion in the elbow joint of the arm. Experiment 1 explored the role eye movements play in sequence learning and whether free eye movements improve sequence learning. The aim of Experiment 2 was to determine the role eye movements in movement sequence learning when the visual angle of the target information is systematically varied and eye movements are minimized by the instruction to fixate. Experiment 3 utilized both a physical practice group as well as a group acquired by observational learning. The purpose was to investigate the role of eye movements in observational learning in comparison to physical learning as well as the influence of eye movements on the development of a movement sequence representation following physical or observational practice. In all three experiments, an eye-tracking system was used to record and analyze eye movements. The dissertation provides five main results. First, movement sequences can be learned without eye movements; however, permitting the use of eye movements supports sequence learning. Second, eye movements facilitate sequence learning, especially when they are used in an early stage of learning, and third, eye movements facilitate sequence learning when the visual information is increased. Fourth, the results from physical practice can be extended to observational practice. Fifth, eye movements play an important role in developing a visual-spatial and motor representation.

Abstract (German)

Das Ziel der Dissertation ist die systematische Untersuchung der Rolle von Augenbewegungen beim motorischen Sequenzlernen. Die Literatur liefert kontroverse Befunde zu der Frage, ob Augenbewegungen zum Erlernen einer motorischen Sequenz notwendig sind. Zur näheren Betrachtung wurden drei Experimente mit zwei verschiedene durchgeführt: 16-elementige Bewegungssequenzen eine Bewegungssequenz, eindimensional auf einer horizontalen Ebene präsentiert (Experiment 1) und eine einfache motorische Sequenzaufgabe, zweidimensional, präsentiert auf einer horizontalen und vertikalen Ebene (Experimente 2 & 3). Alle Sequenzen wurden mittels einer Extensionsund Flexionsbewegung im Ellenbogengelenk des Armes ausgeführt. In Experiment 1 wurde untersucht, welche Rolle Augenbewegungen beim Sequenzlernen spielen und ob freie Augenbewegungen das Sequenzlernen verbessern. Ziel von Experiment 2 war herauszufinden, welche Rolle Augenbewegungen beim Sequenzlernen spielen, wenn der visuelle Winkel der Zielinformation systematisch variiert wird und die Augenbewegungen durch die Anweisung zum Fixieren minimiert werden. In Experiment 3 wurde sowohl eine physische Übungsgruppe also auch eine Gruppe, die durch Beobachtung aneignete, genutzt. Die Intension war zu untersuchen, welche Rolle Augenbewegungen beim Beobachtungslernen im Vergleich zu physischem Lernen spielen. Des Weiteren wurde der Frage nachgegangen, welchen Einfluss Augenbewegungen nach den jeweiligen Übungsformen (physisch/beobachten) auf die Entwicklung einer Bewegungsrepräsentation haben. In allen Experimenten wurde ein Eye-Tracking System verwendet, um Augenbewegungen aufzuzeichnen und zu analysieren. Die Dissertation liefert fünf Hauptergebnisse. Erstens, Bewegungssequenzen können ohne Augenbewegungen gelernt werden, jedoch unterstützen freie Augenbewegungen das Sequenzlernen. Zweitens, Augenbewegungen unterstützen Sequenzlernen vor allem dann, wenn sie im frühen Lernverlauf genutzt werden. Drittens, Augenbewegungen unterstützen Sequenzlernen, wenn die visuelle Information vergrößert wird. Viertens, die Ergebnisse können von physischem Üben auf Üben durch Beobachtung erweitert werden. Fünftens, Augenbewegungen spielen eine wichtige Rolle bei der Entwicklung einer visuellräumlichen und motorischen Repräsentation.

1. Introduction

A very common type of practice to learn a new motor skill is by performing the task physically (Adams, 1987; Shea, Kovacs, & Panzer, 2011; Wulf, Shea, & Lewthwaite, 2010). Another way to acquire new motor skills is to observe others performing the skill, which has been termed observational learning in the motor behavior literature (Badets, Blandin, & Shea, 2006; Blandin & Proteau, 2000; Carroll & Bandura, 1990; McCullagh, Weiss, & Ross, 1989; McCullagh & Weiss, 2002; Scully & Newell, 1985; Vogt & Thomaschke, 2007; Wolpert, Diedrichsen, & Flanagan, 2011, for a review). During both practice types, performers developed a dynamic representation, which is used to define the goal of the task, to program, and to control the execution of the movement. In the sequence learning literature, theoretical schemes such as those proposed by Hikosaka et al. (1999, 2002) suggest that the processing of movement sequence information is distributed in the brain in an independent spatial (e.g., spatial locations of end effectors and/or sequential target positions) and motor (e.g., sequence of activation patterns of the agonist/antagonist muscles and/or achieved joint angles) coordinate system with distinct neural networks, subserving each class of processing. According to this perspective, the learning of movement sequences involves both a fast-developing effector independent component represented in visual-spatial coordinates, as well as a slower developing effector dependent component that is represented in motor coordinates. Recently, inter-manual transfer research provided compelling empirical evidence that both types of practice (physical and observational) develop an effective coordinate system available for sequence production (Boutin et al., 2010; Keele et al., 2003; Shea, Kovacs, & Panzer, 2011; Verwey & Clegg, 2005).

Another line of research proposes a functional equivalence between action generation, action simulation, and perception of action in both, physical and observational

learning (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Jeannerod, 1994; 2001). Indeed, many experiments on observational learning have demonstrated that variables affecting learning through physical practice tend to affect observational learning in a similar way (e.g., Badets & Blandin, 2004, 2010; Wright, Li, & Coady, 1997; Shea, Wulf, Park, & Gaunt, 2001). Neurophysiological and brain imaging studies suggest that a set of common neural structures are activated during both, action production and action observation (e.g., Decety et al., 1997; Grezes & Decety, 2001). However, previous results (see also Hayes et al., 2012; Ong & Hodges, 2010) indicated that physical practice and observational learning relies on different types of representation (visual-spatial or motor coordinate).

Thus, a possible explanation for the differing nature of the representation acquired during either physical or observational learning could be related to eye movements, which were not systematically controlled in previous experiments. Therefore, one question that will be addressed in the continuation of the following experiments involves the determination of eye movements and the development of an efficient representation for movement production. In addition, the current experiments examine the role of eye movements for learning a movement sequence task physically. Previous experiments regarding motor sequence learning have yielded controversial findings on the role of eye movements. Marcus, Karatekin and Markiewicz (2006) showed that eye movements are necessary to learn a movement sequence.

Conversely, the results of other groups (e.g., Coomans et al., 2012; Remillard, 2003) indicated that eye movements are not necessary to learn a movement sequence. Remillard (2003) investigated the effect of eye movements by varying the distance of stimuli during sequence learning. In his experiment, the distance between the stimuli was systematically varied from 3.9° (small angle) to 14° (wide angle), hypothesizing that for a smaller angle, eye movements are not necessary to get all information, but beyond a certain

angle, eye movements become important in order to visualize the stimulus. His results showed that participants learned the sequence independent of the width of the angle. Remillard (2003) concluded that eye movements are not necessary in order to learn a sequence task. In an adapted serial reaction time (SRT) task experiment, Coomans et al. (2012) showed that participants learned a motor sequence without executing oculomotor movements. In this task, participants had to react to a pair of visual stimuli by pressing the corresponding keys as fast as possible. The targets in their task were presented in a visual field < 1° in which eye movements were not needed to visualize the target. To minimize eye movements, participants had to fixate on a cross, and the stimuli were presented only for 100ms. However, Coomans and colleagues only provided participants with verbal instruction to fixate on the cross. They did not use an eye-tracking system, and thus fixations were not controlled. Their results showed that eye movements are not necessary to learn a motor sequence task.

Marcus and colleagues (2006) used an SRT task (Nissen & Bullemer, 1987) to investigate the role of eye movements in physical and observational practice. They demonstrated in their experiment that eye movements reached the stimulus location prior to the stimulus onset. These anticipatory eye movements reflect sequence learning and lead to the conclusion that eye movements are necessary to learn a motor sequence task. There are conflicting conclusions regarding weather eye movements are necessary in order to learn a motor sequence. In summary, there seem to be two different lines of thought in literature, which are "Eye movements are necessary and/or eye movements are not necessary to learn a motor sequence".

In motor sequence learning, theories propose that learning consists of different stages (Bapi, Doya, & Harner, 2000; Hikosaka et al., 1999; Panzer et al., 2009; Verwey & Eikelboom, 2003). In an early stage of learning, movements are performed in a more

discrete manner. At the beginning of practice, this means that e.g. arm movements, move from one point to the other in a step-by-step consecutive manner. Later in practice, these arm movements become more sequential, fluent and smooth (Verwey & Eikelboom, 2003; Shea, Kovacs, & Panzer, 2011, for a review). Schmidt and McCabe (1976) showed that continuous visual control and attention are high in the early stage of motor sequence learning. Later in practice, visual control seems to decreases. Sailer and colleagues (2005) determined that visual control strategies change depending on the phase of learning, from pursuit at an early stage of learning to fixating on the final position at a late stage of learning.

Based on previous findings on the role of eye movements for motor sequence learning (e.g., Bird, Osman, Saggerson, & Heyes, 2005; Coomans et al., 2012; Heyes & Foster, 2002; Hikosaka et al., 1996; Kelly, Burton, Riedel, & Lynch, 2003; Marcus et al., 2006; Maslovat, Hayes, Horn, & Hodges, 2010; Press & Kilner, 2013; Remillard, 2003; Shea, Panzer, & Kennedy, 2016; Verwey, Shea, & Wright, 2015), this dissertation systematically investigated the influence of eye movements on motor sequence learning for physical as well as for observational practice.

Experiment 1 was designed to go into detail regarding the question of the role of eye movements¹ in learning a multi-element sequence. According to the theoretical perspectives of sequence learning which show that continuous visual control and attention are needed in an early stage of learning (Hikosaka et al., 1999), the hypothesis was that participants who were permitted to use eye movements would have an advantage in performance compared to participants instructed to fixate. Further, participants permitted

¹ Eye movements can be classified as fixation, saccades, pupil widening or pupil narrowing. The focus of the following experiments is on fixation and saccades. Note, there are also other conditions, such as tremor, micro saccades and drifts, which the author does not want to go in detail in this context.

to use eye movements should also reduce the requirement of visual control in the later stage of learning. Hikosaka and colleagues (1999) used functional magnetic resonance imaging (fMRI) in their study. They proposed that practice results in a shift of activity in neural structures. Further, they showed that, in an early stage of practice, the association cortices, and later in practice the motor cortices, are primarily involved in sequence learning. The associative cortex is related to the processing of visual-spatial information, whereas the motor cortex is related to somatosensory information. In the early stage of practice, controlled processes need continuous visual control of the location of the target. However, this visual control of the target becomes less important during practice because of the shift in reliance from controlled processes to automatic processes. According to Hikosaka et al. (1999), permitting the use of eye movements should offer an advantage, as they are important in the early stage of learning. However, fixating eye movements could lead to an inhibition of the development of a sequence representation, which is responsible for sequence production.

Building up on Experiment 1, Experiment 2 was designed to continue to investigate the role of eye movements on sequence learning when the visual angle of the target information is systematically varied and eye movements are minimized by the instruction to fixate. Although Remillard (2003) showed that eye movements do not seem to be necessary for learning a motor sequence regarding the distance of the target, Marcus et al. (2006) proposed that eye movements are an integral part of sequence learning. The purpose of the experiment was to systematically investigate the role of eye movements in motor sequence learning when eye movements are minimized and the visual angle of the target information is varied.

In Experiment 2, in contrast to the traditional SRT task (e.g., Nissen & Bullemer, 1987; Willingham, Nissen, & Bullemer, 1989), a sequence task where stimuli were

presented in two dimensions was used. Marcus et al. (2006) displayed the stimuli on a horizontal plane (one dimension), but the sequence used in Experiment 2 was displayed in a horizontal as well as in a vertical plane (two dimensions). In the traditional and most commonly used SRT task, participants have to press one of four buttons as a response to a target presented in a special location on a screen (Moisello et al., 2009). These targets are presented in a repeating order according to a sequence.

However, Experiment 2 used a simple motor sequence task presented in horizontal and vertical plane (two dimensions). Using two dimensions increases the need for using eye movements to obtain all visual information about the target position because the target can now be either on the vertical or the horizontal position. Further, two different target sizes (named "small" and "magnified") were used in the experiment. The magnified target size should make eye movements obligatory while performing the sequence task since eyes in this condition have to move over a long range. During the experiment, participants' eye movements were recorded via an eye-tracking system. Again, the intention was to combine the variation of stimuli size (see Remillard, 2003) and the instruction to fixate (Marcus et al., 2006). If eye movements are not necessary for sequence learning (Remillard, 2003), sequence learning should occur regardless of whether participants are instructed to fixate and the increase of the visual angle. However, if eye movements are an integral part of sequence learning (Marcus et al., 2006), sequence learning should be impaired when participants are instructed to fixate, especially when the visual angle is increased.

In Experiments 1 and 2, the motor sequence was performed physically by a flexion and extension arm movement. Experiment 3 extended the previous findings from physical practice to observational practice. In addition to a physical practice group, this experiment used an observational practice group. Furthermore, the task of Experiment 2 was utilized here again. The purpose of the experiment was to study the development of a movement sequence representation. However, while the performance and learning of movement sequences and the development of a movement sequence representation have received a good bit of experimental attention, little if any focused attention has been directed to participants' eye movements during movement sequences learning and how eye movements are involved in the development of a movement sequence representation. As described earlier, Hikosaka and colleagues (1999) suggested that intracortical bidirectional (loop circuits) connections develop between the neural structures of the association cortices to the motor cortex, basal ganglia and the cerebellum during practice. Visual-spatial information is processed at the prefrontal and parietal cortices, anterior basal ganglia (head of the caudate), and posterior lobe of the cerebellum, and motor information is processed at the motor cortex, mid-posterior basal ganglia (putamen), anterior lobe of the cerebellum, and dentate nucleus circuits.

In addition, Hikosaka and colleagues (1999) proposed that early on in sequence learning, similar brain structures (association cortices) are responsible for the processing of visual and auditory input information and oculomotor output information to control eye movements. Based on the theoretical scheme of Hikosaka et al. (1999), the expectation was that development of motor and visual-spatial representation would differ between the different experimental groups of participants instructed to fixate or permitted to use eye movements. According to the assumption that the association cortices are important in the early stage of learning (processing visual input information and control eye movements), participants instructed to fixate may have an inhibition in the development of an efficient sequence representation leading to a disadvantage in sequence production. Furthermore, participants with physical practice compared to those with observational practice have additional motor information as well.

2. Tasks and Experimental Setup

In Experiment 1, a 16-element movement sequence with eight reversal points was used. In this sequence, the rightmost and leftmost target position was in an angle of view of about 24 degrees (Ellenbuerger et al., 2012; Marcus et al., 2006). Nine elements were presented in a horizontal order. Only four out of the nine elements were a target to which the participants had to move a lever as fast as possible. Participants were only allowed to move the lever via extension and flexion of the elbow. After each trial, participants were informed about their total movement time, which was provided as knowledge of results (KR). This explicit feedback was expected to help participants perform the tasks more effectively (Rosenbaum, 2009).

Experiments 2 and 3 utilized a different presentation of the movement sequence. While in Experiment 1 the target presentation was in a horizontal plane, in Experiments 2 and 3 the visual target of the movement sequence was presented on a horizontal as well as on a vertical plane. The movement sequence used was presented as a spatial temporal pattern, with a duration of 1300ms, and shown in two different sizes (named "magnified" and "small"). Participants moved a lever through the sequence pattern via flexion and extension arm movements. In Experiment 2 as well as in Experiment 3, participants received KR. After performing, the target pattern and the produced movement pattern were superimposed on the screen, and the root mean squared error (RMSE) was shown as a form of KR. The lower the RMSE, the more accurate is the participants' performance.

All experiments in this dissertation were based on an extended KR learning paradigm with a retention test and several transfer tests to examine specific issues. The retention test was designed to measure learning approximately 24 hours after acquisition and was performed under the same conditions as experienced during the acquisition phase. Further, participants who were permitted to use their eyes developed an internal representation of the task that was capable of sustaining performance in a retention test. In the experiments of Marcus et al. (2006) and Coomans et al. (2012), sequence learning was measured by a random sequence and not after a retention interval. Instead of a random sequence, a retention interval induced memory consolidation processes (see Albouy et al., 2006).

The transfer test was different in all three experiments. In Experiment 1, the transfer paradigm consisted of two transfer tests: a transfer opposite test, whereas groups of FIX and FREE changed their condition; and a transfer test, named NOVISION test. In the NOVISION test, participants were provided no illumination of the targets. These transfer tests provide evidence regarding to which extent eye movements are involved in sequence learning as well as if visual information is stored in memory to support sequence production. In Experiment 2, the transfer paradigm was a transfer test in which participants of all groups were permitted to use eve movements while performing the task. The test was designed to determine the extent to which eye movements influenced sequence learning. In Experiment 3, the transfer paradigm consisted of two contralateral transfer tests (mirror and non-mirror transfer). In the mirror transfer test, the target was presented in a mirror image compared to the acquisition, and the motor coordinates were the same as during the acquisition test with the exception of visual-spatial information being mirrored. This required the same pattern of homologous muscle activation and the same relative joint angles as during acquisition. Participants had to perform this test with their contralateral unpracticed limb (compared to the acquisition phase) while the visual information of the target position was presented via a mirror presentation. In the non-mirror transfer test, which was also performed with the unpracticed contralateral limb, the visual-spatial coordinates were the same as during acquisition, although the movement of the limb was mirrored. This required an unpracticed pattern of homologous muscle activation and unpracticed relative joint angles compared to acquisition. These two transfer tests were designed to determine if physical and/or observational practice enhances the development of either the motor coordinate system (mirror transfer test) or the visual-spatial coordinate system (non-mirror transfer test).

3. Overview

The dissertation consists of three already published peer-reviewed research articles. The entire listings of publication, including those, which are not part of this thesis, are listed in the chapter "Publications".

 Vieluf, S., Massing, M., Blandin, Y., Leinen, P., & Panzer, S. (2015). The role of eye movements in motor sequence learning. *Human Movement Science*, 40, 220-236. doi: 10.1016/j.humov.2015.01.004.

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 Massing, M., Blandin, Y., & Panzer, S. (2016). Magnifying visual target information and the role of eye movements in motor sequence learning. *Acta Psychologica*, 163, 59-64. doi: 10.1016/j.actpsy.2015.11.004.

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 Massing, M., Blandin, Y., & Panzer, S. (2018). The influence of eye-movements on the development of a movement sequence representation during observational and physical practice. *Acta Psychologica*, 182, 1-8. doi: 10.1016/j.actpsy.2017.10.008.

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4. Study 1

The role of eye movements in motor sequence learning

Solveig Vieluf^{1,2}, Matthias Massing¹, Yannick Blandin³, Peter Leinen¹, & Stefan Panzer

¹ Institute of Sport Science, Saarland University, Saarbrücken, Germany

² Aix-Marseille Université, CNRS, ISM UMR 7287, Marseille, France

³ CeRCA, CNRS UMR 7295, University of Poitiers, Poitiers, France

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5. Study 2

Magnifying visual target information and the role of eye movements in motor sequence learning

Matthias Massing¹, Yannick Blandin², & Stefan Panzer¹

¹ Institute of Sport Science, Saarland University, Saarbrücken, Germany

² CeRCA, CNRS UMR 7295, University of Poitiers, Poitiers, France

Published in Acta Psychologica, 2016, 163, 59-64

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6. Study 3

The influence of eye-movements on the development of a movement sequence representation during observational and physical practice

Matthias Massing¹, Yannick Blandin², & Stefan Panzer¹

¹ Institute of Sport Science, Saarland University, Saarbrücken, Germany

² CeRCA, CNRS UMR 7295, University of Poitiers, Poitiers, France

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7. Summary

Three experiments were conducted, all aimed at providing further understanding of how sequence learning and eye movements interact. The main objective of Experiment 1 was to more closely address the question of the role eye movements play during sequence learning. Experiment 2 was intended to determine the role of eye movements in movement sequence learning when the visual angle of the target information is systematically varied and eye movements are minimized by the instruction to fixate² and Experiment 3 examined the role of eye movements in the development of a movement sequence representation following physical or observational practice.

The main findings of the experiments presented in this dissertation are as follows:

The hypothesis of Experiment 1 was that participants who were permitted to use eye movements would have an advantage in performance compared to participants instructed to fixate. Experiment 1 showed that a movement sequence can be acquired without eye movements. However, permitting the use of eye movements enhanced sequence learning, whereas the instruction to fixate impaired the learning process. The results of the experiment also provided evidence that eye movements seem to be important at an initial stage of learning.

The question in Experiment 2 addressed the role of eye movements in motor sequence learning when the visual angle of the target information is systematically increased and eye movements are minimized by the instruction to fixate. If eye movements are not necessary for learning a motor sequence, sequence learning should occur regardless

² Note: An eye-tracking system was used in all experiments to control whether or not participants of the fixed groups complied with the instructions regarding fixation. In all three experiments, the percentage of dwell time in the fixation area was > 90% suggesting that all participants followed the instruction to fixate.

of the instruction to fixate and the increase of the visual angle. However, if eye movements are necessary for learning a motor sequence, sequence learning should be impaired when participants are instructed to fixate and especially when the visual angle is increased. Experiment 2 provided evidence that a movement sequence can be learned in the same manner with or without eye movements when the target information is presented closely. Nevertheless, eye movements enhance sequence learning when the target information is magnified.

Experiment 3 dealt with the question as to whether there is a difference in the development of motor and visual-spatial representation with regard to the different experimental groups (eyes free/fixed, physical practice/observational practice). The hypothesis was that participants instructed to fixate might have an inhibition in the development of an efficient sequence representation, which would lead to a disadvantage in sequence production. The results of Experiment 3 indicated that eye movements are important during both physical and observational practice and support the development of a movement sequence representation. Furthermore, observational practice is limited to a development of a visual-spatial representation, which is primarily used for sequence production. However, physical practice supports the development of a motor representation as well as a visual-spatial representation.

Previous studies have tended to rely heavily upon serial reaction time tasks (SRT task; e.g., Coomans et al., 2012; Marcus et al., 2006) requiring participants to manually press keys in response to a stimulus. In this type of task, participants initially react to a visual stimulus by pressing the corresponding key as quickly as possible. Instead of a SRT task, the experiments designed in this dissertation utilized more dynamic tasks. Participants had to perform the sequences using extension and flexion arm movements. These dynamic sequences require the precise control of agonist and antagonist muscle groups and the

management of movement dynamics in order to precisely regulate forces as well as store and utilize elastic forces and momentum during movement reversals, which are not required for discrete key presses. It should be noted that the processing demands, and therefore the representations for key press sequences, might differ in importance in subtle ways from those of continuous movement sequences. Sequences performed by pressing a key corresponding to a target require a sequential pattern of muscle activation. However, the precise regulation of forces and the management of movement dynamics are not required to the same extent as in many movement sequences where a specific pattern of flexion and extension movements is required. In fact, as noted earlier, key press tasks have often been used to study the cognitive processes involved in sequence production because these processes are more easily isolated when the motor demands of the task are reduced (Shea, Panzer, & Kennedy, 2016).

In addition, key press tasks do not afford the participant the opportunity to more continually visually monitor the progress of the movement. They can be performed by simple movements while the finger of the participant rests on the corresponding key, making spatial precision minimal and visual monitoring low. In contrast, the tasks in Experiments 1, 2 and 3 demanded continual visual control at the initial stage of learning. Continuous visual information about the spatial location of the target is needed at an early stage of learning, whereas later, continuous visual control of the target decreases and motor information becomes more important. It must be noted that using different types of tasks such as key pressing tasks, as in the Remillard (2003) experiments, allow us to assess more specifically the contribution of eye movements and their underlying representations depending on those specific tasks. While skill acquisition, motor learning, transfer, and the development of a representation of the motor skill have received a good bit of experimental attention (see Keele et al., 2003; Shea et al., 2011 for overviews), little attention has been

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directed to eye movements and the development of a representation for motor learning and observational learning (see Sailer, Flanagan, & Johansson, 2005).

In this dissertation, retention tests were used to determine a measurement of learning approximately 24 hours after acquisition. Participants performed all retention tests under the same condition as the day before. In the previous experiments by Marcus et al. (2006) and Coomans et al. (2012), learning was measured by a random sequence on the same day. Unlike the retention test, this random sequence did not deliver memory consolidation processes. Further, in a retention test, participants have to retrieve sequence information for sequence production from long-term memory (Schmidt & Lee, 1999). A rest interval of 24 hours enables encoding and consolidation processes that transform sequence information from a relatively unstable into a permanent form and requires retrieval processes from long-term memory to perform the sequence again (Kandel, Schwartz, & Jessell, 2000). This was not obvious in the random test utilized in previous experiments (Coomans et al., 2012; Marcus et al., 2006). Therefore, one goal of this dissertation was to use retention tests instead of random sequences to measure the extent of learning.

The first experiment continued to systematically investigate the role of eye movements for learning a motor sequence. More precisely, it aimed to examine the influence of eye movements on learning a multi-element movement sequence. Again, based on Coomans et al. (2012), Marcus et al. (2006) and Remillard (2003), findings in regard to the necessity of eye movements for sequence learning seem to be contradictory. For the first experiment, a 16-element movement sequence was used, with the targets arranged in a horizontal plane. The experimental groups' instructions varied from free eye movements to instructing participants to fixate in order to minimize eye movements. The design consisted of an acquisition, retention and two transfer tests. The main findings

showed that participants could learn the multi-element movement sequence even when instructed to fixate. However, participants who were allowed to use eye movements outperformed those participants instructed to fixate in the acquisition, retention and the two transfer tests. Although participants had the option to use eye movements in the retention test, they could not compensate for the disadvantage during the acquisition phase. Thus, eye movements seem to play an important role at the initial stage of learning. The target distance could be one explanation why both groups learned the movement sequences. Although participants were given the instruction to fixate, visual information was presented in a small visual angle and thus in a small field of view. When information about the target is presented in a small field of view, eye movements are not necessary to get all visual information needed. Based on this idea, the question emerged as to whether the increase of the visual angle or the instruction to fixate (or both) affected sequence learning.

Based on this question, the purpose of Experiment 2 was to investigate the role of eye movements when the visual angle of target information is varied. The idea was to combine the size of visual target information (Remillard, 2003) and the instruction to fixate (Coomans et al., 2012) to figure out if the benefit of eye movements is related to the size of the target or to the permission to use free eye movements. Four groups were compared in this experiment with regard to the instruction to fixate or not and the target sizes of small and magnified. All participants performed an acquisition, retention and transfer test. The results indicated that all four experimental groups improved their performance during acquisition. These results are consistent with Remillard (2003) and Coomans et al. (2012) and indicate that eye movements are not necessary for sequence production. However, the results also showed that permitting to use eye movements by Marcus et al. (2006) and Coomans et al. (2012), learning is measured by a random sequence rather than by a retention test. A retention interval induces memory consolidation processes. Therefore, in a

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retention test (24 hrs later), participants must have access to motor memory in order to obtain sequence information for sequence execution. The eye movements used during sequence acquisition induced salient visual–spatial information, which contributes to the development of an efficient sequence memory. Participants of the free groups induced more salient sequence information when moving their eyes over a greater distance, leading to an efficient sequence memory. The transfer test showed that eye movements seem to be important in the early stage of learning, and performance disadvantage cannot be regained later in practice.

In summary, the results highlighted the role of eye movements for a magnified and a small target. Eye movements do not seem to be necessary to learn a movement sequence when the visual target is small. However, they provide a little benefit (5% significance level) for sequence performance. Permitting to use eye movements enhances performance when the target is magnified, and the instruction to fixate deteriorates performance. Participants in the magnified condition have to move their eyes over a wide range, and eye movements facilitate sequence performance. All four groups learned the movement sequence regardless of whether they were instructed to fixate or permitted to use eye movements, but permitting to use eye movements induced superior sequence performance as shown during acquisition.

The third experiment was conducted to investigate the role of eye movements for physical and observational practice. Further, the experiment also focused on the extent to which eye movements influence the development of a sequence representation. A twodimensional, spatial-temporal target wave form was presented to the participants, and two conditions with two groups were used: a physical practice condition, where participants performed the sequence during acquisition by extension and flexion arm movements; and an observational practice condition, where participants learned the sequence during acquisition by observing a learning model. Two groups were utilized in both conditions, one permitted to use eve movements and one instructed to fixate. The design consisted of an acquisition, retention and two transfer tests. The results replicated the previous findings of Experiments 1 and 2 showing that permitting to use eye movements facilitates movement sequence learning. Further, the results extend the findings from physical practice to observational practice. Eye movements seem to play a role not only for physical practice but also for observational practice. In addition, eye movements play an important role for sequence representation, as they are involved in gaining visual-spatial and motor information. The results showed that eye movements are involved in the development of a specific representation (either a visual-spatial or a motor sequence representation) during physical and observational practice. This specific representation is determined via an intermanual transfer test following physical and observational practice. The two transfer tests provided a measure to determine the extent to which eye movements influence the development of a sequence representation and if eye movements influence sequence learning. It seems that oculomotor information is needed to develop a visual-spatial and motor representation.

The final outcomes from the three experiments concerning eye movements in motor sequence learning are described here. First, movement sequences can be learned without eye movements; however, permitting the use of eye movements supports sequence learning. Second, eye movements facilitate sequence learning especially when they are used in the early stage of practice. Third, free eye movements facilitate sequence learning when the visual target information is increased. Fourth, those findings can be extended to observational learning, and eye movements enhance sequence learning in physical practice as well as in observational practice. Fifth, eye movements during movement sequence learning play an important role in developing a motor and visual-spatial representation.

8. Theoretical Implications

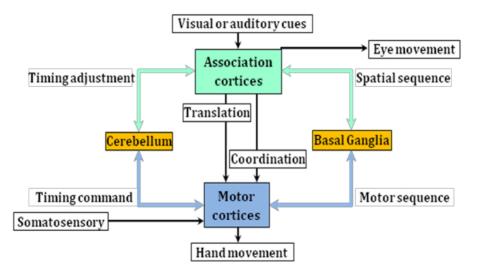
The Hikosaka (1999) proposal was the theoretical background underlying all three experiments. The overall findings of this dissertation are in accordance with this scheme in several ways, which are discussed in this chapter. Further, the results were also in line with the results of the behavioral experiments used by Hikosaka et al. (1995, 1996), Miyashita, Rand, Miyachi, & Hikosaka (1996) and Rand et al. (1998) (see Hikosaka et al., (1999), for a review), which were utilized to propose the hypothetical scheme of the parallel neural network model.

Hikosaka and colleagues used sequence learning tasks for their experiments with both humans and monkeys. Participants had to perform a sequential button-press task in which the correct order was learned by trial and error. The tasks used in this dissertation differed from the button-press task of Hikosaka et al. (1999). Again, participants in the experiments within this dissertation had to perform a visually represented, spatial-temporal sequence or 16-element movement sequence, via bidirectional/reciprocal lever movements. However, all of these sequential movement tasks are similar due to their need to involve multiple joints as well as fine-tuning of velocity, force, timing and acceleration. All tasks have those movement parameters in common. An advantage of the experimental design of this study is the use of the same movement sequence task in Experiments 2 and 3, meaning that the results were not influenced by the characteristic of using different sequences and ensuring that the results of this dissertation were not confounded by the use of different tasks. Other groups for example, have used different types of tasks (e.g., SRT tasks and pairing tasks) within their studies. The results of these different tasks were then compared with each other. One problem with this approach is that differences in tasks have an influence on the results. Experimental setups try to approach reality and test hypotheses with the help of different tasks, starting with a simple experimental task under constant conditions and going all the way to a task that is very close to a real-life situation (Heuer, 1988). However, the transfer of a system is not identical to the transfer of a subsystem, and the reality differs from the sum of many individual subsystems. Basic research provides theoretical information and knowledge about existing subsystems with their individual properties. For this reason, results from different types of tasks cannot be transferred because they depend on different properties. The SRT task used in Marcus et al. (2006) (based on Beldarrain, Grafman, Pascual-Leone, & Garcia-Monco, 1999) consists of four elements with four targets within a ten element sequence. The task used in Vieluf et al. (2015) consists of nine elements with four targets within a 16-element sequence. This task is more complex and has different requirements. By using the same task in Experiments 2 and 3 it is possible to arrange individual examinations in such a way that they gradually approach the more complex reality in terms of research situation and research problem. The multi-element task of Experiment 1 is on the perceptual level different in contrast to the waveform task used in Experiment 2 and 3, as it is visually triggered. That means participants have to look at each element of the sequence at the early stage of learning because the next target element appears when the previous target element is passed. However, the waveform task requires a more pursuing control. That means that participants at the early stage of learning have to continuously control the cursor while performing.

According to the attention shift hypothesis (Rizzolatti, Riggio, Dascola, & Umiltá, 1987), attention and eye movements are strongly linked to each other. In the early stage of learning, when the motor program is initiated, attention is directed to the target. Experiment 1 showed that participants of the "Free" condition reduced their estimated number of saccades as well as dwell time on targets by the end of the acquisition, indicating that participants no longer moved their eyes from one target to the next even

though at this point of practice they still required some overt attention. Therefore, the results are partially in line with the attention shift hypothesis.

The parallel neural network scheme of Hikosaka and colleagues indicated that sequence learning is processed in parallel in two independent cortical systems. One system using spatial coordinates and the other one using motor coordinates. Early in learning, visual-spatial information is active preferentially, whereas later in practice more motor information is active preferentially. The coding of a corresponding representation is done in parallel in two different coordinate systems, a visual system (visual-spatial code) and a motor system (motor code). It is also assumed that the visual-spatial code develops faster than the motor code. Further, the motor code has an executive function in an early stage of learning. Hikosaka et al. (1999) provided neural correlates of the parallel learning mechanism depicted in Figure 1. Again, the results in all three experiments showed that participants permitted to use eye movements had a performance advantage in contrast to participants instructed to fixate. It seems that participants receive visual cues, which are beneficial in the early stage of learning. Experiment 2 showed that although participants, who were instructed to fixate and then are permitted to use eye movements in a transfer test cannot catch up to the performance of participants permitted to use eye movements during the acquisition. These results are in accordance with the scheme of Hikosaka and colleagues and provide evidence for the importance of visual-spatial information at the early stage of learning.



modified: Hikosaka et al., 1999

Fig.1: Correlates of the parallel neural network scheme

In addition, Experiment 3 delved deeper into the question of developing a representation of a movement sequence when the sequence is either learned physically or by observation. The results of the previous experiments showed, that the physical practice group outperformed the observational group on the mirror transfer test, while the observational practice group showed superior performance on the non-mirror transfer test. These findings are in line with other groups (Gruetzmacher et al., 2011; Panzer et al., 2009) showing that physical practice of a simple-temporal movement task leads to a movement representation based on motor coordinates. On the other hand, observational practice supports the development of the visual-spatial representation (Boutin et al., 2010; Ellenbuerger et al., 2012). Further, the instruction to fixate precludes the development of both an efficient visual-spatial and a motor representation.

According to Hikosaka et al. (1999) and the parallel neural network scheme, the visual-spatial as well as the motor representation develop in parallel. However, the visual-spatial representation is primarily responsible for response production during the early stage of learning, whereas with practice, the motor representation becomes responsible for response production. The results of Experiment 3 showed that permitting to use eye-

movements leads to a superior performance on the retention and transfer tests. Of note, participants in the FIX groups were allowed to use eye movements during the retention and transfer test as well. However, the participants permitted to use eye movements showed a superior development of an efficient sequence representation. Physical practice leads to additional somatosensory information, which is processed in the motor cortices, but observational practice enhances the development of a visual-spatial representation because participants receive more visual cues, which are processed in the associative cortices.

The associative cortices are also responsible for controlling eye movements. Experiments 1 and 3 showed that participants decreased their eye movements during the acquisition phase and therefore reduced visual control. Those results are in accordance with the correlation scheme of Hikosaka (1999), which indicates that visual cues are important in the early stage of sequence learning. However, later in practice, somatosensory cues, which are processed in the motor cortices, are more important.

The experiments in this dissertation provided empirical evidence in the field of motor sequence learning and the role of eye movements. They provide behavioral data that are in accordance with the parallel neural network scheme of Hikosaka et al. (1999). Further, they went more in detail to the question of the role of eye movements in sequence learning and especially to the ongoing controversial debate regarding whether eye movements are necessary to learn a motor sequence task or not. According to Remillard (2003), eye movements are not necessary to learn a movement sequence. The experiments in this dissertation confirm those results as well as expand upon them. They showed that eye movements are not necessary but do enhances sequence learning. This dissertation provides additional knowledge in the field of sequence representation along with replicating existing results. It showed that observational learning leads to a more visual-spatial representation whereas physical practice leads to a more motor representation

(Ellenbuerger et al., 2011; Panzer et al., 2009), which is also in accordance with the parallel neural network scheme of Hikosaka and colleagues. The experiments can replicate the findings that in an initial stage of sequence learning, movements are discrete (step-by-step manner) by relying on the sensorimotor transformation for each action, whereas later in practice movements become more sequential (Shea, Kovacs, & Panzer, 2011; Verwey & Eikelboom, 2003).

The results of Experiments 1 and 2 with regard to anchor points are in line with the results of Foerster, Carbone, Koesling and Schneider (2011), Johansson, Westling, Bäckström and Flanagan (2011) and Press and Kilner (2013). Because the control through eye movements depends on the stage of learning and visual seeking is decreasing during practice, anchor points are a mechanism that supports sequence learning.

9. Future Directions

As an outlook for future research, the previous findings of this dissertation can be applied to practical applications but can also be investigate more in detail in basic research.

All experiments indicated an advantage in performance for participants who were permitted to use eye movements compared to those who were instructed to fixate. In all experiments, between 100 and 150 trials were used for the acquisition. An approach would be that, if the FIX groups are able to perform more acquisition trials, they might reach the exact same performance level as the FREE groups. It could be that participants instructed to fixate learn a movement sequence more slowly compared to participants permitted to use eye movement. One explanation for this is that the results in this dissertation showed that participants in the FIX condition learned the movement sequences even though they were instructed to fixate. However, fixation can be a form of dual task. During a dual tasks condition, participants have to perform two tasks simultaneously. It could be that performing the movement tasks used in all three experiments via arm movements and the fixation on a fixation point results in a kind of dual task. The instruction to fixate induces inhibitory processes that might act as dual task interference. Further, interference between those two tasks could lead to deterioration in performance. For that reason participants instructed to fixate might need more acquisition trials to get the same information compared to participants permitted to use eye movements. Therefore, future research could be focused on the number of acquisition trials and the possibility to expand them.

With reference to this topic, another idea is to instruct participants permitted to use eye movements to follow each target while performing the sequence. On the one hand, this approach might increase learning, but on the other hand, it would create the same dual task condition as described above for the fixation group. Following the targets during acquisition should lead to an increase in attention. Since there is a relationship between attention and memory, one can assume that this could further lead to an improvement in learning (see Nissen & Bullemer, 1987).

As mentioned in regard to Experiment 1, the instruction to fixate and performing a movement sequence could be a dual task condition. This would lead to an additional cognitive load, which results in performance deterioration. Coomans et al. (2012) used a task in their experiment in which the authors attempted to reduce the eye movements of participants. The group used a very short stimulus (< 100 ms), to which participants had to react to. The idea was that the short time the stimulus was presented was too short to have additional eye movements (with that minimizes saccades) and therefore participants would only fixate on the stimulus. Applying this concept to the previous experiments produces the idea to use very short stimuli instead of a fixation point within a sequence. Future research could follow up at this point to investigate if performance disadvantages are based

on a dual task (fixation and movement) or the instruction to fixate and thus limited visual and motor information.

An important problem to consider is the initial level of performance. As shown in Experiment 2, the performance of the FIX group and the FREE group in the magnified condition differed. Therefore, it seems reasonable that the instruction to fixate deteriorated movement sequence performance at the beginning of the learning process - or may be the FIX group started on a lower performance level? Experiment 2, used a pre-test to evaluate the performance of the experimental groups at the beginning of learning. This was done to make sure that both experimental groups had the same initial level of performance from the beginning. Another way to ensure that both groups start at the same initial level of performance would be to use a random sequence. During a random sequence, the same amount of elements used in the movement task is placed in a pseudo-random order. However, it must have the same number of reversals as well as the same length as the original sequence.

Future experiments therefore should focus on the initial performance level of the two experimental groups. However, in an observational condition, such as in Experiment 3, measurement of the initial performance cannot be obtained because there occurs always a certain bias. During a pre-test such as in Experiment 2, participants of an observation group would get additional motor information, resulting in a bias in the condition of observational practice. This would mean that those participants not only learned the movement sequence through observation but also via additional physical information (physical practice). In particular, this additional motor information would influence the initial observational learning process.

An interesting aspect within Experiment 1 is the "anchor points". Experiment 1 showed that the dwell time on all targets decreased during acquisition. More specifically,

the dwell time on the outer targets decreased towards zero, yet the dwell time on the inner targets did not. In Vieluf et al. (2015) the inner targets serve as "anchor points". Since the movement sequence in this experiment was presented in one dimension, on a horizontal plane, the question remains as to whether those anchor points are dependent of the dimension in which the sequence is presented. As mentioned previously, Experiment 1 was presented in one dimension. Can there also be anchor points in a sequence presented in two dimensions when performing a visual-spatial movement task? Rentsch and Rand (2014) analyzed eye-hand coordination in their study with regard to different rotation angles. The task was to move the hand to a target, and visual feedback was given by a cursor. The results showed that participants mostly looked at a mid area compared to other areas in the workspace. The authors interpreted this area as "a compromise between having parafoveal/foveal vision near the cursor and fixating on a useful goal to guide the cursor in the direction of the target". Also interesting was the finding that in Experiment 1 (presented in one dimension) and Experiment 3 (presented in two dimensions) those anchor points were always in the inner area of the template. These results are in line with Rentsch and Rand (2014) because the anchor points in Experiments 1 and 3 were in a mid area as well.

Yet, another important area for research would be to determine if anchor points are always at the center of a template and, if so, whether participants instructed to fixate at the center have an advantage over those who were instructed to fixate at the outer area of a template. A further question is whether the fixation of various areas influence sequence performance. Deubel (2004) examined the role of landmarks in his experiment, which play the same role as the anchor points in the previous experiments. He tried to answer the question in which spatial range objects are effective as landmarks. His results showed that the effectiveness of a landmark is limited to spatial range near the target. However, he did not use a sequence with several target points in his experiment. Additionally, his design

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includes distractors. The question here could be whether or not targets within a sequence act as distractors or landmarks (anchor points).

An important aspect of eve movements and another interesting approach for future research is the question, which information is "really" extracted. Adams (1966) described in his work that looking is not equal to seeing, meaning even when a participant is looking at a target, this does not mean he is seeing it. Another example in this context is the foveal field. Participants receive visual information of a target within the visual angle of the foveal field, even though they are not looking at it directly. Although we can track eye movements during experiments via the eye-tracking systems, this does not mean we know what participants see and which visual information they extract. Experiments 1 and 3 only offer one possible approach. Both experiments showed that visual control decreases during the acquisition phase. Further, Experiment 1 also figured out that eye movements, as well as saccades, were reduced. Due to the fact that eye movements are important in the early stage of learning and eye movements were reduced later in practice, one can assume that those eye movements made at the early stage of learning are done to "see" the target, not only for looking. However, the experiments also showed anticipatory eye movements of participants. This leads to the assumption that these eye movements were made to "look" at the target. Summarizing the above, it can be said that we only have indications to differentiate between looking and seeing³. For this reason, future experiments can be focused on the question of what information participants exactly are extracting during sequence learning. A suggestion to find out could be a dual task experiment requiring participants need to react to targets within which, in a randomized order, digits would be

³ To go more into detail for this question, experiments with the use of fMRI or MRI could be useful. With these techniques it is possible to visualize cortical areas that are active during either looking or seeing. It can be differentiated whether participants are looking at a target or seeing. However, this visualization would only provide additional information.

presented that participants have to remember. Such a design could identify if participants "see" or "look" at the target. The recognition of the numbers within the targets presupposes a conscious perception and thus "seeing".

However, these examples are intended to provide only a brief overview of future directions in this field. These suggestions are intended to help to find new approaches and paths based on the findings of this dissertation research. Although these current experiments within the dissertation provide another piece of knowledge of the role of eye movements in sequence learning, they also raise further questions that need to be investigated.

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