SEQUENTIAL MOTOR SKILL

Cognition, perception and action

Marit F. L. Ruitenberg

Sequential motor skill:
Cognition, perception, and action

Marit F. L. Ruitenberg

Doctoral committee

Chair: Prof. dr. K. I. van Oudenhoven-van der Zee

Promotor: Prof. dr. ing. W. B. Verwey
Assistant-promotor: Dr. E. L. Abrahamse

Members: Dr. J. J. Adam
Prof. dr. I. Koch
Prof. dr. S. Panzer
Prof. dr. J. M. Pieters
Prof. dr. P. H. Veltink

The research in this dissertation was made possible by a MaGW grant (No. 400-07-097) from the Netherlands Organization for Scientific Research (NWO).

Cover image: courtesy of Tiberiu Stan
Print: Ipskamp Drukkers, Enschede

SEQUENTIAL MOTOR SKILL: COGNITION, PERCEPTION AND ACTION

PROEFSCHRIFT

ter verkrijging van
de graad van doctor aan de Universiteit Twente,
op gezag van de rector magnificus,
prof. dr. H. Brinksma,
volgens besluit van het College voor Promoties
in het openbaar te verdedigen
op vrijdag 31 mei 2013 om 12.45 uur

door

Marit Frederica Leoni Ruitenberg

geboren op 7 april 1985

te Boskoop

This dissertation has been approved by the promotor:
Prof. dr. ing. W. B. Verwey

and the assistant-promotor:
Dr. E. L. Abrahamse

ISBN : 978-90-365-3537-3
DOI: 10.3990/1.9789036535373

Table of contents

Chapter 1

Introduction

Based in part on

Elger L. Abrahamse
Marit F. L. Ruitenberg
Elian De Kleine
Willem B. Verwey

Frontiers in Human Neuroscience, 7 (2013)

Many of our daily activities are testimony to the possession of motor skill. One may think of riding a bike, lacing a shoe, or writing one's signature. Accordingly, within the fields of cognitive psychology and cognitive neuroscience ample research has been devoted to understanding how the cognitive system is able to represent these movement patterns and control the motor system. This dissertation contributes to our understanding of motor skill by addressing cognitive, perceptual and neural contributions to (the learning of) sequential motor behavior.

Motor sequence learning refers to the acquisition of the skill to produce a sequence of movements in a seemingly automatic manner. Such learning is typically based on repeated practice, following explicit instruction, trial-and-error discovery, and/or (implicit or explicit) detection of regularity. In fact, most, if not all, of our goal-directed actions can be seen as to incorporate a sequential structure that, eventually, allows action performance with limited effort or attentional monitoring. A task that is well-suited for studying the human capacity to acquire sequential motor skill is the discrete sequence production (DSP) task (e.g., Verwey, 1999), which is employed in the studies described in this dissertation. In recent years, work with the DSP task has provided insight in the learning and execution of well-learned, discrete movement patterns. We consider research with the DSP task as a way to study the building blocks of more complex sequential actions that are present in our everyday behavior (Eysenck & Frith, 1977; Gallistel, 1980; Paillard, 1960). As such, the DSP task is representative for the way such real-world actions are acquired and controlled.

Developing a motor skill typically takes time, though. We all remember the hardship of learning how to ride a bike, or learning how to swim (both of which are essential when living in the Netherlands). From the notion of time efficiency, the study of motor skill therefore is in need of experimental paradigms that enable the fast development of a motor skill. Taking the simplest of motor skills—that is, the execution of a brief and fixed series of key presses—the DSP task does just that. In this chapter the DSP task and the typical phenomena associated with it will be introduced. The dual processor model (DPM: Verwey, 2001) of sequence production, which addresses the cognitive processes involved in sequential motor skill, is then discussed. Next, three so-called sequence execution modes are described and a tentative neuropsychological architecture that may underlie sequencing performance in each of these modes is proposed. Finally, the role of perception in sequential motor skill is discussed

1. DSP TASK: A BRIEF USER'S MANUAL

1.1. Experimental setting

In the DSP task, participants are seated in front of a desktop computer and rest four to eight fingers on the designated keys of the keyboard (see Figure 1.1). A similar number of placeholders (e.g., small squares) are displayed on the screen in front of the participants. Each of these placeholders spatially corresponds to one of the keys of the keyboard. Whenever a placeholder is filled with a color, the participant presses the corresponding key as fast as possible. Each next stimulus is displayed only after pressing the required key to the previous stimulus. A typical DSP sequence involves the random presentation of two fixed series of 2 to 7 stimuli, evoking the execution of two sequences of key presses. This implies that a DSP task with, for example, two alternative 6-key sequences turns with practice from two series of six choice response time tasks into a single 2-choice response time task in which the entire 6-key sequences constitute the responses. We use S_n to denote the n-th stimulus of a sequence, R_n to denote the n-th response in the sequence, and T_n to denote the response time associated with S_n.

The DSP task was originally inspired by earlier studies that employed discrete keying sequences (e.g., Kornbrot, 1989; Povel & Collard, 1982; Rosenbaum et al., 1983). The use of sequences of key presses to study sequential motor skill has the benefit that it allows exploring sequential control per se, because executing a single sequence element takes very little time (e.g., MacKay, 1982; Rhodes et al., 2004). That is, response times in a keying sequence constitute a sensitive indicator for the underlying control processes. This is less the case when, for example, series of arm movements are studied. There, control processes may overlap with the execution of individual sequence elements so that execution times

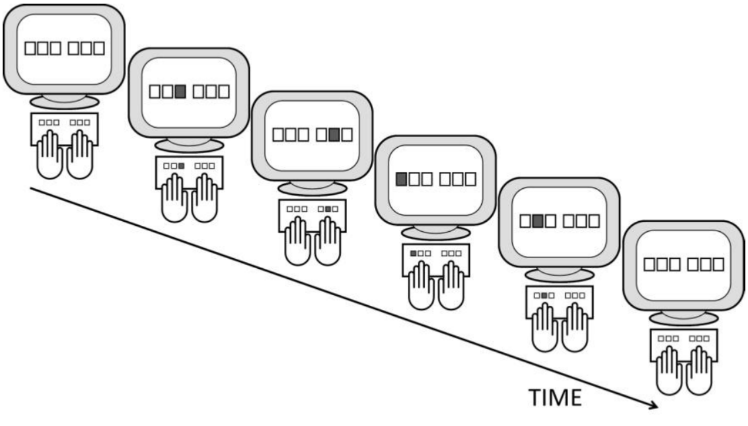

Figure 1.1 A depiction of a typical DSP setting and a timeline of a 4-key sequence.

do not always index the duration of the underlying sequential control processes.

Two methodological features of the DSP task are worth noting. First, the DSP task starts off with a practice phase to enable the development of the building blocks—typically referred to as *motor chunks*—that underlie the true sequence skill in the DSP task. Motor chunks are assumed to represent a limited number of responses that can be selected and executed as if they are a single response in a control hierarchy (Book, 1908; Pew, 1966; Newell & Rosenbloom, 1981; Miller et al., 1960; Verwey, 1996). Following practice, these motor chunks are studied in a test phase in which a novel ('unfamiliar') sequence is usually taken as control condition. Second, by counterbalancing the fingers of individual participants across the sequential positions of the sequence, finger-specific effects at individual sequential positions are ruled out because each of the fingers contributes equally to the RTs at each sequential position. For example, when participants are using the D, F, G, J, K, and L keys on a keyboard, one participant may practice the 6-key sequence KFGDJL, the next participant the 6-key sequence LGJFKD (each key is shifted rightward relative to the first participant), and so on. This counterbalancing procedure also implies that the same sequences can be used as familiar and as unfamiliar sequences, so that response time differences between familiar and unfamiliar sequences are not related to inconspicuous differences in keying order but rather are clean indicators of the underlying control processes.

1.2. Typical phenomena

The literature on the DSP task reports a number of robust observations associated with the production of short movement sequences. These phenomena give rise to theoretical insights in the control of sequential behavior, and relate to distinct phases of discrete sequence skill, the spontaneous segmentation of longer sequences, as well as individual differences in the development of explicit sequence knowledge.

Processing phases of sequence skill

The first phase of performing a well-learned series of key presses can be referred to as the initiation, and involves just T_1. In case of a choice RT paradigm such as the typical DSP task, T_1 is assumed to involve the selection and preparation of the sequence. As can be seen from Figure 1.2, this first key press is typically much slower than subsequent key presses (e.g., Verwey, 1999). This slow start is caused, in part, by suboptimal temporal anticipation as to when S_1 is presented, as the slow first response can be observed even when a short random series of key presses is carried out (Verwey, 2003b). However, when there is a fixed keying order the difference between the first and later Ts increases consid-

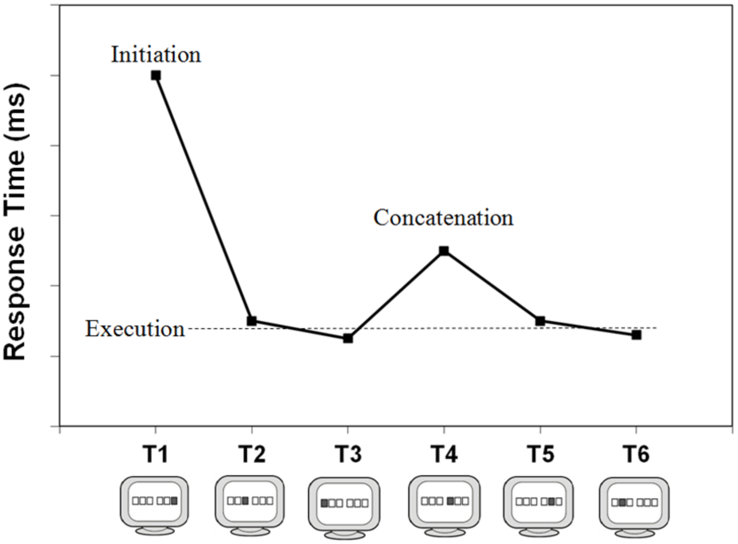

Figure 1.2 The typical reaction time pattern associated with the phases of executing familiar keying sequences: initiation, concatenation, and execution.

erably with practice because of the increasing possibility to prepare the later key presses (Verwey et al., 2010). Possibly, the tendency to prepare an increasing number of elements also affects T_1 itself: The fastening effect of practice on T_1 may be counteracted by the time it takes to prepare an increasing number of responses in advance as the sequence and the task get more familiar.

In line with the notion that T_1 involves selection and preparation of forthcoming key presses, T_1 has been found to increase with the number of elements (i.e., key presses) in the sequence (e.g., Verwey, 1999). This sequence length effect is commonly explained by the notion that individual response elements are loaded immediately before sequence initiation into a short term motor buffer (Klapp, 1995; Rhodes et al., 2004; Sternberg et al., 1978). The sequence length effect appears to level off as sequences become longer (Rosenbaum et al., 1987; Sternberg et al., 1978, 1988). This is attributed to the notion that only a limited number of responses can be prepared in the motor buffer, and that preparation of later responses is postponed until after sequence initiation. This is referred to as concurrent, or online, programming (e.g., Piek et al., 1993; Semjen & Gottsdanker, 1990). A related phenomenon is that the sequence length effect on T_1 reduces with practice. This has been observed in studies with various tasks (Canic & Franks, 1989; Hulstijn & Van Galen, 1983; Klapp, 1995), including the DSP task (Verwey, 1999). As this reducing sequence length effect with practice is associated with sequence-specific improvement (Verwey, 1999), it is assumed that this reducing sequence length effect indexes the development of a motor chunk that allows an entire sequence—or at least the first part of it—to be initiated like a single response.

The key presses following sequence initiation are typically very fast—sometimes with RTs below 100 ms. This is possible because they only involve execution, as selection and preparation processes of individual responses have already occurred during the initiation phase. Together, these key presses are referred to as the (mere) execution key presses (see Figure 1.2). Various studies have shown that initiation and execution key presses can be dissociated through experimental manipulations. For example, Verwey (1999) performed a study in which participants practiced entire DSP keying sequences in response to a particular stimulus (e.g., the number 2 was associated with one particular sequence). When instructed to reverse the learned stimulus-sequence mapping, initiation of the first key press was slowed while the other key presses in the sequence were not. In another study, participants practiced two sequences while using a particular finger setting, involving three fingers of each hand (Verwey et al., 2009). In the test phase, participants performed the sequences while using the familiar finger setting, as well as an unfamiliar finger setting (involving three other fingers of both hands). Results indicated that using a different finger setting for sequence production slowed execution, but did not affect initiation. Together, these studies demonstrate that initiation and execution indeed involve distinct processes.

Segmentation and concatenation

Usually, longer sequences (of more than about four key presses) show a relatively slow response around halfway through the sequence (Bo & Seidler, 2009; Brown & Carr, 1989; Kennerley et al., 2004; Verwey, Lammens, & Van Honk, 2002). Based on this observation, and the aforementioned finding that the sequence length effect levels off as sequence length increases, Verwey and Eikelboom (2003) argued that longer, fixed sequences involve a division into multiple motor chunks due to assumed limitations in the length of single motor chunks—in strong analogy to the well-known chunk-based capacity limitations of working memory (Cowan, 2000; Miller, 1956). Detailed examination of the effects of extensive practice and regularities in key pressing order suggested that most participants executed a 6-key sequence as two or more successive segments. From this notion, the relatively slow response halfway through seems to index the transition from one segment to the next, which involves higher cognitive processes such as preparation processes for the upcoming motor chunk (e.g., Verwey et al., 2010), or strategic parsing (Wymbs et al., 2012).

Segmentation—that is, the division of a sequence in successive parts—is related to what is referred to as concatenation: the processes that allow distinct motor chunks to be executed in rapid succession as smoothly as possible (and that eventually may result in initially separated motor chunks to become a single larger motor chunk). In Figure 1.2, this so-called concatenation point of sequence processing is depicted. Concatenation involves other processes than mere execution of key presses, as suggested by findings that execution and concatenation are affected by different manipulations. That is, the response time reflecting the concatenation point reduced less than RTs from execution key presses after changing the location of the hand relative to the body (De Kleine & Verwey, 2009a), when using fingers adjacent to the ones used during practice (Verwey et al., 2009), and when discrete sequences were executed by dyslexics (De Kleine & Verwey, 2009b). Conversely, the concatenation point was lengthened more than the execution key presses after applying transcranial magnetic stimulation (TMS) to the pre-supplementary motor area (pre-SMA; Kennerley et al., 2004). Initiation and concatenation are assumed to both involve loading and initiating the upcoming motor chunk, but the initiation phase will most likely include more general preparatory processes too (Verwey, 2003b).

Across a group of participants a single relatively long response time (assumed to index concatenation) cannot always be easily observed, as segmentation may occur at different sequential locations for different persons (Bo & Seidler, 2009; Sakai et al., 2003; Kennerley et al., 2004; Verwey, 2003b; Verwey & Eikelboom, 2003). Consequently, there are notable individual differences in the number and length of motor chunks that participants develop during sequence acquisition. These individual differences are thought to be related to the capacity of the motor buffer, which, in turn, may be associated with that of working memory. Bo and Seidler (2009) demonstrated that the length of motor chunks that were formed during the learning of a 12-element sequence could be predicted by individual differences in visuo-spatial working memory capacity: Participants with low capacity spontaneously developed shorter chunks, while participants with high capacity developed relatively long chunks. In a follow-up study Bo et al. (2009) confirmed this finding for elderly participants, in that the age-related decline in visuo-spatial working memory capacity was associated with reduced motor chunk length. These results support the notion that working memory capacity is an important determinant for sequence learning, specifically in motor chunk development, and fits well with the notion that the motor buffer can be considered part of working memory (Verwey, 1999).

Explicit sequence knowledge

It is usually accepted that sequence learning in general can result in both implicit and explicit knowledge. The development of implicit knowledge refers to a learning process that proceeds in the absence of conscious awareness of the end product of learning. For example, learners may show sequence-related performance gains, but at the same time claim to have no verbalizable knowledge about the nature of the learned sequence (or even claim to not have noticed the sequential structure). Explicit knowledge may be based on explicit sequence descriptions in the task instructions, but it is usually developed by testing hypotheses about the nature of the regularity of events (e.g., Haider & Frensch, 2005; Rünger & Frensch, 2010).

Participants in DSP studies are commonly informed that they are performing fixed keying sequences. In combination with the saliency of DSP sequences, this has led to the notion that the DSP task is an explicit sequence learning paradigm (Bo & Seidler, 2009). However, research with the DSP task has demonstrated that participants do not always possess explicit, in-depth and verbalizable knowledge of the order in which the elements were carried out (e.g., Verwey et al., 2010). That is, they have no structural knowledge even though they know that there is fixed regularity in the sequences (i.e., judgment knowledge, Dienes & Scott, 2005). Furthermore, even when participants were able to report on the structure of their sequences, a substantial number of them indicated to have reconstructed this knowledge in a recall task after the experiment by tapping the sequences in their mind or on the table (e.g., Verwey & Abrahamse, 2012; Verwey et al., 2010).

Two potential explanations are worth considering for the lack of explicit, structural knowledge of the DSP sequences. First, it may be that participants obtain substantial (or full) explicit knowledge of the sequential structure early on in training, but later gradually lose out on it as performance becomes more and more automatized. Alternatively, some participants may never develop structural sequence knowledge. This may be influenced by individual differences in testing hypotheses on element order—possibly related to performance gains based on implicit mechanisms that reduce the motivation to do so. Interestingly, participants with substantial structural knowledge are often only a little faster than less aware participants—if at all faster. This indicates that skill in this task does not depend much on explicit (structural) knowledge (Verwey, 2010; Verwey et al., 2010; Verwey et al., 2009). The latter may relate to the notion that in the DSP task motor coding may be best suitable because it is highly efficient in controlling movement executing (Saling & Phillips, 2007). Moreover, utilizing motor codes may result in such fast responses in the DSP that (simultaneously) translating other, explicit, types of sequence coding into movements takes too much time to influence execution much.

2. COGNITIVE PROCESSING IN DISCRETE SEQUENCE SKILL

The next section provides an overview of the dual processor model (DPM) of discrete sequence skill, which has resulted from work with the DSP task. Additionally, three execution modes for carrying out discrete sequences are introduced, which are then tentatively related to neural structures that are involved in sequence production.

2.1. Dual processor model

Early studies with the DSP task led Verwey (2001) to propose the DPM. Over the last years this model has gradually evolved, and here its current state is discussed. In essence, the DPM claims that two distinct processors are active in discrete sequence skill: a cognitive processor and a motor processor. The cognitive processor has a multitude of roles that differ between early and late practice. During early practice, it is responsible for translating an externally presented stimulus into the associated response. It then prompts the motor processor to execute the response. In case of relatively novel but explicitly known sequences, it may also load, one by one and before execution, a limited number of individual responses in the motor buffer. As noted above, this motor buffer is assumed to be a part of working memory. However, as short series of responses are repeatedly programmed by preloading them into the motor buffer, these movement series are assumed to gradually integrate into a single representation, the motor chunk. The availability of a motor chunk allows the cognitive processor to eventually select and load these motor chunks from long term memory into the motor buffer in a single processing step, as if each motor chunk constitutes a single response (Verwey, 1999).

After loading the motor buffer, the cognitive processor triggers the motor processor to start reading the codes for the individual movements from the motor buffer and to execute the movement series in a relatively autonomous fashion (as also postulated by Sternberg et al., 1978). The rapidity with which familiar sequences can be selected and executed through this buffer-mediated process, is what makes up the sequence skill. According to the DPM sequential movement skills can be considered automatic to the extent that little cognitive involvement is required: Motor chunk execution is handled largely by the autonomous motor processor (cf. Bargh, 1992; Tzelgov, 1997), and, with practice, the entire motor chunk may be triggered by external stimuli as if they involve prepared reflexes (cf. Hommel, 2000).

The model has two additional features. First, when the task, participant strategy and available processing resources allow it, the cognitive processor remains engaged in S-R translation while motor chunks are being carried out by the motor processor. This leads to a race between two response selection processes: response selection on the base of the motor processor reading response-related codes from the motor buffer, and response selection by the cognitive processor on basis of continued S-R translations. The execution of each individual key press thus involves both execution processes by the motor processor and preparation processes by the cognitive processor. To better separate between these processes, De Kleine and Van der Lubbe (2011) developed a modified version of the DSP task in which a full series of key-specific stimuli is first presented, after which a small interval is followed by a go or a no-go cue. In case of a go cue, participants are to execute the response sequence that was just before indicated by the series of key-specific stimuli on the screen. Conversely, in case of a no-go cue responding should be withheld. In this so-called go/no-go version of the DSP task the online preparation processes are prevented, as key-specific stimuli that allow for the online S-R translations by the cognitive processor are absent during actual performance of the sequences. This implies that the execution phase during sequencing performance in this go/no-go task is process-pure and only involves execution processes by the motor processor. The go/no-go DSP task is employed in chapters 3 and 4 of this dissertation.

As a second additional feature, the loading of each motor chunk into the motor buffer is initially regulated by the cognitive processor, yet may automatize for later chunks when a fixed sequence involves several motor chunks. Associations between successive motor chunks are assumed to resemble associative learning between individual responses in, for example, the serial reaction time (SRT) task. In this task, participants perform a location-based choice RT task in which the stimulus order is fixed (e.g., Nissen & Bullemer, 1987). Though participants are typically unaware of the precise nature of this order – or do not even notice that there is a fixed order—learning is witnessed by performance measures. This type of learning is attributed to the development of associations between responses and is often referred to as implicit learning (e.g., Destrebecqz & Cleeremans, 2001). Empirical support for such associative learning on the motor chunk level was provided by Verwey et al. (2010) and Verwey et al. (2013), who showed that the concatenation interval was not slowed more by a secondary task than other key presses. This suggests that, after substantial practice, the cognitive processor is no longer necessarily involved in the concatenation process when motor chunks are executed in a fixed order.

2.2. Modes of sequence execution

Performing discrete keying sequences probably involves different execution modes. Indeed, Verwey (2003a) already noted that sequencing performance in the DSP task can be based on at least two. The first is a *reaction mode* in which participants use each key-specific stimulus to select a response. This mode is used when encountering new sequences, and performance involves closed loop control. As a sequence is executed repeatedly, participants learn the order of stimuli and responses and switch to performing the sequence (or short parts of it; i.e., motor chunks) in response to just the first stimulus. Subsequent stimuli can be ignored and participants are said to be performing in the *chunking mode*. This mode can be envisaged as open-loop control in the sense that key-specific stimuli after the first are no longer needed (though, as said, they may still be used when the cognitive processor races with the motor processor).

Recently, indications have been found that discrete keying sequences can be carried out in a third execution mode. Earlier studies had demonstrated that when participants switch from slow to fast execution of a familiar sequence they briefly produce the sequence at some intermediate rate (Verwey, 2003a), and that elderly people do not use motor chunks in discrete keying sequences but still benefit from practice (Verwey, 2010; Verwey et al., 2011). Inspired by these findings, Verwey and Abrahamse (2012) tested the notion that an SRT-like *associative mode* develops with DSP practice too. In this mode successive reactions are primed by the preceding ones but still require stimulus processing for actual execution—as would occur in SRT learning (see Abrahamse et al., 2010). Verwey and Abrahamse (2012) argued that in the DSP task the effect of the associative mode would emerge only when the much faster chunking mode is not used. In their study, skilled participants performed a condition in which familiar, discrete keying sequences were carried out while most of them included 2 deviants (i.e., key-specific stimuli at unpredictable positions) that effectively disabled the chunking mode. As expected, the few sequences in this condition without deviants were executed much slower than the familiar sequences in a non-manipulated condition. Importantly, however, they were executed faster than unfamiliar sequences. Analysis of the response time distributions showed that this effect could not be attributed to sequences occasionally being performed in the chunking mode. The authors interpreted the intermediate execution rate as resulting from reactions to stimuli being primed by the preceding responses (cf. Verwey, 2003a). The development of this associative mode seems reasonable given that responding to successive stimuli in early DSP practice mimics the SRT task.

It can thus be proposed that familiar movement sequences can be executed in two different modes, namely the associative mode which continues to require external guidance by movement-specific stimuli and involves no use of motor chunks, and the chunking mode which is based on advance preparation of motor chunks and which does not require guidance by movement-specific stimuli. Unfamiliar movement sequences, on the other hand, are performed in the reaction mode. The next section attempts to tentatively integrate these three execution modes with several neural structures involved in sequential motor skill.

2.3. Neural underpinnings of sequencing performance

The neurological basis of sequence skill has been studied extensively over the last two decades (for overviews see e.g., Ashby et al., 2010; Hikosaka et al., 1999; Stocco et al., 2010; Penhune & Steele, 2012). Many studies have used techniques such as positron emission tomography (PET; e.g., Jenkins et al., 1994; Jenkins et al., 2000), functional magnetic resonance imaging (fMRI; e.g., Toni et al., 1998; Wymbs et al., 2012), and transcranial magnetic stimulation (TMS; e.g., Kennerley et al., 2004; Verwey et al., 2002). In addition, studies involving patient populations or participants of different age groups have provided insight in contributions of various brain areas to sequence skill. For example, the decline with age of (amongst others) the frontal cortex and the basal ganglia functions have been related to the finding that middle-aged and elderly people show limited development and use of motor chunks for sequencing performance (Verwey, 2010; Verwey et al., 2011). Below, the three execution modes in which sequences can be carried out are tentatively mapped on specific areas of the brain that contribute to sequence skill. In brief, it is suggested that early in training performance is largely S-R based and related to the associative cortico-striatal loop in concert with the prefrontal cortex. With practice, sensorimotor cortico-striatal loops gradually take over and enable both more automatic S-R translations and sequencing performance on the basis of internal representations (i.e., motor chunks)—though a specific associative loop may remain involved for the actual loading of motor chunks. Table 1.1 provides an overview of the proposed neural basis of discrete sequencing performance.

When a sequence is performed in the reaction mode, the execution of each individual movement on the basis of an external stimulus probably involves areas that are consistently related to spatial response selection, such as the premotor cortex (PMC), the parietal cortex (PC) and the prefrontal cortex (PFC) (Dassonville et al., 2001; Iacoboni et al., 1996; Jiang & Kanwisher, 2003; Merriam et al., 2001; Schumacher & D'Esposito, 2002; Schumacher et al., 2003, 2005, 2007). The associative striatum may enable a functional network between prefrontal and posterior areas (i.e., associative cortico-striatal loop; Seger, 2008) to support the initial S-R translation processes that underlie the reaction mode (i.e., performance is driven by goal-directed control based on the instructed S-R mappings that are held in working memory). Indeed, activity in the associative striatum has been strongly linked to the early stages of training in sequence learning and habit formation tasks (Ashby et al., 2010; Jankowski et al., 2009). Moreover, it has been shown that activ-

Table 1.1 The proposed neural architecture of sequencing skill in the reaction, associative and chunking modes of sequence execution.

Execution mode	Neural network	Function
Reaction mode	Associative cortico-striatal loop: PFC, PMC, associative striatum	Initially > PFC: learning of S-R coupling Later > PMC: S-R translations
Associative mode	Sensorimotor cortico-striatal loop: PMC, sensorimotor striatum	PMC: S-R translations
Chunking mode	Associative loop: pre-SMA	Pre-SMA: Motor chunk selection and loading
	Sensorimotor cortico-striatal loop: SMA, basal ganglia	SMA: Sequence execution Basal ganglia: transition between motor chunks

ity in the associative striatum (i.e., anterior caudate) is closely correlated with (the rate of) learning the associations between visual cues and specific motor responses (Williams & Eskandar, 2006). However, the involvement of PFC may soon decrease as the highly compatible spatial S-R mapping of the DSP task allows for less controlled response selection that may involve PMC in concert with the (associative/sensorimotor) striatum—in line with the special role that is assumed for PMC in translating spatial information into motor output (Hikosaka et al., 1999) and with PMC involvement in habit formation (i.e., automatic S-R translation; Ashby et al., 2010).

With more practice and the development of a sequence representation, activity is likely to (further) shift from associative cortico-striatal loops towards sensorimotor cortico-striatal loops involving the sensorimotor striatum, premotor (PMC, supplementary motor area [SMA]) and motor cortices. Support for this notion comes from studies showing that the sensorimotor striatum is more involved in performing highly practiced sequences than in performing new sequences (Miyachi et al., 1997, 2002). In addition, at the cortical level PMC activity has been found to decrease with practice, while SMA activity gradually increases (Jenkins et al., 1994; Toni et al., 1998; Wymbs & Grafton, 2013). It is assumed that SMA is strongly related to memory-based sequence performance (Haaland et al., 2004; Mushiake et al., 1991), thus independent of external action cueing, while PMC underlies skill that is stimulus-based.

As discussed above, well-practiced movement sequences can be performed in the so-called chunking and associative modes. Performance in the chunking mode is dominated by the cognitive processor selecting and loading a motor chunk that is subsequently executed by the motor processor. The crucial role of the basal ganglia (BG) for motor chunking has become evident over the last decades. Studies on stroke (Boyd et al., 2009) and Parkinson's disease (e.g., Hayes et al., 1998; Tremblay et al., 2010) led to the conclusion that the ability to form motor chunks is impaired in patients with BG damage. Recent studies further suggest that the segmentation of longer sequences into multiple smaller chunks is based on fronto-parietal networks (e.g., Pammi et al., 2012). These findings fit well with two studies by Verwey and colleagues who showed that the ability to segment longer sequences into chunks is impaired in elderly people (Verwey, 2010; Verwey et al., 2011), which could be related to reduced cortical capacity (Raz et al., 2005; Resnick et al., 2003). Wymbs et al. (2012) related concatenation processes required for the fluid transitions between motor chunks to the bilateral putamen of the BG. While the overall involvement of BG may be evident, we here speculate about the chunking mode in some more detail, specifically considering the contribution of the (pre-)SMA.

On the basis of a study by Kennerley et al. (2004) we propose that loading the motor buffer is related to the pre-SMA. In their TMS study, Kennerley et al. showed that for extensively practiced sequences a) the pre-SMA is involved in the initiation of a motor chunk, but b) that this only holds when the motor chunk needs to be retrieved from memory as a "superordinate set of movements without the aid of a visuomotor association" (p. 978). Conversely, the pre-SMA was shown to not be involved in general execution processes. Pre-SMA, then, through its dense connections with PFC, is assumed here to selectively activate the relevant long-term memory representations (i.e., load the motor buffer) that are stored elsewhere. Because pre-SMA is typically related to the associative loop with the basal ganglia, the loading of the motor buffer may require a stable involvement of the associative pre-SMA loop in even more advanced sequence skill. Chunking-based performance is thus proposed to rely on the loop between the sensorimotor striatum and SMA, with an associative pre-SMA loop may remain involved for the actual loading of motor chunks. This fits well with the notion that SMA is typically involved in memory-based performance: Though stimuli are still presented in the DSP task even after substantial practice, these are assumed to be no longer dominant in the response selection process. We thus propose that initiation of well-learned action sequences is based on sequence (or motor chunk) selection and loading through PFC (Averbeck et al., 2006) and pre-SMA, after which a sensorimotor-SMA loop is subsequently prompted to commence execution of this sequence.

Whereas the sensorimotor-SMA loop may thus underlie sequencing performance in the chunking mode, the associative mode may build from a sensorimotor-PMC loop because performance in the associative mode is still partly under stimulus-based control (cf. Verwey & Abrahamse, 2012). The latter loop will be engaged either when practice has not yet allowed development of strong enough representations for memory-based performance (i.e., the chunking mode driven by the sensorimotor-SMA loop), or when the chunking mode has been disengaged through experimental manipulations. This fits well with studies that relate both the sensorimotor cortico-striatal loop and the PMC to implicit sequence learning in the SRT task (e.g., Bischoff-Grethe et al., 2004; Grafton et al., 2002; Seger, 2006), which is typically seen as a form of associative learning (e.g., Abrahamse et al., 2010) that remains at least partly stimulus-driven and does not include motor chunking (Jiménez et al., 2011).

3. Perceptual processing: Context-dependent learning

As outlined above, the reaction, chunking and associative modes differ in the extent to which performance relies on the processing of external stimulus information. This section addresses the role of perceptual processing in discrete sequence skill in more detail. Perceptual information that is relevant for the task at hand typically involves stimuli that are necessary for response selection (e.g., key-specific stimuli in the DSP task). The role of such perceptual information shifts with practice, in that it typically starts off being essential for performance but gradually becomes less important. Studies employing the DSP task have demonstrated that sequence execution is initially stimulus-based as each individual stimulus has to be translated into a response. As practice continues and sequence representations (i.e., motor chunks) develop, successful performance relies less on stimuli. Participants can then select and load the motor chunks from memory, after which the individual movements are carried out in the correct order. Although stimuli thus are no longer required, it should be noted that their presence can still affect performance even when movement sequences are automated. Verwey (1999, 2010) and Verwey et al. (2011) observed that performance slightly decreases when highly practiced sequences have to be performed on basis of just the first sequence-specific stimulus. This supports the notion of a race between two response selection processes, namely making online S-R translations by the cognitive processor and reading elements from the motor buffer by the motor processor, to generate the fastest possible responses. While the role of task-relevant perceptual information in discrete sequence skill may be evident, it has also been suggested that the processing of task-irrelevant information can affect performance. Below, I describe how irrelevant information may be processed and introduce the notion of context-dependent learning. Furthermore, it is discussed which processes involved in sequence production may be sensitive to such perceptual information.

3.1. Processing task-irrelevant information

When perceptual features of a task are not essential for accurate performance, they can be seen as the task's *context*—that is, environmental features that are not required for task performance, but that can become associated with the task because of their selective presence during performance. The importance of seemingly irrelevant environmental features for task performance is illustrated by the finding that transfer from training to real-world situations is often suboptimal, even though performance of the learned skill is thought to rely on the same underlying knowledge. Such transfer asymmetry has been observed for skills learned in a virtual environment, such as surgical or flight simulators (e.g., Kozak, Hancock, Arthur, & Chrysler, 1993), but also applies to skills that are learned in the real world (e.g., home advantage in sports; Pollard, 2008). It is important to understand how and when changes in perceptual features can affect performance, as this could have consequences for the design of training programs (see also Abrahamse & Noordzij, 2011).

In their work on context effects, Wright and Shea (1991) distinguished perceptual features that are relevant for a task at hand (intentional stimuli) from those that are task-irrelevant (incidental stimuli). Whereas the former thus are essential for successful task performance, the latter are not—they merely make up the context of the task. Incidental stimuli have been further classified into (e.g., Smith & Vela, 2001): (1) Extra-item global context stimuli, such as the testing room, the experimenter, and the participant's mental, emotional, or physiological state. (2) Extra-item local context stimuli that have been intentionally encoded during practice, like when during learning one stimulus is always paired with another stimulus. (3) Intra-item context stimuli which are task-irrelevant features of the intentional stimuli, such as modality of presentation, color, symbolic format, and language. In this dissertation, the term context effects refers to effects of a change in any task-irrelevant feature, regardless of whether or not it is part of the imperative stimulus.

Various researchers observed that skilled performance benefits from reinstatement of the context in which it was acquired, and that the skill cannot fully be transferred to another context: a phenomenon that has been referred to by the concepts of context-dependent learning (e.g., Wright & Shea, 1991), contextual or procedural reinstatement (e.g., Healy, Wohldmann, Parker, & Bourne, 2005; Wright & Shea, 1991) and specificity of learning (e.g., Healy et al., 2005). They all denote the general principle that transfer occurs to the extent that there is overlap in features between training and testing. The notion of context-dependent learning was first reported for verbal memory performance. A famous example is the study of Godden and Baddeley (1975), in which recall performance of a learned list of words declined when participants who were trained on land were tested under water (and vice versa). Verbal memory performance has also been demonstrated to be sensitive to contexts like physiological state (Eich, 1980) and background music (Smith, 1985). The work on verbal memory performance has inspired the notion of context-dependence in motor skills, as the learning of (sequential) motor skills is assumed to rely—at least partly—on memory, too (e.g., Verwey, 1999; 2001). Indeed, several studies confirmed the notion of context-dependent learning for performance in perceptual-motor sequence learning tasks (e.g., Abrahamse & Verwey, 2008; Anderson, Wright, & Immink, 1998; D'Angelo, Milliken, Jiménez, Lupiáñez, 2013; Magnuson, Wright, & Verwey, 2004; Wright & Shea, 1991; Wright, Shea, Li, & Whitacre, 1996). In the studies of Anderson et al. (1998) and Wright and Shea (1991), for example, the intentional feature of each stimulus in the learned sequence was the spatial location on the screen (using four horizontally outlined location markers) and participants responded with a spatially compatible key press. Stimulus displays in these two studies also involved incidental stimulus features, namely background color, accompanying tone, and shape and position of the stimuli on the screen (top, middle or bottom). Participants practiced three sequences of 4 key presses, each sequence within a unique combination of incidental features. It was found that sequencing performance decreased when these incidental features were changed in a subsequent test phase, thus indicating context-dependent sequence learning.

The common explanation of context-dependent learning is that context cues become associated with the task due to their mere presence during task acquisition, and subsequently facilitate memory retrieval processes (e.g., Healy et al., 2005; Wright & Shea, 1991). When these cues are changed during testing, this may hinder retrieval of the learned skill from memory, thereby resulting in impaired performance (cf. encoding-specificity; Tulving & Thompson, 1973). However, it has also been suggested that context-dependence results from interference: Performance may also decline because selection of the correct responses is more difficult following a context reversal, as the context may prime the alternative sequence (Shea & Wright, 1995). Both accounts would predict that context-dependence would emerge with practice, as associations between the sequence and context need to be formed. The context information that is part of the imperative stimuli thus initially would not affect performance. In contrast, when task-irrelevant perceptual information is not part of the imperative stimuli, it may initially interfere with optimal task performance as it yields selection between relevant and irrelevant information. Indeed, in everyday life we also need to select information that is relevant for our behavior and ignore irrelevant information that might distract from optimal performance—for example, think of playing a game of field hockey, where you should attend to the events at the playing field but ignore the supporters. As several studies suggest that people can learn to ignore such irrelevant information and, moreover, can learn what exactly they are ignoring (e.g., Cock et al., 2002; Deroost et al., 2008, Fox, 1995), it could be predicted that changing the initially distracting information may create renewed interference. This may affect performance, thus creating a sort of context-dependence. The feasibility of such a second type of context-dependent learning (in addition to context-dependent retrieval) will be examined in chapter 2 of this dissertation.

3.2. Context effects on cognitive processing during sequence skill

As mentioned earlier in this introduction, the DPM proposes that the production of skilled movement sequences involves motor chunk selection and buffer loading by the cognitive processor during the preparation phase, followed by execution of the motor buffer content by the motor processor during the execution phase. Although this model does not explicitly include a role for the processing of task irrelevant features during sequencing performance, inferences can be made on how perceptual changes may affect functions of the cognitive processor and the motor processor.

Assuming that context effects necessarily involve perceptual processing, it would follow that motor processor efforts are not sensitive to contextual information and that context-dependence would thus be restricted to the operations carried out by the cognitive processor. This would mean that preparation processes in the typical DSP task, and in particular the decision moment at which sequence selection takes place on the basis of the (first) imperative stimulus, would be most sensitive to perceptual changes. Indeed, Magnuson et al. (2004) provided some initial support for the notion that the search and retrieval processes used as part of response selection are facilitated by the reinstatement of the learning context. Preparation processes are also thought to be involved in the single relatively long response time that is often observed during the execution of longer discrete sequences. This response time reflects the transition between motor chunks (i.e., concatenation) and is thought to involve the selection and retrieval of the upcoming motor chunk. As such, it may also be sensitive to changes in perceptual information.

Besides being involved in preparation processes in terms of the selection and retrieval of sequences and/or motor chunks, it has been proposed that the cognitive processor can assist the motor processor in generating responses by means of direct S-R translations (Verwey, 2001, 2003b). As these online S-R translations are based on perceptual—visual-spatial—stimuli that are converted into a response, they may be susceptible to context effects as well. In the DSP task, then, processing throughout the production of a sequence can be said to be sensitive to perceptual changes, as the cognitive processor is involved in each key press. When considering the go/no-go version of the DSP task, however, it should be noted that such S-R translations do not occur during the execution phase because the key-specific stimuli are all presented beforehand. In a go/no-go DSP task, then, one would expect the cognitive processor to be responsible for motor chunk selection and buffer loading, but not for assisting the motor processor online. Consequently, only the key presses in which the cognitive processor is involved (i.e., the first key press and the key press reflecting concatenation) should be sensitive to perceptual changes. Overall, based on the DPM it may be predicted that context-dependence should be reflected in operations in which the cognitive processor is involved.

4. Overview of this dissertation

The studies presented in this dissertation address the (neuro)cognitive underpinnings of sequential motor skill, in particular in relationship to the role of perceptual information and the development of automaticity in such skill. The majority of the empirical chapters (chapters 2-4) focusses on the role of perceptual information in sequential behavior, and specifically examines the context-dependence of sequencing performance in the DSP task.

Chapter 2 explores the feasibility of a new form of context-dependence, namely context-dependent filtering. We investigate whether the continuous pairing of an irrelevant stimulus along with imperative stimulus results in the learning of (filtering out) the irrelevant information. If this would be the case, sequencing performance is assumed to be hindered when the learned pairs of irrelevant and imperative stimuli are changed during testing. In chapters 3 and 4, the notion of context-dependence for memory-based sequencing skill in the go/no-go DSP task is studied. We differentiate between the sensitivity to perceptual changes of sequence preparation versus execution processes. These chapters on the effects of perceptual changes on sequencing performance also address the role of practice in this matter.

Chapter 5 examines developmental differences in the cognitive mechanism underlying discrete sequence skill. We studied whether preadolescent children, like young adults, learn to perform sequential movements in an automated fashion. Previous studies demonstrated that the development and use of motor chunks for sequencing performance was limited in middle-aged and elderly people (Verwey, 2010; Verwey et al., 2011). It has been suggested that this relates to the degeneration of frontal and other brain areas with older age. As these areas are known to mature during childhood, it could be hypothesized that sequencing skill differs between children and young adults as well.

The final empirical chapter addresses the neural basis of sequencing performance in the DSP task. Specifically, in chapter 6 the roles of the PMC and pre-SMA during sequence execution in the reaction, associative and chunking modes are investigated. It is proposed that the S-R translations by the cognitive processor during externally guided performance in the reaction and associative modes can be related to the PMC, while the loading of motor chunks into the motor buffer during representation-based sequencing skill in the chunking mode is related to the pre-SMA. The dissertation ends with a summary and discussion of the obtained results in chapter 7.

Chapter 2

Context-dependent motor skill and the role of practice

Marit F. L. Ruitenberg
Elian De Kleine
Rob H. J. Van der Lubbe
Willem B. Verwey
Elger L. Abrahamse

Psychological Research, 76, 812-820 (2012)

Research has shown that retrieval of learned information is better when the original learning context is reinstated during testing than when this context is changed. Recently, such contextual dependencies have also been found for perceptual-motor behavior. The current study investigated the nature of context-dependent learning in the discrete sequence production task, and in addition examined whether the amount of practice affects the extent to which sequences are sensitive to contextual alterations. It was found that changing contextual cues—but not the removal of such cues—had a detrimental effect on performance. Moreover, this effect was observed only after limited practice, but not after extensive practice. Our findings support the notion of a novel type of contextdependent learning during initial motor skill acquisition and demonstrate that this context-dependence reduces with practice. It is proposed that a gradual development with practice from stimulus-driven to representation-driven sequence execution underlies this practice effect.

1. INTRODUCTION

It has often been observed that performance of a learned skill is better when the learning context is reinstated at test as opposed to testing in another environment (Smith & Vela, 2001). Such contextual dependencies have been demonstrated for verbal memory performance using contexts like physical environment (Godden & Baddeley, 1975), physiological state (Eich, 1980), and background music (Smith, 1985). In addition, contextual dependencies have been reported for perceptual-motor skills (e.g., Abrahamse & Verwey, 2008; Anderson, Wright, & Immink, 1998; Wright & Shea, 1991). One major aspect of motor skill involves sequence learning, i.e., the acquisition of serially organized behavior. Most complex motor actions that people perform in daily life (e.g., writing, driving, and playing guitar) consist of a series of simple movements that are executed in a specific sequential order. The present study investigated, first, the nature of context-dependent learning in sequencing skill, and second, the role of the amount of practice in the extent to which sequencing skill becomes context-dependent.

A number of studies have explored context-dependent learning in perceptual-motor sequence learning tasks. In the studies of Anderson et al. (1998) and Wright and Shea (1991) the intentional—that is, imperative—feature of each stimulus in the learned sequence was the spatial location on the screen (using four horizontally outlined location markers) and participants responded with a spatially compatible key press. Stimulus displays in these two studies also involved incidental stimulus features—features that are not essential for successful task performance—namely background color, accompanying tone, and shape and position of the stimuli on the screen (top, middle or bottom). Participants practiced three 4-key sequences, each sequence within a unique combination of incidental features. Sequencing performance decreased when these incidental features were changed in a subsequent test phase, thus indicating context-dependent sequence learning.[1] In another sequencing study, Abrahamse and Verwey (2008) used a serial reaction time (SRT) task to explore context-dependent learning with static stimulus features. In an SRT task, participants perform a location-based choice RT task in which the stimulus order is fixed (e.g., Nissen & Bullemer, 1987). Though participants are often unaware of (the precise nature of) this order, learning is witnessed by performance measures—this type of learning is called implicit learning (e.g., Destrebecqz & Cleeremans, 2001). Abrahamse and Verwey (2008) showed that implicit learning can be context-dependent, as task-irrelevant changes in the stimulus display reduced performance.

The observation that skilled performance benefits from reinstatement of the context in which it was acquired, and that the skill cannot fully be transferred to another context, has been referred to by the concepts of context-dependent learning (e.g., Wright & Shea, 1991), procedural reinstatement (e.g., Healy, Wohldmann, Parker, & Bourne, 2005) and specificity of learning (e.g., Healy et al., 2005). They all adhere to the general principle that transfer occurs to the extent that there is overlap in features between training and testing. The common explanation of context-dependent learning is that context cues become associated with the task due to their mere presence during task acquisition, and subsequently facilitate memory retrieval processes (e.g., Healy et al., 2005; Wright & Shea, 1991). When these cues are changed during testing, this may hinder retrieval of the learned skill from memory, thereby resulting in impaired performance. We refer to this mechanism as *context-dependent retrieval.*

It could be theorized, however, that performance and context-dependent learning processes are related to each other in yet another way that—to the best of our knowledge—has not been recognized so far. This notion is inspired by the SRT studies of Cock, Berry and Buchner (2002) and Deroost, Zeischka and Soetens (2008). In otherwise typical SRT tasks, these researchers presented irrelevant stimuli simultaneously with the imperative stimuli, at another location and in a different color. It was shown that people could learn to ignore the sequence of locations of the irrelevant stimuli, as later responding to this sequence of previously irrelevant locations was impaired relative to fully unfamiliar (or random) sequences. This learning process, which they termed negative priming, predicts that performance should be impaired when the locations of irrelevant stimuli (i.e., the "context") are changed after practice. Hence, this strongly suggests a second relationship between performance and context-dependent learning: context is initially interfering with optimal performance (e.g., because it forces a visual search), but people learn to cope with such interference through biasing attentional selection by means of a filter. This would imply that after changing the context, the filter may no longer work and the performance drops. As a first goal of this study, we aim to explore the prospect of such *context-dependent filtering* as a potential second type of context-dependent learning—besides the more common notion of context-dependent retrieval.

The second goal of this study relates to the role of practice in context-dependent learning of discrete movement sequences. Wright and Shea (1991) hinted at the possibility that the amount of practice modulates context-dependent learning, and specifically that context dependency decreases as practice progresses. This notion is in line with work of Fitts and Posner (1967) who proposed that during initial motor skill learning specific environmental cues become associated with the required movements. With extended practice, however, automaticity is reached: the skill can be performed without attention and—more important for the present study—without dependence on environmental cues. Support for such a shift from controlled to more automated skill execution comes from the finding that with extensive practice, people can execute discrete keying sequences without the aid of key-specific cues (Verwey, 1999, 2010). While initially using each key-specific cue for executing individual sequence elements (i.e., the reaction mode), people shift to executing the entire sequence in response to (just) the first stimulus, while ignoring subsequent stimuli (i.e., the sequencing/chunking mode). Similarly, Hikosaka et al. (1999) proposed that a sequential skill starts off from visual-spatial coordinates and with further practice becomes increasingly motor based and therewith less stimulus-dependent. The need for environmental cues thus decreases, implying that the skill would become less susceptible to contextual changes. Therefore, and in line with Wright and Shea's (1991) prediction, we hypothesize that contextual dependencies in sequencing skill performance gradually reduce with practice.

In the current study, we employed a discrete sequence production (DSP) task to explore (a) the prospect of two distinct types of context-dependent learning, and (b) the role of practice. This task is highly suitable for studying the processes underlying motor sequence learning as it allows the development of automated skill in a relatively controlled setting (for a more detailed discussion, see Verwey, Abrahamse, & De Kleine, 2010). In its typical version, participants are presented two sequences of two to seven stimuli in a fixed order to which they respond by means of spatially compatible key presses. With practice, the sequences are learned and execution rates increase. It is assumed that improvement occurs because familiar series of key presses are represented in a single memory representation, called a motor chunk (e.g., Verwey, 1999). In order to induce context dependency in the present study, we presented the irrelevant stimuli on the same spatial dimension as the relevant stimuli. According to the principle of intentional weighting (i.e., top–down selection of task-relevant feature dimensions; Hommel, Müsseler, Aschersleben, & Prinz, 2001) this should ensure that the incidental information is encoded during task execution, as it is assigned the same weight as the intentional information. Hence, while usually only one stimulus is presented per display, we presented two differently colored stimuli simultaneously—one intentional and one incidental stimulus—in an otherwise standard DSP task. The role of practice was explored by manipulating the number of practice blocks between different practice groups, and the test phase involved three distinct conditions to explore context-dependent retrieval and filtering.

First, in the *changed context condition* we presented the irrelevant stimuli at different locations compared to the practice phase. Second, in the *removed context condition* we simply removed all irrelevant stimuli. Finally, the performance on these two test conditions was compared to a third test condition in which nothing changed relative to practice, the *same context condition*. According to the notion of context-dependent retrieval, similar performance impairments should occur for both the changed and removed context conditions in the test phase, as both are characterized by removing the incidental cues that are supposed to facilitate memory retrieval. Conversely, from the notion of context-dependent filtering, predictions are less straightforward as different filtering strategies may be used. First, if a *location-based filter* is adopted—as can be expected from the studies of Cock et al. (2002) and Deroost et al. (2008)—we predict that changing the context adversely affects performance because the novel irrelevant stimulus locations do not match the learned-to-ignore locations, and people thus have to learn anew to cope with this novel situation (i.e., they have to learn to ignore another series of locations). Removing the irrelevant information, however, should not impact performance as it does not require renewed learning and application of the acquired filter should not lead to interference. Second, it could also be speculated that people adopt a *color-based filter*, learning to ignore all stimuli with a specific color or only attending to the target color. In this case, one would expect similar performance irrespective of whether irrelevant stimuli are changed, removed, or left intact in the test phase (relative to practice).

Overall, in the present study we explored, first, whether learning to deal with an interfering context may constitute another type of context-dependent learning than the typical interpretation in terms of memory retrieval. As outlined above, the test phase of the current study nicely predicts different outcomes for context-dependent facilitation, location-based filtering, and color-based filtering. Second, we explore the precise role of practice in context-dependent learning, predicting that contextual dependencies reduce with practice as sequence execution gradually becomes less dependent on external stimulation.

2. METHOD

2.1. Participants

Participants were 48 students (17 male, 31 female) of the Faculty of Behavioral Sciences at the University of Twente. They were aged 18–27 years (*M* = 22) and participated as part of a course requirement. According to Annett's (1970) Handedness Inventory 44 subjects were right handed, two were left handed and two were ambidextrous.[2] All participants gave their written informed consent and reported not having problems with their sight (corrections via glasses or contact lenses were allowed). The study was approved by the ethics committee of the Faculty of Behavioral Sciences of the University of Twente.

2.2. Apparatus

We used E-Prime© 2.0 for stimulus presentation and data registration. The program ran on a Pentium IV class PC. Stimuli were presented on a 17 inch Philips 107 T5 display.

2.3. Task and procedure

At the start of the experiment, all participants were instructed to place the little, ring, middle and index fingers of their left hand on the c, v, b and n keys, respectively. Four horizontally aligned white square stimulus placeholders were presented against a black background, and each key corresponded to a specific stimulus location on the screen. Two of the stimulus placeholders were then filled with a color, one with red and one with blue. Half of the participants responded to the red square and the other half to the blue square (i.e., the relevant stimulus). They were not informed about the other colored square (i.e., the irrelevant stimulus). A correct response to each relevant stimulus was given by pressing the corresponding key, e.g., c, for the leftmost square. Immediately after a response was given, the next combination of relevant and irrelevant stimuli in the sequence was presented. Following a correct response to the last stimulus of each sequence, the stimulus placeholders were presented for 1,000 ms before the first combination of relevant and irrelevant stimuli of the next sequence was displayed. The relevant and irrelevant stimuli were consistently matched throughout practice, so that each relevant sequence was paired with only one irrelevant sequence.

Participants were instructed to respond as fast and as accurately as possible. They received feedback regarding mean response time and accuracy before each break. If a participant's error rate was below 3% or above 8%, a message stating "respond faster" or "respond more accurately" was shown, respectively.

In the practice phase, participants learned two 7-key sequences of a fixed order. To prevent finger-specific effects on individual sequence locations, we created four versions of one sequence (*vnbnvbc*, *nvcvncb*, *bcncbnv* and *cbvbcvn*), two of which were presented to each participant as relevant sequences and two as irrelevant sequences. Across participants each sequence was as often relevant as irrelevant. Half of the participants practiced 100 trials of each sequence, distributed across two blocks. The other half practiced 300 trials of each sequence, distributed across six blocks.

The test phase consisted of three test blocks (see Fig. 2.1). In the same context test block, the relevant and irrelevant sequences were identical to those in the practice phase. In the changed context test block, the relevant sequences were paired with new irrelevant

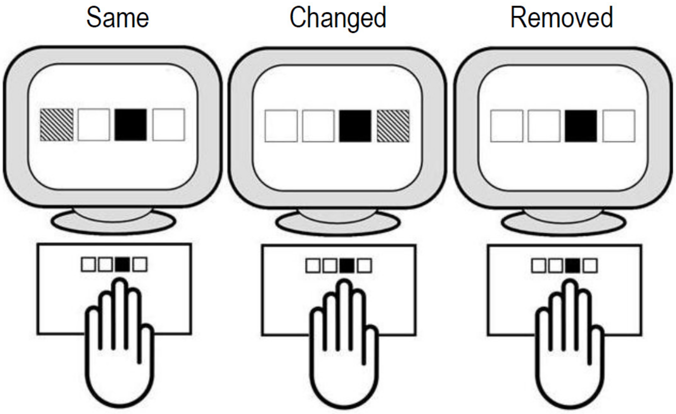

Figure 2.1 An example of a single stimulus within a sequence for the same, changed and removed context test conditions. The black square is the intentional stimulus, while the striped square is the incidental stimulus.

sequences, consisting of mirrored versions of the old irrelevant sequences. Finally, there was a removed context test block in which only the learned sequences were shown while the irrelevant stimuli were removed. The order of the test blocks was fully counterbalanced over participants. Finally, participants completed a questionnaire, in which they were asked to recall both the relevant and accompanying irrelevant sequences.

Each block (both practice and test) included 50 trials per sequence, which were presented in a random order. There was a short 30-s break halfway through each block and a 3-min break in between blocks.

2.4. Data analysis

The first two trials (i.e., sequences) of every block and the first two trials directly following a pause were discarded from the analyses. Additionally, we eliminated trials in which one or more errors had been made. We calculated mean response times (RTs) per key within the sequences for every participant in each block. RT was defined as the time between stimulus presentation and depression of the appropriate response key. To analyze the practice and test phase, mixed factorial analyses of variance (ANOVAs) were performed. Planned comparisons were performed to specifically address our hypotheses.

3. RESULTS

3.1. Practice phase

For the limited and extended practice condition ANOVAs with Block (2 or 6) and Key (7) were performed. As Figure 2.2 shows, mean RTs decreased across the practice

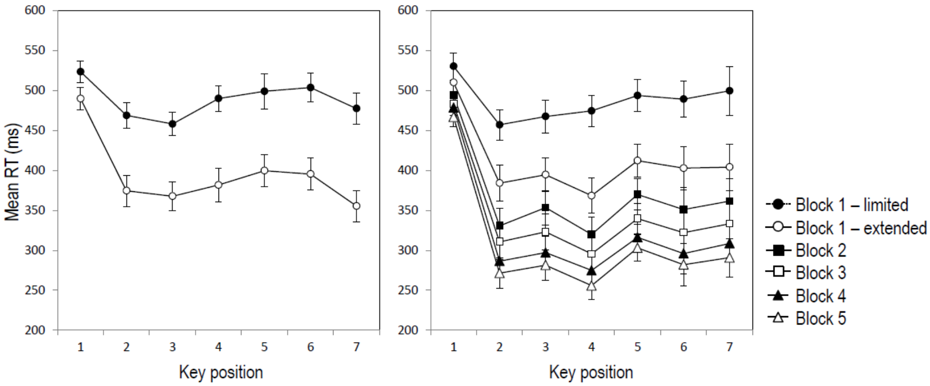

Figure 2.2 Mean RT per key as a function of practice block for both the limited (left panel) and extended (right panel) practice condition. Error bars represent standard errors.

blocks, *F*(1,23)=167.42, *p*<.001 for limited practice and *F*(5,110)=126.38, *p*<.001 for extended practice. Some key presses were executed faster than others, *F*(6,138)=11.20, *p*<.001 for limited practice and *F*(6,132)=27.76, *p*<.001 for extended practice. A Block × Key interaction suggested that across the blocks some keys improved more than others, *F*(6,138)=10.67, *p*<.001 and *F*(30,660)=12.41, *p*<.001 for limited and extended practice, respectively (see Fig. 2.2). Finally, an ANOVA on the first two practice blocks with Block (2), Key (7) and Practice (2; limited vs. extended) showed no main or interaction effects of Practice, *ps*>.13, suggesting that performance of the practice groups on these blocks did not differ.

3.2. Test phase

Results of an ANOVA on RTs with Test condition (3), Key (7) and Practice (2) showed that participants responded faster after extended practice than after limited practice (280 vs. 330 ms), *F*(1,46)=6.41, *p*< .05. Performance in the various test conditions differed (299 vs. 318 vs. 297 ms for the same, changed and removed context, respectively), *F*(2,92)=8.38, *p*<.001. Moreover, a Test condition × Practice interaction suggested that the differences in performance on the test conditions were dependent on prior practice, *F*(2,92)=3.44, *p*<.05 (see Fig. 2.3). Some key presses were executed faster than others, *F*(6,276)=116.69, *p*< .001. This effect is likely to be caused by the longer RT on key 1 as compared to other keys. A Key × Practice interaction suggested that some keys were affected more by practice than others, *F*(6,276)=4.39, *p*<.001, and a Test condition × Key interaction indicated that key presses within the sequence were differently affected by the various contexts, *F*(12,552)=4.39, *p*<.001. Figure 2.3 suggests that these effects are primarily due to key 1.

To further investigate the aforementioned Test condition × Practice interaction and ex-

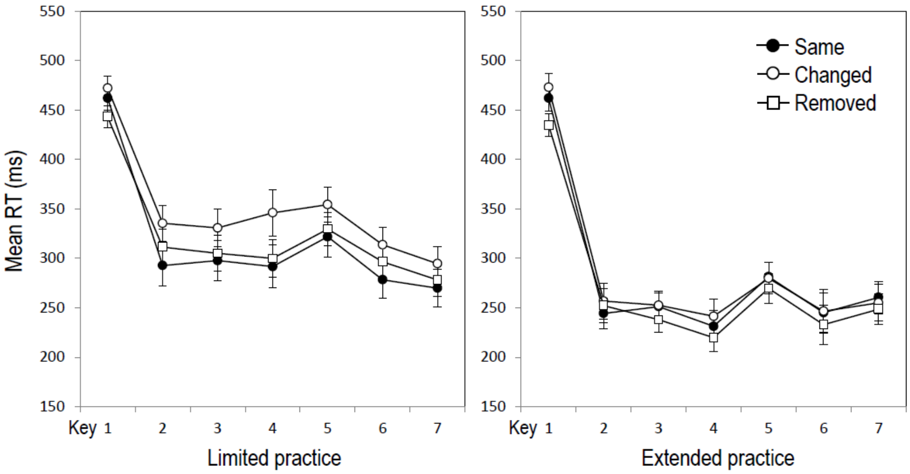

Figure 2.3 Mean RT per key for the same, changed and removed context conditions for both the limited practice (left panel) and extended practice (right panel) condition. Error bars represent standard errors.

plore our hypothesis, planned comparisons were performed. First, a planned comparison showed that RTs were shorter in the same than in the changed context, *F*(1,46)=10.61, *p*<.01. This supports our hypothesis that changing the context affects sequence–skill performance. To further explore the hypothesis that this effect is dependent on the amount of practice, we performed a planned comparison for the limited practice group only. Results showed that performance was significantly better in the same context than in the changed context (316 vs. 350 ms), *F*(1,46)=16.74, *p*<.001. In contrast, a similar planned comparison for the extended practice group yielded no significant result (282 vs. 286 ms for the same and changed context, respectively), *p*=.61. The interaction between the practice conditions and performance in the same versus changed contexts was significant, *F*(1,46)=6.40, *p*<.05. Finally, results of a planned comparison showed that performance in the same and removed context did not differ, *p*=.71, neither after limited nor after extended practice, *ps*>.18. So, while RTs were slower in the changed than in the same and removed context conditions after limited practice, this effect disappeared after more extensive practice.

As the above-mentioned Test condition × Key interaction and inspection of Fig. 2.3 suggested that key 1 was differently affected by the context manipulations than the other keys, we further examined the difference between key 1 and the other keys. First, we performed an ANOVA on RTs of key 1 with Test condition (3) and Practice (2). Results showed a main effect of Test condition, *F*(2,68)=13.81, *p*<.001. There were no main or interaction effects of Practice. Paired t tests showed that responses to the first stimulus were faster in the removed context (439 ms) than in the same and changed context (462 and 473 ms), *ts*(47)>4.79, *ps*<.001, while RTs of key 1 in the same and changed context did not differ significantly, $p>.06$. The effect of context on performance thus was different for key 1 compared to the overall context effect, and was uninfluenced by practice. Removing key 1 from the original ANOVA yielded similar results, with significant main effects of Practice, $F(1,46)=7.17$, $p<.05$, and Test, $F(2,92)=6.48$, $p<.01$, as well as a significant Practice × Test interaction, $F(2,92)=3.76$, $p<.05$—hence, verifying that the pattern of practice and context effects was present for keys 2–7. Also, planned comparisons for these keys showed that performance in the same context was better than that in the changed context (272 vs. 292 ms), $F(1,46)=9.80$, $p<.01$. A similar planned comparison showed a significant difference for the limited practice group (229 vs. 329 ms), $F(1,46)=16.72$, $p<.001$, but not for the extended practice group, $p>.73$. This interaction was significant as well, $F(1,46)=7.04$, $p<.05$. Again, there were no differences in performance between the same and removed context, $p=.85$, neither after limited nor after extended practice, $ps>.23$. So, the effect of practice on context dependency occurs after responding to the first stimulus of a sequence.

Finally, we examined the effects of practice and context on the accuracy of participants' performance in the test conditions, by calculating the proportion of erroneous responses per key in each context condition. The average proportion of errors was 3.1%. Error proportions were submitted to an ANOVA with Test condition (3), Key (7) and Practice (2). Results showed that most errors were made on the second key (4.4% on key 2 vs. 3.5% or less on other keys), $F(6,276)=5.79$, $p<.001$. There were no other main or interaction effects, $ps>.21$. Responses to the irrelevant instead of relevant stimulus accounted for 28% of errors in the same and changed contexts. For each context condition, the proportion of responses to irrelevant stimuli was compared to chance level of generating an erroneous response (which is 33% as three keys could be erroneously pressed) with a one-sample t test. Results indicated that in the same context condition the proportion of responses to irrelevant stimuli (26%) were reliably lower than chance level, $t(47)=2.66$, $p<.001$. In the changed context, however, the responses to the irrelevant stimuli (30%) did not differ from chance level, $p=.14$. This finding suggests that participants have learned not to respond to the locations of to-be-ignored stimuli in the practice phase.

3.3. Awareness

Results of the awareness questionnaire showed that in the extended practice group 12 participants (50%) correctly reproduced both relevant sequences and 5 participants (21%) recalled one relevant sequence. Only two participants (8%) in this group correctly recalled both irrelevant sequences and one participant (4%) recalled just one irrelevant sequence. In the limited practice group, nine participants (37%) recalled both relevant sequences and five participants (21%) recalled one relevant sequence. One participant (4%) correctly recalled both irrelevant sequences and one other participant recalled just one irrelevant sequence. For both practice groups, recalling of the relevant sequences was better than recalling of the irrelevant sequences, *ts*(23)>4.45, *ps*< .001. Participants who recalled one or both irrelevant sequences also recalled the accompanying relevant sequences. Differences in performance between the same and changed contexts were not correlated to recall of the relevant, *r*(48)=−0.02, *p*=.89, or irrelevant sequences, *r*(35)=−0.08, *p*=.61, suggesting that performance impairment does not depend on a person's explicit knowledge about the original context.

4. Discussion

The present study explored context-dependent learning in the DSP task, and provided two major conclusions. First, our data suggest that context effects are not always due to the facilitation of memory retrieval processes during contextual reinstatement, but also to learning to deal effectively with irrelevant information by means of what we here refer to as a filter. Second, in line with the notion that stimulus information is decreasingly required for proper performance on an automatized skill, we observed that context dependencies diminished as practice increased. These findings provide further empirical support for context-dependent learning of discrete motor sequences (cf. Anderson et al., 1998; Wright & Shea, 1991), and in addition show for the first time that the context dependency of perceptual-motor skill is—at least under some circumstances—modulated by the amount of practice. Below we will discuss these findings in more detail.

We observed that participants' performance in the limited practice group was impaired when irrelevant stimulus locations were changed, but not when they were removed. This provides support for the notion that people can learn to deal effectively with stimulus conflict through context-dependent filtering, by learning to ignore the conflicting information (cf. Cock et al., 2002; Deroost et al., 2008). When the irrelevant information was changed in the test phase, incidental stimulation was no longer received from the expected—and learned-to-ignore—locations, and therefore rendered useless the filter that had developed during practice. Conversely, the performance was unaffected by removal of the irrelevant stimuli (with exception of the first key press), as it did not require renewed learning of to-be-ignored locations and application of the acquired filter did not lead to interference.

An issue for future research may be to understand the mechanism underlying such filtering. One question may relate to what exactly is filtered out? Based on our current results, we believe we can already elaborate on this to some extent. First, it cannot be a color-filter, as the changed context—presented in the same color—negatively affected performance compared to the same context. Second, a filter based on the locations of irrelevant stimuli from the display information can account for the current results: while changing the context required a new conflict to be solved (i.e., new locations had to be ignored), removing the context did not require renewed learning and the strategy of ignoring certain locations thus could still be used without affecting performance. Moreover, the finding that the proportion erroneous responses to irrelevant stimuli was significantly lower than chance level in the learned context, confirms that participants learned not to respond to the to-be-ignored locations during practice. Finally, we cannot exclude the possibility that the filter was based on a combination of color and location features—hence, a sort of task-filter. As noted, future research should aim to further examine the precise nature of this filter.

Another question pertaining to the here proposed filter relates to its precise relationship to the task-relevant information. One possibility is that participants learned to ignore the order of to-be-ignored locations along with the order of relevant stimuli, and thus learned a to-be-ignored sequence (i.e., a spatial–temporal filter; cf. Cock et al., 2002; Deroost et al., 2008). For example, participants could learn that with the first key press of a sequence, the third stimulus location and/or corresponding key press should be inhibited; with the second key press, the fourth location and/or key press should be inhibited; etc. However, in the changed context condition not only the locations of the irrelevant stimuli, but also the coordination of relevant and irrelevant stimuli was different from what participant had learned in the practice phase. That is, while in the practice phase each relevant stimulus location was always paired with one specific irrelevant stimulus location (e.g., relevant 'c' was always paired with irrelevant 'b' in the sequence), this coordination changed during testing (e.g., the first relevant 'c' in the sequence was paired with irrelevant 'b', while the second 'c' was paired with 'v'). Another possibility, then, is that the locations of the irrelevant stimuli were learned relative to those of the relevant stimuli—indicating that the to-be-ignored information could be anticipated through predicting the next task-relevant stimulus (i.e., a purely spatial filter).

Noteworthy is that the current findings do not correspond with the common view on context-dependent learning, namely that retrieval of a skill representation from memory is always facilitated when the original learning context is reinstated (e.g., Healy et al., 2005; Wright & Shea, 1991; see also Abrahamse & Verwey, 2008). It is often claimed that contextual cues are integrated within an overall skill representation, and that the reinstatement of such cues aids retrieval. If in the present study the irrelevant stimuli had indeed been integrated within the sequence representation, one would predict superior performance in the same context condition compared to both the changed and removed context condition, which was not observed. As such, we believe that the results of the current study provide support for a novel type of context-dependent learning, namely context-dependent filtering. Future research should zoom in on both these types of context-dependent learning and investigate under which conditions either type is developed and/or is expressed.

The second goal of the present study was to investigate the role of practice in context-dependent learning. We hypothesized that contextual dependencies would diminish as practice increased (cf. Wright & Shea, 1991) because reliance on external stimuli reduces with practice (Hikosaka et al., 1999; Verwey, 1999). Indeed, contextual dependencies were found only after limited practice and not after extended practice. As already briefly hinted at in the introduction, we propose that the mechanism underlying the effect of practice on context dependencies (at least within the realm of the DSP task) pertains to the source of evidence that people use for response selection on a trial-by-trial base. Before generating a response, people accumulate evidence (e.g., stimulus color, location) until the required response can be correctly identified (Brown & Heathcote, 2008). Such evidence can be provided both by external information (i.e., a stimulus) and/or by internal information (i.e., a sequence representation). The relative importance of internal evidence increases with practice, as sequence representations gradually become stronger during skill acquisition (see Cleeremans & Jiménez, 2002). Sequence execution thus shifts from being externally driven toward being internally driven (Tubau, Hommel, & López-Moliner, 2007): participants gradually shift from identifying each key-specific stimulus in the reaction mode, to using an internal representation in the sequencing/chunking mode (Hikosaka et al., 1999; Verwey, 1999, 2010). In the latter case, the evidence provided by the sequence representation—the internal information—is sufficient for signaling the appropriate response (cf. Tubau et al., 2007). Participants no longer needed to process stimulus information for the execution of subsequent key presses after initiation of the first key press of the sequence. Consequently, external stimulus information could be mostly ignored and performance was unaffected by either context manipulation.

The increasing independence of stimulus information with practice does not apply to the first key press of a sequence. Participants always performed two sequences, so the first stimulus needed to be processed in order to select the appropriate sequence. Accordingly, we observed that RTs of the first key press of a sequence were actually faster in the removed than in the same and changed context of the current study, irrespective of the amount of prior practice. This suggests that detecting the first imperative stimulus of the sequence involved a visual search procedure when irrelevant stimuli were present. Yet, key presses following the first of a sequence were not significantly affected by removing the irrelevant stimuli, indicating that visual search was not needed for later stimuli. The differential involvement of sequence learning between the first key press and later ones can explain this discrepancy regarding context dependence. The first key press relies on the randomly selected sequences and thus is unpredictable, whereas later key presses can be predicted on the basis of the acquired sequence information—hence, on some internal representation (e.g., a motor chunk). RTs of the first key press were similar in the same and changed context, which is reasonable as detecting the first stimulus involved visual search in both conditions.

It should be noted that the demonstrated effect of practice on context dependence does not necessarily exclude the possibility that the link between learned sequences and their contexts strengthens with practice. It could well be that—even though the link between task and context becomes stronger—changes in context have no or a little effect once a level of automaticity in sequencing skill has been reached. As participants start to build internal sequence representations, the need for using the environment (i.e., the key-specific stimuli on the screen) decreases, thereby resulting in reduced context dependence. This reasoning could apply not only to context-dependent filtering, but also to context-dependent retrieval—though future studies should explore the specific effects of practice on the latter. Moreover, it is important to note that the effects of practice may be task-specific. For tasks in which the stimulus input remains essential even after extensive practice, for example in the case of probabilistic SRT tasks (e.g., Schvaneveldt & Gomez,1998), one would predict to find increasingly stronger effects of context change with practice.

Finally, let us briefly discuss—and counter—two alternative explanations for the current findings. First, one might argue that performance-differences between the test conditions are due merely to continuous distraction by the irrelevant stimuli. However, from such an account one would predict performance in the removed context to be better than in either the same or changed context—yet this was not observed. This led us to interpret findings with the additional notion of a filter that developed with practice to effectively deal with the conflicting information. In addition, a purely attention-based account cannot explain why context dependency would reduce with practice. Second, results of the awareness questionnaire showed that recall of the relevant sequences was better than recall of the irrelevant sequences, but that recall was not correlated with the extent to which the performance was affected by changing the context. This precludes an explanation in terms of awareness and shows that performance impairment upon contextual changes does not depend on whether the original context has actually been explicitly learned.

In summary, the present study demonstrated that sequence learning in the DSP task is initially context-dependent. Results showed that when an irrelevant sequence was presented along with and on the same spatial dimension as an imperative sequence, changing this irrelevant sequence resulted in impaired performance. This indicates that the participants not only learned to perform the relevant sequences, but concurrently learned to ignore the locations of the irrelevant stimuli—thus, supporting the notion of context-dependent filtering. Moreover, the present study showed for the first time that sequence learning becomes less context-dependent with practice. This effect seems due to a gradual development with practice from stimulus-driven (i.e., based on external information) to representation-driven (i.e., based on internal information) sequence execution (cf. Verwey, 1999; Verwey et al., 2010). Altogether, we thus believe the current results reflect a combination of the notions of (a) a location-based filter and (b) a decreasing importance of external stimuli with practice.

Notes

1. One may doubt, however, whether this effect truly involved the effect of incidental context, as the “incidental” features possibly became intentional over time. That is, participants may have used (one of) these features for sequence identification and/or execution as they probably required less effort to be processed compared to the intentional feature. In line with this possibility, Ruitenberg, Verwey and Abrahamse (unpublished work) found no indications of context-dependent sequence learning when the incidental context was static during training (i.e., all sequences were trained within the same context), and could therefore not be used for sequence identification.

2. Removing the left-handed and ambidextrous participants from the analyses did not yield a different pattern of results.

Acknowledgments

We would like to thank Annika Rausch for her assistance in running the experiment.

Chapter 3

Context-dependent motor skill: Perceptual processing in memory-based sequence production

Marit F. L. Ruitenberg
Elger L. Abrahamse
Elian De Kleine
Willem B. Verwey

Experimental Brain Research, 222, 31-40 (2012)

Previous studies have shown that motor sequencing skill can benefit from the reinstatement of the learning context—even with respect to features that are formally not required for appropriate task performance. The present study explored whether such context-dependence develops when sequence execution is fully memory-based—and thus no longer assisted by stimulus–response translations. Specifically, we aimed to distinguish between preparation and execution processes. Participants performed two keying sequences in a go/no-go version of the discrete sequence production task in which the context consisted of the color in which the target keys of a particular sequence were displayed. In a subsequent test phase, these colors either were the same as during practice, were reversed for the two sequences or were novel. Results showed that, irrespective of the amount of practice, performance across all key presses in the reversed context condition was impaired relative to performance in the same and novel contexts. This suggests that the online preparation and/or execution of single key presses of the sequence is context-dependent. We propose that a cognitive processor is responsible both for these online processes and for advance sequence preparation and that combined findings from the current and previous studies build toward the notion that the cognitive processor is highly sensitive to changes in context across the various roles that it performs.

1. INTRODUCTION

Over the last decades, various studies have explored context-dependence within the domain of (sequential) motor skill (e.g., Abrahamse & Verwey, 2008; Anderson et al., 1998; Ruitenberg et al., 2012; Shea & Wright, 1995; Wright & Shea, 1991). The notion of context-dependence—which originates from the literature on verbal memory (e.g., Eich, 1980; Godden & Baddeley, 1975; Smith, 1985)—holds that memory retrieval is better in the environment in which the memory trace was initially acquired as opposed to retrieval in a different environment. Hence, context refers to characteristics of the task setting that are not formally required for proper task execution, but that may become relevant with practice. In the current study, we further explored and extended the conclusions from a recent study in which we reported context-dependence for discrete sequencing skill (Ruitenberg et al., 2012). Specifically, here (I) we set out to disentangle the potential context-dependence of preparation and execution phases in memory-based sequencing skill. Additionally, (II) we aimed to test the major account of context-dependence as a form of cue-facilitated memory retrieval (see Healy et al., 2005; Ruitenberg et al., 2012). Finally, (III) we explored the role of the amount of practice as we previously showed this can modulate the extent to which sequencing skill is context dependent (Ruitenberg et al., 2012). We employed the discrete sequence production (DSP) task (e.g., Verwey, 1999), as this task allows for the fast acquisition of sequencing skill, and we believe that keying sequences are well suited to study the underlying control processes of sequential skill. More specifically, we actually employed a go/no-go version of this task to have distinct preparation and execution phases (De Kleine & Van der Lubbe, 2011).

In the DSP task, participants practice two fixed and discrete sequences of key presses by responding to series of key-specific stimuli. Initially, sequences are performed in a reaction mode as each stimulus has to be translated into the appropriate response (see Verwey et al., 2010). With practice, performance gradually improves. At the skilled level, series of successive responses—represented by so-called *motor chunks*—are prepared and executed as if they were a single response; we call this the chunking mode (see Verwey & Abrahamse, 2012; Verwey et al., 2010). Indicative of such motor chunks is a relatively slow initiation (i.e., first key press) followed by very fast later key presses—sometimes with average RTs below 100 ms. With longer sequences, participants spontaneously develop multiple motor chunks that are concatenated during execution (Bo & Seidler, 2009; Kennerley et al., 2004; Park & Shea, 2005; Sakai et al., 2003; Verwey et al., 2009; Verwey & Eikelboom, 2003). To better separate motor preparation and execution, De Kleine and Van der Lubbe (2011) introduced a go/no-go version of the DSP task. This version allows distinguish ing between a preparation and an execution phase. All key-specific stimuli of a sequence are displayed at a fixed pace before execution is started in response to a go signal—the sequence thus has to be executed completely from memory. As such, participants cannot execute the sequence based on simple stimulus–response (S-R) translations, like in the traditional DSP task, and this prompts optimal preparation: Only when preparation has been completed can execution of the prepared elements start. Memory-based sequencing skill is an important topic of research because it may come closer to daily life situations than the more stimulus-driven performance in the traditional DSP task.

According to the dual processor model (DPM; Verwey, 2001), skilled sequence performance involves motor chunk selection (including retrieval from long-term memory) and motor buffer loading by a cognitive processor. This preparation phase—which may be called *advance preparation* because it involves preparation of multiple key presses before sequence execution starts—is then followed by the fast execution of the motor buffer content by a dedicated motor processor (i.e., execution phase). So, the cognitive processor is responsible for top-down, intentional control, whereas the motor processor is autonomous and dedicated to reading and executing elements from the motor buffer. Moreover, it has been tentatively proposed that during the execution phase, the cognitive processor can support the motor processor in producing the sequence elements by means of direct S-R translations (Verwey, 2001, 2003b). The relatively fast motor processor can thus possibly be supported by the cognitive processor (i.e., statistical facilitation; see, e.g., Verwey, 2001), so that the fastest possible responses are generated. This online S-R translation process also involves preparation related to triggering each individual response. We refer to this as *online preparation* because it occurs during sequence execution. Importantly for current purposes, we emphasize that such S-R translations do not occur during the execution phase in the go/no-go DSP task because the stimuli are all presented beforehand. In a go/no-go DSP task, then, one would expect the cognitive processor to be involved merely in advance preparation.

Klapp (1995) proposed a related model of motor preparation that is based on the work of Sternberg et al. (1978). Specifically, Klapp proposes that the so-called INT process selects and prepares the individual elements (involving either a single response or an entire chunk) that have to be executed and loads these into the motor buffer, and the SEQ process places these elements in the correct order. The INT and SEQ processes can be strongly related to the functions of the cognitive processor in the DPM. In a next step, the content of the buffer is read and executed by what the DPM refers to as a motor processor.

Both the DPM and Klapp's model—arguably the major models of discrete sequencing skill—follow the logic of traditional stage models of information processing in that the relevant action sequence is selected based on the sensory input through a simple “decision moment” (i.e., sequence selection by the cognitive processor), after which follow motor preparation (e.g., buffer loading by the cognitive processor) and execution (through a motor processor). If we assume that context effects require a link from perception to action, it follows that motor processor efforts are not sensitive to context. Context effects would then be constrained to the operations carried out by the cognitive processor. In the DSP task, this would entail advance preparation processes, and then in particular the decision moment at which sequence selection takes place on the basis of the (first) imperative stimulus; buffer loading processes could be assumed to be unaffected by perceptual processes within the context of traditional processing stages. Indeed, Magnuson et al. (2004) provided some initial support for the notion that the search and retrieval processes used as part of response selection (especially Klapp’s SEQ process) are facilitated by the reinstatement of the learning context. Besides advance preparation, one could envisage also that the cognitive processor’s online S-R translations—when possible—are susceptible to changes in context. So, context-dependence should be reflected in tasks in which the cognitive processor is involved.

Research with the DSP task shows that—in line with various models on sequence production in general—preparation and execution are distinct processes (e.g., Verwey, 1995, 1999; Verwey et al., 2010). Within the context of the DSP task, this has resulted in the notion that (advance) preparation processes are most clearly involved at sequence initiation—reflected in the first response time (T_1) of the sequence. In addition, it has been shown that with longer discrete sequences (around 5–8 elements), one of the key presses after the first (depending on the participant) has a relatively long response time. This relatively slow response is thought to reflect the transition between successive motor chunks (i.e., concatenation, T_C). It is assumed to include additional preparation processes by the cognitive processor (e.g., Bo & Seidler, 2009; Kennerley et al., 2004; Verwey et al., 2010). Hence, T_1 and T_C are assumed to reflect predominantly advance preparation, while all other response times reflect online preparation and execution processes. With respect to the latter, in a go/no-go DSP task, these responses should merely reflect execution processes, because online contribution of the cognitive processer, in terms of S-R translations, is prevented. A strong prediction, then, is that context-dependence of the cognitive processor results in prolonged T_1 and T_C, whereas other response times are unaffected. Nevertheless, previous studies did not explicitly consider this prediction. Studies by Wright and colleagues, for example, did not clearly compare effects on T_1 and T_C with other response times (Anderson et al., 1998; Magnuson et al., 2004; Wright & Shea, 1991). The study by Ruitenberg et al. (2012) could not zoom in on especially the preparation phase because the context manipulation involved the presentation of both a relevant and an irrelevant stimulus, due to which responses to the first stimulus involved not just sequence preparation but also a visual search procedure to determine the stimulus to respond to.

1.1. The present study

In the present study, we extended previous research on context-dependent memory-based sequencing skill. Specifically, we attempted to distinguish between contextual dependencies of the (advance) preparation phase versus the execution phase to further contribute to the literature on context-dependent sequencing skill. To disentangle these phases, we employed the go/no-go version of the DSP task. Participants practiced two 6-key sequences by first observing the six key-specific position stimuli that were presented in succession. After a short interval, a go or no-go signal was presented, respectively, cueing the participant to execute the sequence in the correct order or to withhold from responding. Importantly, for each of these two sequences, the key-specific stimuli were presented in a specific color. This color constituted the context.

In the ensuing test phase, performance was tested in three conditions. The *same context condition* involved the same stimulus colors as during practice for each of the two sequences. In the *reversed context condition*, we switched the colors used for the key-specific stimuli of the two sequences (cf., Abrahamse & Verwey, 2008; Anderson et al., 1998; Wright & Shea, 1991; Wright et al., 1996). Comparing these two conditions allows exploration of contextual dependencies. Context-dependent advance preparation by the cognitive processor would be reflected in effects of context change on the response time to T_1 and T_C. Conversely, context-dependent online preparation and/or execution processes would be assumed to result in comparable effects across all key presses. We predict that context change will predominantly affect T_1 and T_C (in line with Magnuson et al., 2004), as execution is here assumed to be entirely driven by the motor processor (since no stimuli are available during execution to allow the cognitive processor to join the race)—which is assumed to function independently of perceptual input.

We also included a *novel context condition* in which both sequences were indicated by key-specific stimuli presented in the same, new, color. Several researchers have argued that contextual dependencies are mainly related to a facilitation of memory retrieval when cued by context features (e.g., Healy et al., 2005; Wright & Shea, 1991). Impaired performance after a change of context, then, is explained by the notion that the context can no longer serve as a cue for memory retrieval. However, the potential observation in the current study of impaired performance after a switch of context may be explained also by the notion that the alternative sequence is primed by the color and needs to be inhibited.

Shea and Wright (1995) suggested that a reversed context primes activation of the wrong sequence information, so that selection of the correct responses is hindered and performance decreases. This would imply that performance suffers only following context reversal (i.e., inhibition is required) and not when a novel context is introduced (i.e., inhibition is not required). To experimentally distinguish the reduced facilitation and the inhibition explanations, we compared the same context condition with both the reversed and novel context conditions.

Finally, Ruitenberg et al. (2012) showed that the amount of practice may play an important role in context-dependence. They observed that when a fixed pairing of relevant and irrelevant stimuli from the training phase was changed in the test phase (i.e., irrelevant stimuli were presented at another position than during training), performance dropped. Interestingly, this context-dependence was only observed with relatively little practice, and not with more extensive practice. To examine whether this effect of practice holds for the go/no-go version of the DSP task as well, we here manipulated the amount of practice, too. Although it has been suggested that the context-dependence of preparation processes will increase with practice, as the association between context features and a sequence representation may strengthen with practice (e.g., Healy et al., 2005; Wright & Shea, 1991), we predict that context-dependence reduces with more extensive practice as stimuli in the go/no-go DSP task may be decreasingly processed since the first stimulus suffices for proper sequence preparation (cf. Ruitenberg et al., 2012).

Overall, our central aim was to test the assumption that, in memory-based sequencing skill, advance preparation by the cognitive processor is the process in sequence skill that is sensitive to (task-irrelevant) perceptual changes in the initial learning context—in this case changing the task-irrelevant color of the stimuli. This assumption predicts effects of context mainly on T_1 and T_C. Additionally, we explored whether context effects are caused by reduced facilitation of information retrieval or by inhibition of associated information, and whether context-dependence reduces with practice.

2. METHOD

2.1. Participants

Participants in this study were 48 students (19 male and 29 female) of the University of Twente and the University of Münster. Their mean age was 22 years, ranging from 19 to 27 year. The study was approved by the ethics committee of the Faculty of Behavioral Sciences of the University of Twente.

2.2. Apparatus

E-Prime© 2.0 was used for stimulus presentation and data registration. The program ran on a Pentium IV class PC. Stimuli were presented on a 17 inch Philips 107 T5 display.

2.3. Task and procedure

Participants placed their index and middle fingers of both hands on the c, v, b and n keys of a computer keyboard. A fixation cross was presented in the center of the screen, along with four horizontally aligned squares (Fig. 3.1). The four stimulus squares spatially corresponded with the alignment of the four response keys. The squares and the fixation cross were drawn with a silver color line on a black background. After 1,000 ms, one square was filled for 750 ms, next a second square and so on until the sixth square had been filled. The default screen then reappeared for 1,500 ms. Next, the fixation cross was colored either red or blue. The red fixation cross was presented for 3,000 ms and indicated that sequence execution had to be withheld (a no-go trial[1]), whereas the blue fixation cross, presented for 100 ms, indicated that participants had to repeat the presented sequence by pressing the appropriate keys in the correct order (a go trial). Participants were instructed to respond as fast and accurately as possible. An error message appeared when a participant reacted before the go/no-go signal. In addition, feedback was provided upon completion of a response sequence to indicate whether errors had been made. After each completed sequence, the default screen would appear for 1,000 ms before the first stimulus of the next sequence was presented.

Participants practiced two 6-key sequences during the practice phase, which were presented in random order. In order to prevent finger-specific effects on individual response times, we created four versions of each sequence, namely ncbvbc, bnvcvn, vbcncb, cvnbnv and cbvnbc, vnbcnv, bcnvcb and nvcbvn. The two sequences that a participant practiced never started with the same key press. During practice, one sequence was always presented in blue while the other one was always presented in yellow (colors were counterbalanced over sequences). A practice block consisted of 100 go and 20 no-go trials, and the two sequences were presented in random order. Participants in the limited practice condition completed one block (50 trials per sequence), whereas participants in the extended practice condition completed five blocks (250 trials per sequence). There were a short 30-s break halfway through each block and a 2-min break at the end of each block.

During the test phase, which followed the practice phase after a 2-min break, participants performed the sequences in one of three context conditions. In the same context condition, the sequences were presented in the same colors as during the practice phase. In the

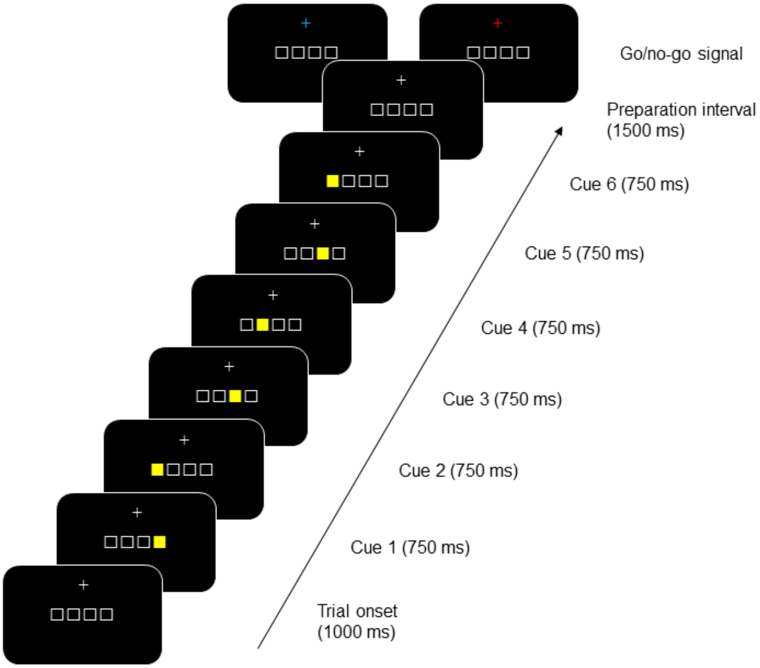

Figure 3.1 An overview of stimulus presentation in the go/no-go DSP task. Key-specific cues were presented for 750 ms. After a 1,500-ms preparation interval, a go or no-go signal was presented. In case of a go signal, the + turned blue, while in case of a no-go signal it turned red .

reversed context condition, the sequence that was formerly presented in blue was now presented in yellow, and vice versa. In the novel context condition, the learned sequences

both were presented in red. Each test block comprised ten go and two no-go trials. As in the practice blocks, sequences were presented randomly.

Finally, participants were asked to complete a questionnaire that measured their awareness of the sequences. Participants were asked to write down both of the sequences they had performed during the experiment (recall test). Then, they were asked to identify (by choosing from twelve alternatives) their two learned sequences (recognition test).

3. RESULTS

Response time (RT) was defined as the time between onset of the go signal and depression of the first key and as the time between the onsets of two consecutive key presses within a sequence. RTs of sequences in which erroneous key presses were made were discarded from the analyses below. We calculated mean RTs per key press within the sequence for each participant. RTs exceeding the group mean by more than three standard deviations were replaced by the respective group mean (this affected 1% of the data). Including the actual color of the sequence as a variable in the analyses did not have any main or interaction effects, all *ps*>.15. Therefore, this variable was excluded from the analyses below.

3.1. Practice phase

For the limited practice group, we performed a mixed factorial analysis of variance (ANOVA) on RTs with Key position within the sequence (6; hereafter referred to as Key) as repeated measure and Test condition (3; same vs. reversed vs. new) as between-subject variable. Results showed that some key presses were executed faster than others, *F*(5,105)=40.33, *p*<.001, which can be attributed to the relatively slow first key press as compared to ensuing key presses (see Fig. 3.2); the RT on key 1 reflects a reaction to the go signal and thus initiation of the sequence, whereas RTs on other keys reflect responses based on sequence knowledge. There were no other significant effects, *ps*>.17.

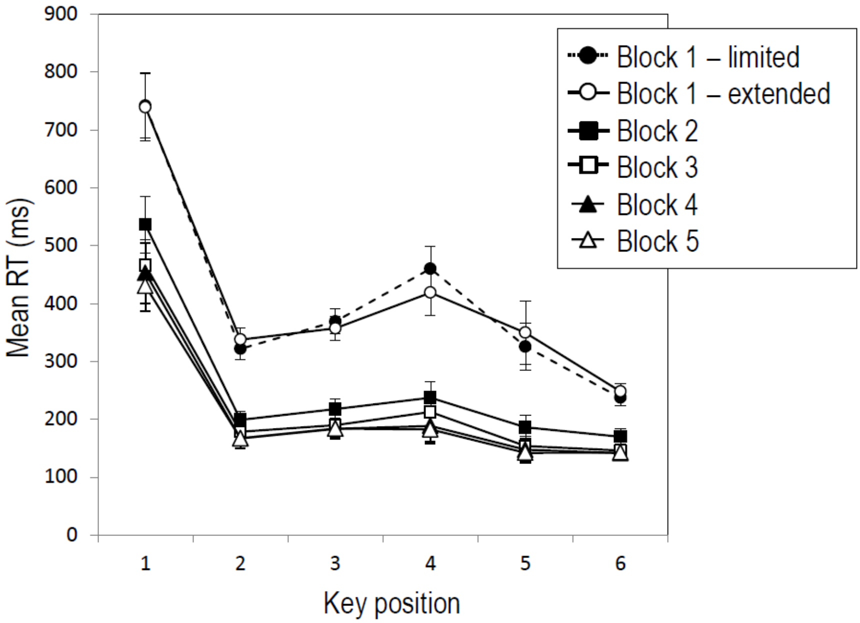

Figure 3.2 Mean RTs (ms) in the practice blocks as a function of key position within the sequence, both for the limited practice group (one block) and extended practice group (five blocks). Error bars represent standard errors.

For the extended practice group, a mixed ANOVA was performed with Block (5) and Key (6) as repeated measures and Test condition (3) as between-subject variable. Figure 3.2 shows that mean RTs decreased across the practice blocks, *F*(4,80)=142.14, *p*<.001. As in the limited practice group, some key presses were executed faster than others, *F*(5,100)=54.61, *p*<.001. As explained above, this can be attributed to the relatively slow responses on the first key press as compared to the ensuing key presses. A Block × Key interaction suggested that there was more improvement in some keys across blocks, *F*(20,400)=5.43, *p*<.001. The sixth key press improved less between block 1 and 2 (79 ms) than any of the other key presses (*M* = 167 ms), *ps*<.05. While RTs still improved across blocks 3 to 5, *F*(2,42)=5.73, *p*<.05, the improvement was similar for all keys, *p*=.19. There were no main or interaction effects of Test condition, *ps*>.18.

A mixed ANOVA on RTs in the first practice block with Key (6) as repeated measure and Practice group (2; limited vs. extended) and Test condition (3) as between-subject variables only showed an effect of Key, *F*(5,205)=76.16, *p*<.001. This was attributable to the relatively slow first key press as compared to the ensuing key presses. There were no main or interaction effects of Practice group, *ps*>.44, suggesting that performance of the practice groups on the first block did not differ. Results showed no other effects, *ps*>.34.

Finally, we analyzed the percentage of correctly executed key presses (PC) by using mixed ANOVAs including the same variables as described above. For the limited practice group, PC of the key presses ranged from 80% (key 5) to 91% (key 1), *F*(5,105)=10.79, *p*<.001. For the extended practice group, results showed a similar pattern across the practice groups, with PC ranging from 92% (key 5) to 97% (key 1), *F*(5,100)=21.38, *p*<.001. Mean PC improved strongly between the first and second practice blocks (89% vs. 96%) and remained stable during the ensuing blocks, *F*(4,80)=22.33, *p*<.001. A Block × Key interaction suggested that the improvement in accuracy across blocks differed for the various key presses, *F*(20,400)=5.29, *p*<.01. This can be attributed to the fact that key 5 had to be improved more than the other keys to reach the 96% PC, as its accuracy in the first practice block was lower compared with that of the other keys. Possibly, the first four elements of the sequence could be memorized relatively easy, given that people on average can hold three or four sequence elements in their working memory (Bo et al., 2009; Bo & Seidler, 2009), resulting in relatively high accuracy. The high accuracy on the sixth key press can be explained in terms of a recency effect: Participants well remembered the last stimulus they had seen before the preparation interval, causing their response to be relatively accurate. There was no such mechanism for the fifth key press, so that it was initially the most difficult to memorize and thus had the lowest accuracy.

3.2. Test phase

We analyzed participants' performance in the three context conditions via a mixed ANOVA on RTs with Key (6) as repeated measure and Practice group (2) and Test condition (3) as between-subject variables. Results indicated that some key presses were executed faster than others, *F*(5,210)=90.32, *p*<.001, which is due to the longer RT on key 1 as compared to other keys (as in the practice phase). RTs were shorter after extended than after limited practice (211 ms vs. 315 ms), *F*(1,42)=20.95, *p*<.001. However, a Key × Practice group interaction suggested that this beneficial effect of practice differed for the two practice groups, *F*(5,210)=3.10, *p*<.05. Post hoc ANOVAs confirmed that RTs of all key presses were shorter after extended than limited practiced, *Fs*>4.94, *ps*<.05, but that the first and fourth key presses showed the greatest difference (183, 69, 111, 175, 71 and 53 ms, respectively, for keys 1–6). Indeed, when repeating the aforementioned ANOVA without keys 1 and 4, results no longer showed the interaction, *p*=.11.

Most importantly, results showed that performance in the various test conditions differed, *F*(2,42)=3.88, *p*<.05 (see Fig. 3.3). Planned comparisons indicated that RTs were longer in the reversed context condition (308 ms) compared with both the same context condition (242 ms) and the novel context condition (240 ms), *ps*<.05. RTs in the same and novel

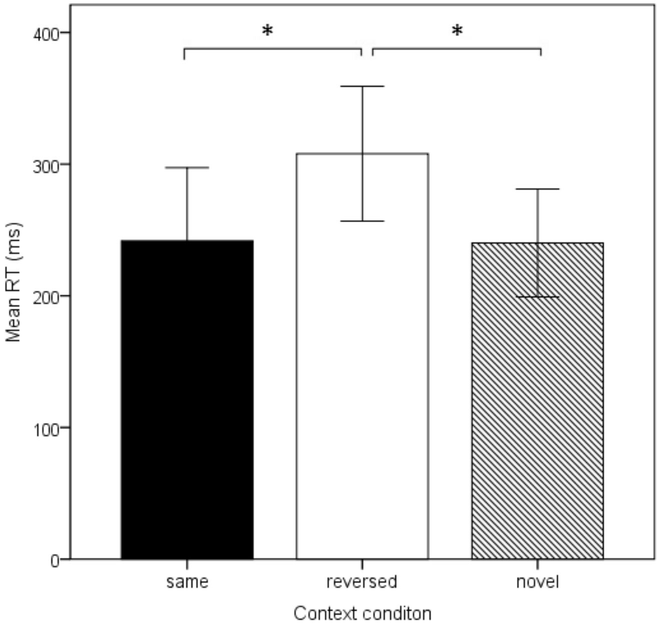

Figure 3.3 RTs (ms) in the same, reversed and novel context conditions across practice groups. Error bars represent standard errors.

context test conditions did not differ, *p*=.95. The ANOVA showed no significant interaction between Test condition and Practice group, *p*=.85, suggesting that performance differences between the test conditions were not moderated by the amount of practice. Furthermore, there was no interaction between Test condition and Key, indicating that all key presses were slowed equally in the reversed context condition, *p*=.43. There were no other interaction effects, *ps*>.51.

As averaging RTs across participants may conceal individual differences in chunking patterns (see, e.g., Verwey, 2003a; Verwey et al., 2009; Verwey & Eikelboom, 2003), this may consequently mask potential differential effects of context on motor chunk preparation and execution. Therefore, we performed an additional analysis in which we differentiated between these two phases of a motor chunk. The first key press of each sequence was assumed to reflect preparation of the first chunk and was thus defined as a preparation point (i.e., T_1). To determine whether for a specific participant other preparation points (T_C) had developed within the sequences, we ran one-tailed paired t tests (*p*<.05) on RTs of the third, fourth and fifth key press of each sequence to evaluate whether each element was significantly longer than both its preceding and succeeding key presses (cf. Bo & Seidler, 2009; Kennerley et al., 2004). The second and sixth key presses were not evaluated as such, because we assume that the second key press of a sequence is always included in the first chunk and that the sixth key press is always within the last chunk. As chunking patterns may be different for the two sequences that a participant performed, we analyzed these sequences separately. This procedure yielded additional preparation points (i.e., T_C) for 23 participants, indicating that they segmented one or both sequences. RTs of the first key press and RTs of key presses that were classified as being significantly slower than its adjacent key presses were averaged to compute the mean preparation RT per participant per sequence. The RTs of the remaining key presses were averaged to compute the mean execution RT. The RTs were subjected to a mixed ANOVA with Process (2; preparation vs. execution) and Sequence (2) as repeated measures and Practice group (2) and Test condition (3) as between-subject variables. Results showed that preparation was not differently affected by the context manipulations than execution, *p*=.80.

Finally, in order to test whether there were differences between the test conditions in terms of accuracy, we calculated the percentage of correctly executed key presses (PC). The mean PC across the test blocks was 94%. A mixed ANOVA on PC with Key (6), Practice group (2) and Test condition (3) showed a Key × Practice interaction, *F*(5,210)=2.86, *p*<.05. Compared with the extended practice group, participants in the limited practice group were more accurate on keys 1–5, but less on key 6. This can be explained in terms of a recency effect: Participants in the limited practice group well remembered the last stimulus they had seen before the preparation interval, causing the final response to be most accurate. This effect did not occur with more practice, as participants could then use their sequence knowledge for execution instead of having to remember each individual stimulus. There were no other significant main or interaction effects, *ps*>.08.

3.3. Awareness

To examine participants' awareness of the sequences, we determined the number of correctly recalled and recognized sequences for every participant. With respect to recall, results of the awareness questionnaire showed that 16 participants (67%) in the limited practice group and 22 participants (92%) in the extended practice group correctly reproduced both learned sequences. Six participants (25%) in the limited and 2 (8%) in the extended practice group recalled one sequence. A total of 17 participants (71%) in the limited practice group correctly recognized both their sequences, as compared to 23 participants (96%) in the extended practice group. Six participants (25%) in the limited and one participant (4%) in the extended practice group recognized one of their sequences. Both recall and recognition were better after extended practice than after limited practice, $\chi^2 s(df{=}1)>4.56$, *ps*<.05. Recall and recognition performance correlated with mean sequence execution time in the test phase, *rs*<−.30, *ps*<.05, indicating that participants with more awareness were faster at executing their sequences.

4. DISCUSSION

The present study explored the potential development of context-dependence for advance sequence preparation and execution processes in memory-based sequencing skill. Specifically, in a go/no-go DSP task, we studied the effects on performance of reversed context and novel context manipulations and examined whether these effects would be mediated by practice. The results showed (I) that performance across all key presses was more or less equally impaired when the stimulus color was reversed during testing, which confirms context-dependence but contrasts with our hypothesis that only the first key presses of a motor chunk—that is, T_1 and T_C—would be affected (cf. Magnuson et al., 2004). Moreover, we observed (II) that sequencing performance was unaffected in the novel relative to the same context condition, which supports the inhibition hypothesis. Finally, (III) the effect of reversing the stimulus color was independent of the amount of practice. Although inspection of performance impairment upon a context reversal showed that RTs were slowed more in the limited practice group than in the extended practice group (107 vs. 57 ms), this difference was not significant and the present results thus do not provide a clear insight into the role of practice. The idea that stimuli are decreasingly processed with practice—which is a typical observation in discrete sequence learning—because subjects more and more only require the first stimulus for proper preparation (e.g., Verwey, 2010; Verwey et al., 2010; Verwey et al., 2011), predicts that context-dependence decreases and thus this inspires further testing in a study with enhanced power. Below, we discuss in more detail our major findings regarding the mechanism underlying context effects and its impact on (advance) preparation and execution processes.

4.1. The mechanism underlying context effects

In line with the study by Ruitenberg et al., (2012), we examined whether context-dependence could be explained in terms of facilitation of memory retrieval by reinstatement of the learning context (cf. Healy et al., 2005; Wright & Shea, 1991). Whereas we observed that sequencing performance was significantly impaired when contexts were reversed, sequencing performance in the novel context did not differ from performance in the learning context. This is not in line with the reinstatement hypothesis and rather suggests that interference between the two sequence representations during preparation is causing the here-observed context effect. Such an account of context-dependence in terms of interference has already been forwarded before by Shea and Wright (1995). They proposed that a switched context activates the alternative task (here; alternative sequence), which in turn inhibits activation of the correct task (sequence) and results in slower responses. The present study confirms this proposition and additionally replicated earlier findings that context effects in the DSP task arise only when the context yields interference (cf. Ruitenberg et al., 2012).

4.2. Context effects in the preparation versus execution phase

We observed that interference during the preparation phase due to a context reversal resulted in impaired performance across all key presses of the sequence. This result is surprising in the light of the (above discussed) previous research and existing models on discrete sequencing skill, which would have predicted that only T_1 and T_C will be affected in a memory-based sequence task. We believe we have two findings to explain: first, why was the preparation phase not more sensitive to a context reversal than the execution phase and, second, why was the execution phase—thought to include merely motoric processes in the go/no-go DSP task—context dependent to begin with?

The first observation that T_1 and T_C were not slowed more than later response times from the execution phase suggests that advance preparation did not suffer from a change in context. This may imply that advance preparation is not typically context dependent. However, as this would contradict previous studies (e.g., Magnuson et al., 2004), we believe that an alternative explanation should be considered. With regard to T_1, the time interval that we employed between the (first) moment of context presentation and sequence execution may be important. Magnuson et al. (2004) used 4-element sequences and observed that the time needed for sequence selection increased to about 3,000–3,500 ms upon a context reversal. In the current study, however, the total interval from presentation of the first stimulus to presentation of the go signal amounted to 6,000 ms. Hence, sufficient time may have been available for advance preparation to be performed optimally, even in the face of an unfavorable context.

With regard to T_C, we expected indications of context-dependence, too, as the DPM states that the cognitive processor is involved in the transition between motor chunks. However, Verwey et al. (2010) recently observed that this transition was relatively unaffected by a dual task, and suggested it may not involve preparatory process controlled by the cognitive processor, but instead may be an automated process (possibly controlled by a dedicated concatenation processor). It may be, then, that this particular process is not sensitive to contextual changes, thereby explaining the absence of indications for context-dependence at T_C.

Though very interesting, the second observation of context-dependence in the execution phase is harder to explain, and for now we can only speculate on its account. As noted above, both the DPM and Klapp's model assume that in the current memory-based design responses after the first (with the possible exception of T_C) are executed by a motor processor—using the content of the motor buffer. Anything that adversely affects and thus delays these advance preparation processes would be predicted to only slow the first key press of a motor chunk[2]—whether it is a perceptual conflict arising from mismatch between the stimulus location(s) and stimulus color, a surprise resulting from a state prediction error related to the anticipated and actual color of the stimulus, or interference with preparation of the opposite sequence that needs be overcome. So, what then caused the slowing across all key presses in the reversed context condition?

In the introduction, we described the preparation and execution phases in a go/no-go DSP task as two distinct and relatively process-pure phases, respectively, involving advance preparation processes by the cognitive processor and execution processes by the motor processor. However, if we maintain our central assumption that contextual changes impact performance of the cognitive processor rather than of the motor processor (as the latter is assumed to be merely involved in motoric execution processes), our results suggest that the cognitive processor was involved also in the execution phase. The major task attributed to the cognitive processor in sequencing skill is advance preparation (i.e., sequence selection and buffer loading). Yet, it has been proposed that in traditional

DSP tasks—with continued display of key-specific stimuli—the cognitive processor may contribute to performance online by serving as a direct S-R translator that races with the motor processor (Verwey, 2001). In the go/no-go DSP task, where there are no stimuli presented during sequence execution, such S-R translations are clearly not possible. However, during memory-based execution, the cognitive processor possibly contributes to performance online in a different way, namely by explicitly and intentionally triggering single key presses on the basis of the memory trace(s) held in short- and/or long-term memory.[3] This could provide a first explanation for the current results: Whenever a short-term memory trace is created during a trial in the reversed context condition, this conflicts with an existing long-term memory trace (e.g., motor chunks or explicit knowledge developed during the practice phase) and impairs the performance of the cognitive processor (cf. Botvinick et al., 2001) so that it no longer races with the motor processor. Consequently, performance across all key presses is slowed. Such interference did not occur in the novel context condition, as the short-term and long-term memory traces did not prime alternative sequences.

The current observation that sequence awareness was high relative to typical DSP studies (hence, without the go/no-go inclusion) fits the idea that the cognitive processor uses long-term memory traces. For example, 46% of the participants in the Verwey et al.'s (2010) study recalled their sequences, compared with 79% of the participants in the present study. Such explicit sequence knowledge is assumed to be used by the cognitive processor for triggering individual responses (Verwey et al., 2010). Indeed, the present data show for the first time that sequence awareness was correlated with sequence execution time when no stimuli are presented during actual execution of the sequence. The idea that the cognitive processor may actively use perceptual-motor memory traces could explain this finding. This interesting but speculative notion should be tested further in future research.

Second, we might speculate also that the context effect on the cognitive processor impaired sequencing performance in a less direct manner—that is, by affecting the quality of the motor buffer content. Specifically, it is possible that the content of the motor buffer is of a poorer quality in the reversed context condition because the change of context somehow affected motor buffer loading by the cognitive processor. This would explain the effect across all key presses as observed here, and imply that loading of the motor buffer is not an all-or-none process.

Third, one may argue that the reversed context condition (and the interference that it produced) created some kind of general mind set in the participants which caused them to respond in a more controlled—and thus slower—manner (see for such a suggestion also Abrahamse & Verwey, 2008). However, Verwey (1999) performed a study in which participants learned entire discrete sequences based on associated numbers (e.g., the number 2 indicated that a certain sequence had to be performed). When in a test phase the number-sequence mapping was reversed—essentially creating a similar kind of conflict as in the current study—execution of the first key press, but not later key presses, in the sequence was slowed. This suggests that such a general slowing does not typically occur for sequence production tasks.

Finally, one may argue that the above, speculative explanations are especially appropriate for the extended practice group, as there exists an alternative—and simpler—explanation for the limited practice group. Specifically, it may be that performance is improving substantially in the same context condition for the latter group, as if it were further practice, because performance is far from having reached asymptote after the first and only practice block.[4] From this notion, the relatively poor performance in the reversed context condition can be explained by claiming that the context reversal (but not the novel context) prevented the effective continuation of practice in this block. In the end, however, this explanation is less parsimonious than the above, because still the arguments above are needed to explain the effect in the extended practice condition.

4.3. Conclusions

The present study demonstrated that memory-based sequencing performance was impaired when associated context-colors were reversed, but unaffected when sequences were presented in a new color. This provides further evidence for the notion of context-dependent sequence skill in general. We propose that contextual changes either affected the online contribution of the cognitive processor during sequence execution, or yielded a reduced quality of advance sequence preparation. Overall, the current results shed new light on the production of skilled, discrete keying sequences by indicating a(n) (even more) substantial role for the cognitive processor in memory-based sequencing skill than previously thought—extending beyond advance preparation and contributing to execution by triggering responses based on key-specific stimuli. Moreover, in combination with the findings from previous studies, the current study suggests that the cognitive processor is susceptible to changes in context for both its advance (e.g., Magnuson et al., 2004) and online (this study) contributions.

Notes

1. No-go trials are included to prevent participants from simply learning to start performing the sequence after the 1,500-ms preparation interval has ended. Instead, they have to await the (no-)go signal before deciding whether or not they should actually execute the sequence.

2. One may argue that under some conditions, motor buffer loading continues after sequence execution has started (on the basis of, for example, explicit knowledge). Indeed, such an assumption may be supported to some extent by the study of Verwey (2001) who showed that loading of the second motor chunk could be performed during execution of the first motor chunk. However, even then, one would not expect all key presses of the sequence to be affected, and thus expect to find an interaction with Key.

3. Short-term memory traces being built during actual stimulus presentation during the test trial, and long-term memory traces being built throughout the many repetitions of the sequence in the practice phase.

4. Improvement from the (last) practice block to the same context condition (i.e., no context changes between practice and test) was significant for the limited practice group (from 409 ms to 299 ms on average), *F*(1,7)=6.98, *p*=.03, but not for the extended practice group (from 206 ms to 196 ms; *p*=.53). This indicates room for performance improvement for the limited practice group and near asymptote performance for the extended practice group.

Acknowledgments

We would like to thank Nadiya El-Sourani for her assistance in running the experiment.

Chapter 4

Context-effects on highly practiced motor chunks in sequencing skill

Marit F. L. Ruitenberg

Manuscript in preparation

The present study examined whether practice mediates the development of context-dependence in memory-based sequencing skill. Additionally, the sensitivity to context-manipulations of preparation versus execution processes was investigated. Participants performed two keying sequences in a discrete sequence production task, either during limited or extended practice. Each sequence was presented in its own color. During testing, participants performed the sequences in three conditions in which the sequence-specific colors were either the same as during practice, reversed or completely novel. The current results provide two new insights in context-dependent sequencing skill. First, performance was only sensitive to context-manipulations after extended practice. Second, the observation that the preparation—but not execution—of highly practiced motor chunks was affected suggests that context mainly affects higher cognitive processes.

1. INTRODUCTION

The ability to acquire and perform action sequences is essential for our everyday behavior, as most complex actions that people perform (e.g., lacing a shoe or playing piano) consist of a series of simple movements that are executed in a specific order. Research has shown that such sequencing skills can become context-dependent—that is, performance has been found to be better in the environment in which the performed skill was originally acquired, as opposed to performance in a different environment (e.g., Abrahamse & Verwey, 2008; Anderson, Wright, & Immink, 1998; Ruitenberg, Abrahamse, De Kleine, & Verwey, 2012a; Ruitenberg, De Kleine, Van der Lubbe, Verwey, & Abrahamse, 2012b; Shea & Wright, 1995; Wright & Shea, 1991). In recent studies we have focused specifically on context-effects in discrete sequence skill—the ability to execute a short series of simple movements at high pace. The observation of context-dependence in such skill is important because it shows the ongoing relevance of perceptual information even in predominantly motor-based tasks. Below, I first discuss how discrete movement sequences are produced, specifically distinguishing between preparation and execution processes in memory-based sequence production. Next, I zoom in on the context-dependence of such sequencing skill and address the possible role of practice. In one of our earlier studies (Ruitenberg et al., 2012a) the overall notion of impaired memory-based sequencing performance upon contextual changes was confirmed, but more specific predictions on (I) the role of practice and (II) the distinct sensitivity to context-effects of preparation and execution processes in such skill were not supported. The present study further investigated these issues.

1.1. Discrete sequence skill

The relatively complex movement patterns that we perform in daily life are often made up of several brief movement sequences that require both motor and cognitive control. A task that is well-suited for studying the cognitive processes underlying sequencing skill is the Discrete Sequence Production (DSP) task (e.g., Verwey, 1999; see also Abrahamse, Ruitenberg, De Kleine, & Verwey, under review; Verwey, Abrahamse, & De Kleine, 2010). The DSP task typically involves series of two to seven stimuli that are presented in a fixed order. Participants respond to each of these stimuli by means of a spatially compatible key press, yielding the learning of fixed, discrete key press sequences. Due to the relatively simple responses in the form of key presses, the motor control component is minimized (e.g., there is little need for joint angle or force control) and as such cognitive control mechanisms involved in sequencing skill can be examined.

Based on work with the DSP task, Verwey (2001) proposed the dual processor model (DPM) of discrete sequence production. According to the DPM, sequencing performance involves sequence selection and motor buffer loading by a cognitive processor (i.e., preparation phase), followed by the fast execution of the motor buffer content by a dedicated motor processor (i.e., execution phase). Initially, the cognitive processor prepares each individual element—that is, key press—by translating each stimulus into the appropriate response, which is then executed by the motor processor. With practice, the sequences are learned and *motor chunks* develop: representations of a series of successive responses that can be prepared and loaded as if they were a single response. The cognitive processor can then select such a chunk on the basis of just the first stimulus that corresponds to that motor chunk, after which the motor processor executes all elements within the chunk. During the execution phase the cognitive processor can support the motor processor in producing the motor chunk elements by means of direct stimulus-response (S-R) translations (Verwey, 2001, 2003b; Verwey & Abrahamse, 2012), so that the fastest possible responses are generated (i.e., statistical facilitation; e.g., Verwey, 2001). As S-R translations also involve preparation related to triggering each individual response, the execution phase of the typical DSP task includes both preparation and execution processes.

To better distinguish between preparation and execution processes during sequence performance, De Kleine and Van der Lubbe (2011) developed the go/no-go DSP task. In this task, all key-specific stimuli of a sequence are displayed at a fixed pace before execution is started in response to a go-signal—participants thus have to perform the sequence completely from memory. As such, the cognitive processor cannot assist the motor processor in the go/no-go DSP task, as the absence of stimuli during the execution phase prevents S-R translations. Consequently, preparation and execution processes are clearly separated in the go/no-go DSP task. Preparation processes are most clearly involved during sequence initiation, which is reflected in the first response time (T_1). In addition, it has been shown that longer sequences (around 5 to 8 elements) are often segmented in two or more motor chunks. The transition from one motor chunk to the next is thought to be reflected in a relatively long response in the sequence (i.e., concatenation, T_C), and is assumed to include additional preparation processes by the cognitive processor (e.g., Bo & Seidler, 2009; Kennerley, Sakai, & Rushworth, 2004; Verwey et al., 2010). In a go/no-go DSP task, all other responses are assumed to merely reflect execution processes driven by the motor processor, because the online contribution of the cognitive processor is prevented. The current study employs this go/no-go version of the DSP task, as it allows studying the context-dependence of preparation and execution processes in memory-based sequencing skill.

1.2. Context-dependent sequencing performance

The notion that skilled performance is facilitated by reinstatement of the context in which it was acquired and that performance is impaired in another context, has been defined as context-dependent learning (e.g., Wright & Shea, 1991), procedural reinstatement (e.g., Healy, Wohldmann, Parker, & Bourne, 2005) and specificity of learning (e.g., Healy et al., 2005). The common explanation for these effects is that context features become associated with the task during acquisition and subsequently enhance performance by acting as a cue for memory retrieval processes (e.g., Healy et al., 2005; Wright & Shea, 1991). This suggests that context-dependent learning involves the integration of perceptual context information into a task representation (cf. feature binding; Hommel, 2004, 2007), such that retrieval of the learned skill from memory—and therewith performance of the task—becomes impaired when the context is changed. Although the concept of context-dependent learning originates from the domain of verbal memory performance (e.g., Godden & Baddeley, 1975; Smith, 1985), it has also been demonstrated for sequential motor performance. For example, Anderson et al. (1998) and Wright and Shea (1991) demonstrated that performing 4-key sequences in a DSP-like task was hindered when sequence-specific contextual features—that were consistently paired with each sequence during practice—were changed during testing.

In addition to such context-dependent retrieval, Ruitenberg et al. (2012b) recently demonstrated a second type of context-dependence in motor skill performance, which they referred to as context-dependent filtering. They observed that sequencing performance in the typical DSP task dropped when the location of irrelevant stimulus information that accompanied each imperative stimulus during practice was changed, but that performance was unaffected when such information was removed. It was suggested that participants had learned to ignore the (order of) locations of irrelevant stimuli during the practice phase, in order to achieve optimal sequencing performance. Interestingly, Ruitenberg et al. (2012b) observed that this type of context-dependence reduced with practice. These results suggest that perceptual context information that needs to be filtered out initially interferes with performance, but that such information is decreasingly processed as practice continues. The latter is in line with the idea that with practice sequencing performance becomes more motor-based and internally guided, so that the need for external guidance by means of stimuli reduces (e.g., Hikosaka et al., 1999; Verwey, 1999). Furthermore, it implies that during such filtering the contextual features are not included in the sequence representation, and thus are unlikely to serve as a cue for memory retrieval processes.

To contribute to a more comprehensive understanding of the role of practice in context-dependent learning, the present study explores whether the amount of practice modulates the development of context-dependent *retrieval* in memory-based sequencing skill. While context-dependent filtering thus involves the learning of to-be-ignored (context) information so that the effect of such information reduces with practice, context-dependent retrieval involves the formation of associations between sequences and sequence-specific contextual features. These associations are assumed to strengthen with practice, so that contextual features become gradually integrated in the sequence representation and can be used as a cue for memory retrieval and therewith performance. This would imply that sequencing performance is best when all features included in the representation are reinstated, but suboptimal when some of these features are changed during testing. Furthermore, as memory-based sequencing performance in the go/no-go DSP task always occurs in the absence of stimuli (since they are presented before the go-signal), the reliance on key-specific stimuli during actual execution of the sequence does not change with practice. In all, it could therefore be predicted that context-dependent retrieval increases with practice.

Based on the DPM, even more specific predictions can be made regarding the processes underlying sequencing skill that will be sensitive to contextual-changes after extended practice. Assuming that context-effects require a link from perception to action, it follows that only preparation processes by the cognitive processor—but not pure execution processes by the motor processor—would be sensitive to context. In line with this notion, Magnuson, Wright, and Verwey (2004) found that search and retrieval processes used as part of response selection are facilitated by reinstatement of the learning context. Besides such general sequence preparation, it could be predicted also that the cognitive processor's online S-R translations are affected by changes in context. As outlined above, the latter are prevented in the go/no-go DSP task (as stimuli are not presented during actual performance of the sequences) and it could therefore be expected that context-dependence of the cognitive processor results in prolonged T_1 and T_C, whereas other response times are unaffected. Given that the former responses are thought to reflect memory-retrieval processes, this hypothesis fits well within the notion of context-dependent retrieval. However, contrasting the idea that context would only affect key presses that reflect preparation processes by the cognitive processor, Ruitenberg et al. (2012a) observed slowing across all key presses of a motor sequence upon a context-reversal. As this counters the prediction of the DPM, the present study reexamines whether the cognitive processor is indeed more sensitive to perceptual changes than the motor processor.

1.3. The present study

In order to examine the effect of practice on the context-dependence of memory-based sequencing skill in the go/no-go DSP task, as well as test the prediction that T_1 and T_C—but not other key presses—would be context-dependent, the present study involved several methodological changes compared to Ruitenberg et al. (2012a). First, participants performed their sequences in each test condition (as opposed to only one of the conditions), so that the effect of context on individual chunking patterns could be examined. As several studies have shown individual differences in chunking patterns (e.g., Bo & Seidler, 2009; Kennerley, et al., 2004; Verwey, 2003a; Verwey, Abrahamse, & Jiménez, 2009), comparing between groups may have concealed differential effects of context on preparation versus execution keys in the previous work. Second, participants performed both a prestructured sequence (including a pause between the presentation of the third and fourth stimulus) and an unstructured sequence (without a pause). The pause in the prestructured sequence is known to induce the same chunking pattern for all participants, while chunking patterns of unstructured sequences are known to differ between participants (see e.g., Verwey, 2003a; Verwey et al., 2009; Verwey & Eikelboom, 2003). Finally, the number of trials in the test phase was increased from 10 to 20 to enhance the power of the study.

Participants practiced one prestructured and one unstructured sequence (each in their own color) in the go/no-go DSP task, either during limited or extended practice. In the test phase, participants performed their sequences in three different context conditions. In the same context condition, the combinations of sequences and stimulus colors were the same as during practice. In the reversed context condition, the colors of the key-specific stimuli were switched between the two sequences. It was expected that T_1 and T_C would be predominantly affected by this manipulation (cf. Magnuson et al., 2004), as other responses are assumed to be entirely driven by the motor processor (since no stimuli are available during execution for S-R translations by the cognitive processor). A novel context condition was also included, in which key-specific stimuli of both sequences were presented in the same, new, color. Several researchers have argued that a contextual change impairs performance because perceptual features can no longer serve as a cue for memory retrieval (e.g., Healy et al., 2005; Wright & Shea, 1991). Alternatively, we recently suggested that performance may also decline because selection of the correct responses is more difficult following a context reversal, as the color may prime the alternative sequence (Ruitenberg et al., 2012a; see also Shea & Wright, 1995). Whereas the former account would imply that performance declines in any context that differs from the learning context, the latter predicts that performance declines only in a reversed context and not in a novel context. To test the feasibility of the reduced facilitation and the inhibition accounts, the same context condition was compared with both the reversed and novel context conditions.

Summarizing, the present study examined whether practice modulates the development of context-dependence in memory-based sequencing performance. Furthermore, it was hypothesized that preparation processes reflected in T_1 and T_C, but not execution processes reflected in the other key presses would be context-dependent. More specifically, T_1 and T_C were expected to slow in the reversed context condition compared to the same (and possibly novel) context conditions.

2. METHOD

2.1. Participants

The participants in this study were 48 students (39 women and 9 men) of the University of Twente, aged 17 to 32 years (mean age = 22 years). According to Annett's (1970) Handedness Inventory 46 participants were right handed and 2 were ambidextrous. Participants reported not to suffer from color-blindness, dyslexia or ADHD, and they had no problems with their sight (glasses or contact lenses were allowed). All participants gave their written informed consent. The study was approved by the ethics committee of the Faculty of Behavioral Sciences of the University of Twente.

2.2. Apparatus

E-Prime© 2.0 was used for stimulus presentation and data registration. The program ran on a Pentium IV class PC. Stimuli were presented on a 17-in Philips 107 T5 display.

2.3. Task and procedure

Participants placed the fingers of their left hand on the c, v, b and n keys of a computer keyboard. A fixation cross was presented in the center of the screen, along with four horizontally aligned squares (see Figure 4.1). They were drawn with a silver color line on a black background. The four stimulus squares spatially corresponded with the four response keys (e.g., the left most square corresponded with the 'c' key). After 1000 ms, one square was filled for 750 ms, next a second square, and so on until the sixth square had been filled. The default screen then reappeared for 1500 ms, after which the fixation cross was colored either red or green. The red fixation cross, presented for 3000 ms, indicated that sequence execution had to be withheld (a no-go trial). No-go trials were included to prevent participants from simply learning to start performing the sequence after the 1500 ms preparation interval has ended. Instead, they have to await the (no-)go signal before deciding whether or not to execute the sequence. The green fixation cross, presented for 100 ms, indicated that participants had to repeat the presented sequence by pressing the appropriate keys in the correct order (a go trial). After each completed sequence, the default screen would appear for 1000 ms before the first stimulus of the next sequence was

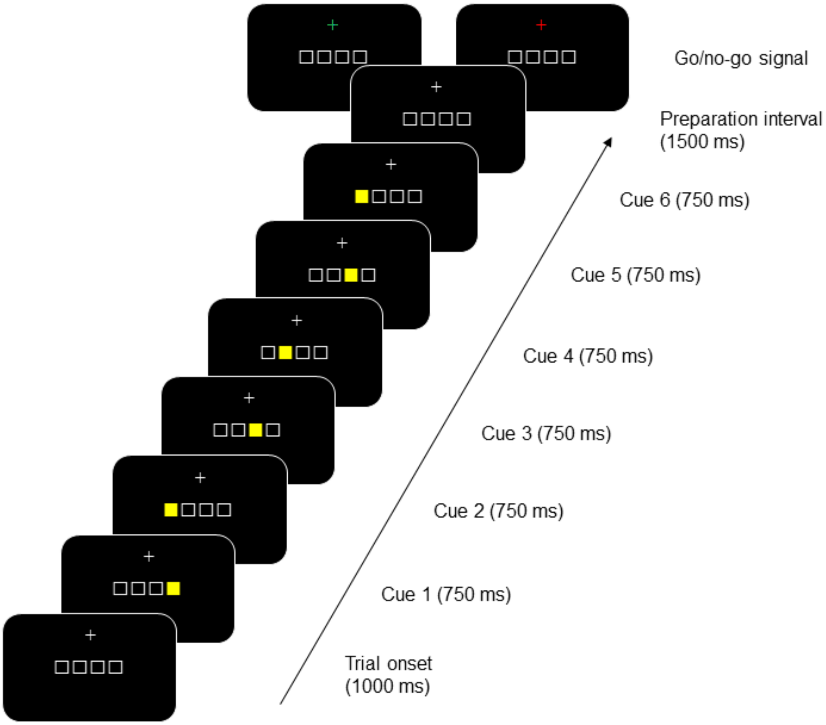

Figure 4.1 An overview of stimulus presentation in the go/no-go DSP task.

presented. Participants were instructed to respond as fast and accurately as possible. An error message appeared when a participant reacted before the go/no-go signal. In addition, feedback was provided upon completion of a response sequence to indicate whether errors had been made.

During the practice phase, participants practiced two 6-key sequences that consisted of a combination of two 3-key sequences, namely cbv, vnc, bcn and nvb. The prestructured sequence involved a repetition of a three-key sequence, that included a pause of either 200, 400 or 600 ms between stimulus 3 and 4 (e.g., bcn-bcn, with ‘-‘ indicating the pause). Three intervals were used to prevent participants from learning a fixed rhythm, and the duration of the pause was determined randomly per trial. The unstructured sequence involved a combination of two different 3-key sequences and did not include a pause (e.g., bcnvnc). In order to prevent finger-specific effects on individual response times, the sequences were counterbalanced across participants. For each participant, the prestructured and unstructured sequence never started with the same key and combinations resulting in repetitions (e.g., cbvvnc) were discarded. One of the sequences was always presented in yellow, while the other sequence was always presented in blue (counterbalanced across participants and prestructured vs. unstructured sequences). A practice block consisted of 50 trials per sequence, as well as 8 no-go trials. The sequences were presented in random order. Half of the participants completed 1 practice block (i.e., limited practice group), the other half completed 6 practice blocks and thus practiced 300 trials per sequence (i.e., extended practice group). There was a short 30-s break halfway through each block and a 2-min break in between blocks. After completion of the final practice block, there was a 2-min break before the test phase was started.

During the test phase, participants performed their sequences in three context conditions. In the same context condition, the sequences were presented in the same color as during practice. In the reversed context condition, the colors of the two sequences were switched. In the novel context condition both sequences were presented in red. Each test block consisted of 20 randomly presented trials per sequence (plus 4 no-go trials) and the order of the three blocks was counterbalanced across participants.

Finally, participants completed a questionnaire that measured their awareness of the sequences. They were asked to recall both of the sequences they had performed during the experiment, by writing down the letters of the keys in the correct order. Then, they were asked to recognize their two learned sequences from a list of twelve alternatives.

3. RESULTS

Response time (RT) was defined as the time between onset of the go-signal and depression of the first key and as the time between two consecutive key presses within a sequence. Sequences in which one or more errors were made were excluded from the analyses. Sequences in which RTs of individual key presses exceeded more than 2 standard deviations from the group mean in a (practice or test) block were also excluded. Mean RTs per key press within the prestructured and unstructured sequences were calculated for each participant.

3.1. Practice phase

The RT data of the limited practice group were subjected to an ANOVA with Key position within the sequence (6; hereafter referred to as Key) and Sequence (2; prestructured vs. unstructured) as within-subject variables. Results showed that some key presses were executed faster than others, $F(5,115)=42.40$, $p<.001$, $\eta_p^2=.65$, which can be attributed to the relatively slow first key press as compared to ensuing key presses: The RT on key 1 reflects a reaction to the go signal and thus initiation of the sequence, whereas RTs on other keys reflect responses based on sequence knowledge (Fig. 4.2; dashed line).

For the extended practice group, an ANOVA on RTs with Block (6), Key (6), and Sequence (2) as within-subject variables was performed. As Figure 4.2 (solid lines) shows, RTs decreased across the practice blocks, $F(5,115)=93.94$, $p<.001$, $\eta_p^2=.80$. A Block × Key interaction suggested that there was more improvement in some keys across blocks, $F(25,575)=4.48$, $p<.001$, $\eta_p^2=.16$. Furthermore, a Sequence × Key interaction suggested that the RT patterns across the six key presses differed for the two sequences, $F(5,115)=2.85$, $p<.05$, $\eta_p^2=.11$. As expected, the difference between T_4 and $T_2T_3T_5T_6$ in the prestructured sequence was larger than in the unstructured sequence (41 ms vs. 3 ms), $t(23)=2.11$, $p<.05$, $d=0.65$, supporting the idea that participants segmented their prestructured sequences into two chunks on T_4.

Finally, results of an ANOVA on RTs of the first practice block with Key (6) and Sequence (2) as within-subject variables and Practice group (2; limited vs. extended) as between-subject variable showed no main or interaction effects of Practice group (*ps*>.45), suggesting that performance of the practice groups in this blocks did not differ.

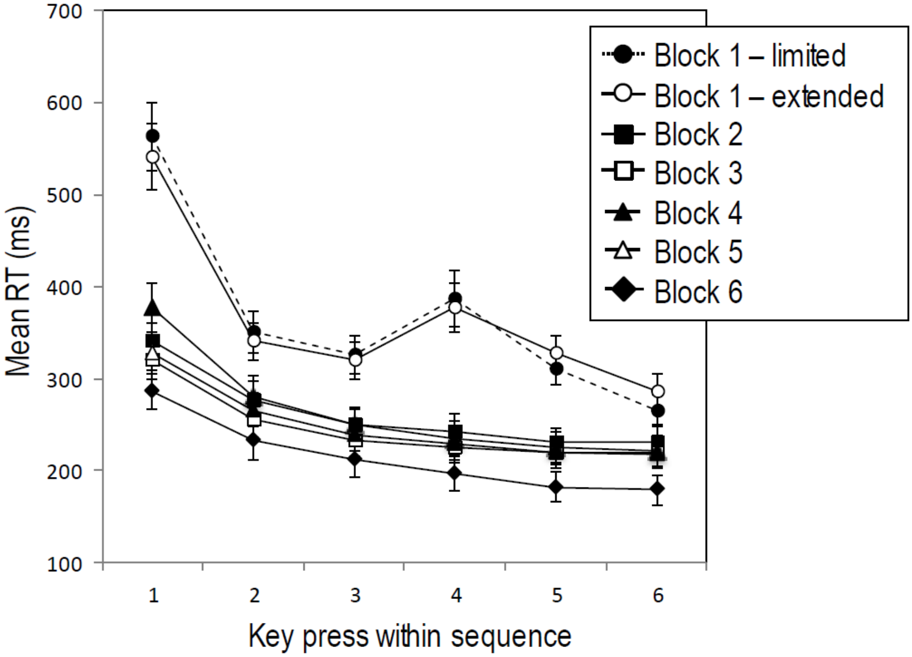

Figure 4.2 Mean RTs (ms) per key position for participants in the limited and extended practice groups as a function of block.

Performance was also analyzed in terms of accuracy by using ANOVAs on error percentages including the same variables as described above. For the limited practice group, errors differed across key position within the sequences, $F(5,115)=30.65$, $p<.001$, $\eta_p^2=.57$. Errors increased from key 1 to key 5 (3.8% to 11.8%), then slightly decreased to key 6 (9.9%). Participants made fewer errors in the prestructured sequence than in the unstructured sequence (6.2% vs. 9.8%), $F(1,23)=7.22$, $p<.05$, $\eta_p^2=.24$, yet a Sequence × Key interaction suggested that this differed per key position, $F(5,115)=3.20$, $p<.05$, $\eta_p^2=.12$. There were no differences in error rates between prestructured and unstructured sequences on T_1-T_3 (4.0% vs. 5.8%, $p=.51$), but participants made fewer errors on T_4-T_6 of the prestructured sequence than on the same keys of the unstructured sequence (8.4% vs. 13.7%), $F(2,46)=6.44$, $p<.05$, $\eta_p^2=.22$.

For the extended practice group, error percentages decreased from 7.9% in the first practice block, to on average 3.3% in blocks 2-6, $F(5,115)=10,23$, $p<.001$, $\eta_p^2=.31$ (the effect of Block was absent when removing the first practice block from the analysis). Results further showed that errors increased with key position in the sequence (2.1% on key 1 to 6.0% on key 6), $F(5,115)=27,69$, $p<.001$, $\eta_p^2=.55$, but this difference reduced with practice, $F(25,575)=3,65$, $p<.01$, $\eta_p^2=.14$. There was no difference in errors between prestructured and unstructured sequences ($p=.13$). Finally, in line with the RT data, results of an ANOVA on errors in the first practice block with Sequence (2), Key (6) and Practice group (2) showed no differences between the groups ($ps>.45$).

3.2. Test phase

Participants' performance in the three context conditions was analyzed via a mixed ANOVA on RTs with Context (3; same vs. reversed vs. novel), Sequence (2) and Key (6) as within-subject variables and Practice (2) as between-subject variable. Results showed that the prestructured sequence was performed faster than the unstructured sequence (248 vs. 266 ms), $F(1,46)=16.34$, $p<.01$, $\eta_p^2=.27$. Furthermore, a Sequence × Key interaction suggested that RT patterns differed for the two sequences, $F(5,230)=3.55$, $p<.01$, $\eta_p^2=.07$. Like in the practice phase, the prestructured sequence was segmented into two chunks on T_4, while the unstructured sequence did not show such stable segmentation across participants. Results showed that performance in the various context conditions differed, $F(2,92)=4.07$, $p<.05$, $\eta_p^2=.09$. Moreover, a Context × Practice interaction suggested that the effect of context depended on the amount of practice, $F(2,92)=2.98$, $p=.05$, $\eta_p^2=.06$. A Context × Practice × Key interaction further suggested that some key presses were differently affected by the context manipulations than others, $F(10,440)=3.19$, $p<.05$, $\eta_p^2=.07$.

To investigate in more detail the interaction between context condition, practice and key, an ANOVA on RTs with Context (3), Sequence (2) and Key (6) was performed for each practice group. Results showed no main or interaction effects of context after limited practice (*ps*>.17). For the extended practice group, however, results showed a main effect of Context, $F(2,46)=7.15$, $p<.01$, $\eta_p^2=.24$. Sequences were performed slower in the switched and reversed context conditions (240 ms and 251 ms, respectively) than in the same context condition (230 ms), $Fs>6.09$, $ps<.05$, $\eta_p^2s>.21$. Moreover, a Context × Key interaction suggested that the key presses within the sequences were differently affected by the context manipulations, $F(10,220)=3.07$, $p<.05$, $\eta_p^2=.12$.

To specifically test the hypothesis that preparation would be differently affected by the context manipulations than execution, mean RTs of key presses that reflect preparation and execution processes, respectively, were determined for both sequences. The prestructured sequence was clearly segmented on T_4, thus enabling us to compare the mean preparation RT (i.e., T_1T_4) with that of the mean execution RT (i.e., $T_2T_3T_5T_6$). Results of an ANOVA on RTs with Context (3) and Process (2; preparation vs. execution) showed an interaction between Context and Process, $F(2,44)=5.17$, $p<.05$, $\eta_p^2=.19$. As expected, preparation was found to be significantly affected by the context manipulations, $F(2,44)=6.72$, $p<.01$, $\eta_p^2=.23$, while execution was not ($p=.10$). Specifically, results showed that RTs of key presses reflection preparation were slower in reversed and novel context than in the same context, $Fs>13.04$, $ps<.01$, $\eta_p^2s>.36$.

As there are large individual differences in how participants segment unstructured sequences, preparation and execution processes in the unstructured sequence are likely to be reflected by different key presses for different participants. The first key press of each sequence was assumed to always reflect preparation of the first chunk, and was thus defined as a preparation point (i.e., T_1). To examine whether other preparation points (T_C) had developed within the sequence during practice, paired t-tests were performed ($p<.05$, one tailed) per participant on RTs of the third, fourth and fifth key press of the sequence in the final practice block to evaluate whether the RT of a given key press was significantly longer than the RT of both its preceding and succeeding key presses (cf. Bo & Seidler, 2009; Kennerley et al., 2004; Ruitenberg et al., 2012a). The second and sixth key press were not evaluated as such, because it was assumed that these key presses were always included in the first and last chunk, respectively. This procedure yielded additional preparation points (i.e., T_C) for 17 of the 24 participants in the extended practice group, indicating that they segmented their unstructured sequence. Results of an ANOVA on RTs with Context (3) and Process (2) showed no significant interaction between Context and Process ($p=.52$), suggesting that in the unstructured sequence preparation and execution processes were not differently affected by context.

Performance in was also examined in terms of accuracy. The percentage of erroneously executed key presses was calculated for each sequence in each context condition and subjected to an ANOVA with Context (3), Sequence (2) and Key (6) as within-subject variables and Practice (2) as between-subject variable. Results showed that error percentages did not differ between the same, reversed and novel context conditions (2.8% vs. 4.1% vs. 3.5%, respectively, *p*=.20).

Finally, results of the awareness questionnaire showed that in the limited practice group 20 participants (83%) correctly reproduced the prestructured sequence and all participants recalled the unstructured sequence. In the extended practice group, 23 participants (96%) recalled the prestructured sequence and 22 participants (92%) recalled the unstructured sequence. To examine whether explicit sequence knowledge was related context-effects in the extended practice group, awareness of the sequences (i.e., recall plus recognition score) was correlated with slowing in RT in each context condition. For the prestructured sequence, awareness did not correlate with slowing of preparation and execution keys in either context condition (*ps*>.49). For the unstructured sequence, there was a negative correlation between awareness and slowing of both preparation and execution in the novel condition, *rs*(24)<-.40, *ps*≤.05. This suggests that when participants had more explicit knowledge of their unstructured sequence, sequencing performance slowed less in the novel context condition.

In summary, results showed that memory-based sequencing performance was unaffected by the context-manipulations after limited practice. After extended practice, the key presses reflecting preparation—but not execution—of motor chunks in the prestructured sequence were slowed in both the reversed and novel context conditions. Performance was impaired across all key presses in the unstructured sequence in the reversed and novel context conditions.

4. Discussion

The present study extended previous research on the role of perceptual context in memory-based sequencing skill, and provides three particularly interesting findings. (I) It further strengthens the notion that performing skilled discrete movement sequences—though typically assumed to be predominantly motor based—is indeed susceptible to and partly dependent on the context in which the skill was acquired (cf. Ruitenberg et al., 2012a). (II) The current study for the first time shows that the impact of context in such skill increases with practice. (III) It strongly suggests that a context's largest impact is on higher cognitive processing, as context-dependence was observed mainly for preparation processes (that are assumed to predominantly include cognitive processor efforts). Below, I will subsequently elaborate on each of these issues. Notably, there were some subtle but clear distinctions with the findings in our previous study, which indicates that the task design and other factors may largely modulate the impact of context on memory-based sequencing skill; this issue is addressed distributed across the sections below.

First, it is typically assumed that sequencing skill is predominantly represented in the brain in terms of motor codes. Therefore, results of previous studies were surprising in the sense that they showed an impact of (changes in) perceptual context on the execution of well-trained movement sequences (e.g., Abrahamse & Verwey, 2008; Ruitenberg et al., 2012a, 2012b). Whereas in the studies of Abrahamse and Verwey (2008) and Ruitenberg et al. (2012b) such context dependency was shown in tasks (respectively the SRT and typical DSP task) that continue to provide stimuli during execution, the impact of context in the current study and that of Ruitenberg et al. (2012a) is even more surprising because stimuli were no longer present at the time of actual performance (go/no-go DSP task). The current study thus strengthens the claims from our previous study and shows that the context-dependence of memory-based sequencing skill can be replicated.

Second, in an earlier study on the role of practice in context-dependent sequence learning in the typical DSP task, Ruitenberg et al. (2012b) observed that context-dependence reduced with practice. They proposed that this is the result of the decreased use of external stimuli with practice, due to which participants no longer need to process the context information. A goal of the present study was to examine whether a modulatory role of practice would also emerge for memory-based sequencing performance in the go/no-go DSP task. In contrast to the findings of Ruitenberg et al. (2012b), results showed contextual dependencies after extended practice, but not after limited practice. This supports the notion that context-dependent learning involves the development of associations between context features and the task, which are likely to strengthen with practice and can facilitate memory retrieval processes (Healy et al., 2005; Wright & Shea, 1991). It also showed that probably in our previous study (Ruitenberg et al., 2012a) the power was too low to show the effects of practice. The differential implementation of context stimuli in the Ruitenberg et al. (2012b) study and the present study is likely to underlie the contradictory findings of these studies: Ruitenberg et al. (2012b) investigated so-called context-dependent filtering, which constitutes a different process than context-dependent retrieval. Filtering out irrelevant contextual information may become easier with practice, as people may learn what needs to be filtered out, thus reducing context-dependence. However, retrieval is thought to be context-dependent because of associations that develop between relevant stimuli and contextual features: It is likely that these associations intensify with practice so that the stimulus-color gradually becomes part of the sequence representation, hence increasing context-dependence. The role of practice in context-dependence thus seems to be moderated by the sort of context-dependent learning (filtering vs. retrieval).

Third, in line with the hypothesis that context would affect preparation but not execution processes, it was observed that the first key press of a motor chunk (i.e., T_1 and T_C) in a prestructured sequence was slowed in both the reversed and novel context compared to the same context. Other key presses, thought to reflect execution processes controlled by the motor processor, were unaffected by the context manipulations. These observations are in line with the idea that preparation processes by the cognitive processor are sensitive to perceptual changes, and suggest that context may facilitate the search for and retrieval of motor chunks (cf. Magnuson et al., 2004). In addition, they support the notion that the stimulus-color may have been integrated in the sequence representation—possibly serving as a memory cue (Healy et al., 2005; Wright & Shea, 1991)—so that preparation was more difficult when the combinations of color and sequences were different from that during skill acquisition.

In the unstructured sequence, however, contextual changes resulted in slowing across all key presses of the sequence. While the effect on key presses that reflect preparation processes can be explained in terms of memory-facilitation in the same context condition, the observation that other key presses were slowed, too, is harder to explain—given its purely motoric tasks, it seems unlikely that the motor processor would be sensitive to perceptual changes. I here briefly propose two potential explanations that will need to be further addressed in future research. First, although the cognitive processor was clearly unable to assist the motor processor by means of S-R translations to trigger responses, its efforts may possibly have been affected in an earlier stage: As selection was more difficult in the reversed and novel context conditions, this may have resulted in poorer quality of information loaded in the motor buffer. Consequently, performance across all key presses was impaired. This may especially apply to performance in the novel context condition, as the absence of sequence-specific stimulus colors yielded sequence selection based on spatial stimulus information only. The finding that more awareness was related to less slowing in the novel context condition suggests that the cognitive processor may have assisted the motor processor during sequence execution on the basis of explicit knowledge (e.g., Verwey & Abrahamse, 2012) possibly by facilitating information retrieval from the motor buffer content. A second possibility is related to the construction of the sequences: Although both involved a combination of two 3-key segments, the segments in the prestructured sequence were practiced twice as often as the segments in the unstructured sequence. It could therefore be speculated that the motor chunks in the prestructured sequence were more automated. Consequently, preparation of these chunks was impaired during testing when the presented context-features accompanying a sequence deviated from those during practice. Once the chunk was fully prepared and loaded into the buffer, it could then be executed without further interference by the context. One might argue that motor chunks in the relatively complex unstructured sequence were less developed, so that the performance in an unfamiliar context provided a sort of overload and triggered a general mode of slower responding (which fits with the notion that preparation and execution processes were equally affected).

As outlined above, the current results showed context-effects on motor chunk preparation that are in line with the notion of memory retrieval facilitation. It should be noted, though, that slowing in the reversed and novel context conditions may have different causes: While preparation in the reversed context condition may have been more difficult because the stimulus color primed preparation of the alternative sequence and/or motor chunk (cf. Ruitenberg et al., 2012a), it may have been slowed in the novel context condition because the absence of sequence-specific stimulus colors hindered selection. Overall, the present study replicates earlier findings that memory-based sequencing performance is susceptible to contextual changes (cf. Magnuson et al., 2004; Ruitenberg et al., 2012a). This suggests that perceptual processing takes place when preparing and/or executing sequences from memory, even though perceptual information is not present during actual execution of sequences. Moreover, the present study demonstrates that practice affects the extent to which contextual changes impact performance. Interestingly, it seems that context-dependent filtering becomes less sensitive to contextual changes with practice (Ruitenberg et al., 2012b), while context-dependent retrieval becomes increasingly sensitive to such changes with practice (present study). The current results offer support for the DPM's prediction that preparation of highly automated motor chunks by the cognitive processor, rather than execution of these chunks by the motor processor, would be sensitive to perceptual changes.

Acknowledgements

I would like to thank Marita Espey for her assistance in running the experiment.

Chapter 5

Sequential motor skill in preadolescent children: The development of automaticity

Marit F. L. Ruitenberg
Elger L. Abrahamse
Willem B. Verwey

In press with
Journal of Experimental Child Psychology

This study investigated to what extent preadolescent children, like young adults, learn to perform sequential movements in an automatic fashion. Twenty-four children (mean age 11.3 years) practiced fixed 3-key and 6-key sequences in the discrete sequence production task, by responding to key-specific stimuli via spatially compatible key presses. We compared their performance with that of 24 young adults (mean aged 22.0 years). Results showed that performance improved with practice for both age groups, although children were generally slower. Compared to young adults, children had less explicit knowledge, but relied more on the available explicit knowledge when executing familiar 6-key sequences. Furthermore, they completed fewer of these sequences on the basis of just the first stimulus, and showed a slower transition between successive segments within the sequences. Together, these findings provide insight in the degree to which preadolescent children develop automaticity in sequential motor skill, suggesting that preadolescent children automatize the processes underlying longer movement sequences slower and/or to a lesser extent than is the case with young adults. The present study is in line with the idea that there are several mechanisms that underlie sequencing skill, and suggests that the use of these mechanisms may be dependent on age.

1. INTRODUCTION

Most complex motor actions that people perform (e.g., driving a car or lacing one's shoes) consist of a series of simpler movements that are executed in a specific order. The overall relevance of such sequential motor skills in everyday life prompts questions about skilled performance across the lifespan. The present study contributes by exploring sequential motor skill in preadolescent children and comparing this with such skill in young adults. In contrast to more basic motor skills—such as pointing (e.g., Badan, Hauert, & Mounoud, 2000), reaching (e.g., Kuhtz-Buschbeck, Stolze, Jöhnk, Boczek-Funcke, & Illert, 1998) and aiming (e.g., Smits-Engelsman, Sugden, & Duysens, 2006)—few studies have addressed fine motor skills like sequential finger movements in children. Moreover, studies that examined such sequencing skill have typically addressed only the development of implicit (i.e., incidental) sequence learning. These studies typically showed that both children and adults improve with practice on the learned sequence, but that children are typically slower (e.g., Dorfberger, Adi-Japha, & Karni, 2007, 2012; Gabbard, Caçola, & Bobbio, 2011; Thomas et al., 2004; Thomas & Nelson, 2001; Savion-Lemieux, Bailey, & Penhune, 2009). However, little is known about children's performance on the execution of brief, discrete series of key presses that allow for strong open-loop control, and the mechanisms underlying such performance.

Discrete movement sequences are assumed to be the building blocks of more complex sequential actions that are present in our everyday behavior. For example, making yourself a cup of coffee builds from movement sequences that underlie reaching for the cup, turning on the tap, and putting the filter in. The so-called Discrete Sequence Production (DSP) task is representative of the way such movement sequences are acquired and controlled, and it allows for the fast development of sequencing skill in a relatively controlled manner (for more detailed discussions, see Abrahamse, Ruitenberg, De Kleine, & Verwey, 2013; Rhodes, Bullock, Verwey, Averbeck, & Page, 2004; Verwey, Abrahamse, & De Kleine, 2010). The DSP task typically involves the sequential display of two series of up to seven stimuli in a fixed order, that each require a response by means of a spatially compatible key press. Because the fixed keying sequences have a recognizable beginning and end, and a response-to-stimulus interval of 0 ms, the DSP task allows the development of automated movements in the form of motor chunks. *Motor chunks* are brief series of successive responses that are represented in a single memory representation, and can be prepared in advance and executed at high pace. The development of motor chunks results in large benefits in terms of speed of responding (sometimes average response latencies are observed below 100 ms for key presses after the first) and in the relative independence from key-specific stimuli after the first stimulus (i.e., open-loop control)—the first stimulus being used for sequence selection. More complex sequences are organized by using more abstract, higher level action representations including several motor chunks.

In the present study we examine whether preadolescent children, like young adults, show indications for automaticity in sequencing skill after practicing discrete keying sequences. We refer to automaticity in sequencing skill as performance that is largely based on motor chunk use, controlled by an autonomous motor processor. We will elaborate on this below (cf. Verwey et al., 2010; Verwey, Abrahamse, De Kleine, & Ruitenberg, 2013). Earlier studies explored the development of automaticity in children with respect to gross motor skills such as running (Whitall, 1991) and reaching (Kuhtz-Buschbeck et al., 1998), and also in more cognitive tasks like number processing (Girelli, Lucangeli, & Butterworth, 2000) and word processing (Spironelli & Angrilli, 2009). By and large, these studies demonstrated that the development of automaticity is limited in children compared to adults. The current study aims to further contribute to the literature on automaticity in children by specifically focusing on fine motor sequencing skills.

1.1. Automaticity in fine sequential motor skill

Research with the DSP task had led to the dual processor model of sequencing skill (Verwey, 2001; see also Abrahamse et al., 2013). This model assumes that two distinct processors are active in discrete sequence skills: a cognitive processor and a motor processor. The relative contribution of these processors to sequencing performance changes with practice, resulting in distinct modes of sequence execution. When initially performing a motor sequence in the DSP task, the sequence is said to be executed in the so-called *reaction mode*. In this mode, each key press of the sequence is executed in isolation from other key presses: The cognitive processor is responsible for the translation of each key-specific stimulus into the appropriate response (i.e., S-R translation), while the motor processor generates each actual response.

After extensive practice, execution may shift to the *chunking mode* in which a movement sequence is executed as one or more motor chunks. In the chunking mode there is no longer a need for selecting, preparing and separately executing all individual elements of the sequence. The actual skill has developed and sequencing is automatic to the extent that the whole sequence can be executed based on the first stimulus (which signals the sequence that should be executed). At this stage, the cognitive processor selects motor chunks and loads them into a temporary motor buffer, from which the motor processor then executes these motor chunks in a relatively automatic—that is, autonomous—fashion (i.e., without the need for cognitive involvement once initiated). The latter renders performance relatively independent of awareness of the motor chunk elements that are executed.

It is typically assumed that the capacity of motor chunks is limited to about three to five key presses (e.g., Bo & Seidler, 2009; Sakai, Kitaguchi, & Hikosaka, 2003; Verwey et al., 2009; Verwey & Eikelboom, 2003), indicating that longer sequences are represented by multiple motor chunks. Indeed, after extensive practice, longer sequences typically include one (or more in case of still longer sequences) slowly executed key press(es) somewhere halfway through the sequence, and this is assumed to reflect retrieval and initiation of an upcoming motor chunk within the sequence. Interestingly, even though one would intuitively attribute these retrieval and initiation processes during sequences execution to the cognitive processor, Verwey et al. (2010) demonstrated that—after substantial practice—the transition between motor chunks is relatively unaffected by a secondary task. This suggests that the transition from one to the other motor chunk *within a fixed sequence* can automatize with practice. This may indicate hierarchical control of longer sequences and is probably highly dependent on the consistency with which motor chunks succeed each other.

Finally, the dual processor model includes one additional feature that is relevant here. Although in the chunking mode the cognitive processor is assumed to load entire motor chunks into a motor buffer—which are then executed by the motor processor—the cognitive processor can additionally engage in S-R translations for each individual key press within a motor chunk in order to assist the relatively fast motor processor. This leads for each key press to a race between two response selection processes (with a response being executed as soon as one of these processes is completed) and results in the fastest possible responses (as supported by the notion of statistical facilitation; Verwey, 2001). Moreover, recent research suggests that—in the absence of external stimuli—the cognitive processor can also use explicit sequence knowledge to elicit responses in parallel to the motor processor (Ruitenberg, Abrahamse, De Kleine, & Verwey, 2012). However, the contribution of explicit knowledge is likely to reduce as motor chunks develop, since sequence representations become more automatic and therewith dominant (Cleeremans & Jiménez, 2002) and also because less time is available to process explicit knowledge during sequence execution at more advanced skill levels (Verwey et al., 2010).

Overall, the dual processor model explains in detail how sequential movements can become highly automatized. Besides the highly automatized execution of motor chunks by an autonomous motor processor, even the transition from one to the next motor chunk may become automatized with practice. This leaves the major part of non-automatized processes to take place before or during the execution of the first key press.

1.2. The present study

To examine the development of automaticity in sequential motor skill in preadolescent children (mean age = 11.3 years, range = 10.6 to 13.2 years), we employed the DSP task in which we had participants practice a 3-key and a 6-key sequence. Given the reduced information processing speed and working memory capacity of children (e.g., Kail, 1991, 2000) we anticipated that they would benefit from dividing the longer 6-key sequences into shorter segments. Such a benefit of practicing longer action sequences in parts first has earlier been shown to enhance sequence learning (e.g., Park, Wilde & Shea, 2004). Therefore, half of the participants in each age group practiced the 6-key sequence with a pause halfway through the sequence in order to induce segmentation into two 3-key segments.

After the practice phase, participants performed a test phase that included three conditions (cf. Verwey, 2010; Verwey, Abrahamse, Ruitenberg, Jiménez, & De Kleine, 2011). In the familiar condition participants performed their practiced 3-key and 6-key sequences in response to key-specific stimuli. In the unfamiliar condition participants carried out unfamiliar 3-key and 6-key sequences, again in response to key-specific stimuli. Finally, in the single-stimulus condition participants were asked to produce their practiced 3-key and 6-key sequences in response to just the first stimulus of each sequence. In this block, participants thus could not rely on external guidance by the stimuli.

We expected preadolescent children to show sequence-specific performance gains, just like young adults. These gains would be indicated by faster execution of familiar than of unfamiliar sequences in the test phase. In addition, the difference between the first key press of a sequence and the subsequent key presses were expected to be larger for familiar than for unfamiliar sequences. We further hypothesized—based on earlier studies—that children are generally slower and less accurate than young adults (cf. Dorfberger et al., 2007, 2012; Gabbard et al., 2011; Thomas & Nelson, 2001; Thomas et al., 2004; Savion-Lemieux et al., 2009). The question remains, though, if preadolescent children show similar development of automaticity as young adults. To this purpose, we performed more detailed analyses.

As discussed above, the dual processor model predicts a gradual development of automaticity in sequencing performance as practice evolves. We used four indicators to determine to what extent children, like young adults, develop such automaticity. A first indicator for automaticity is the rapid execution of familiar sequences, resulting from performance being predominantly controlled by the autonomous motor processor executing motor chunks. Using motor chunks would allow for responses that are faster than would be expected on the basis of typical S-R translations—as is the case in a typical choice RT task, and when performing unfamiliar sequence. Secondly, as the relative contribution of the motor processor increases over time (paralleled by a gradually reduced involvement of the cognitive processor), automaticity is expected to be indicated by a decreasing use of explicit knowledge with practice. Consequently, a correlation between scores on an explicit knowledge test and execution rate of the familiar sequences—specifically for the first few responses of a sequence (Verwey & Abrahamse, 2012)—is only expected as long as the involvement of the cognitive processor is high, but should approach zero when automaticity develops. A third indicator for automaticity is that sequences can be performed based on just the first stimulus of that sequence, which suffices for sequence selection and preparation. In case of automatization, participants should thus be able to correctly perform their sequences in the single-stimulus condition—and without large drops in performance speed. Fourth, we investigated whether segmentation (i.e., dividing a sequence into multiple shorter segments, e.g., motor chunks) would be observed in the unstructured sequence, and we examined the transition between these spontaneously created segments within a sequence. The transition process of one motor chunk to the next has been found to become highly automated—and therewith fast—with practice in young adults (Verwey et al., 2010; Verwey et al., 2013). As a fourth indicator for automaticity, we therefore inspected this transition process for both age groups.

2. METHOD

2.1. Participants

Participants were 24 preadolescent children (11 male, 13 female) aged between 10.6 to 13.2 years[1] (mean age = 11.3 years). Prior to the study, each child's parent or guardian received an information letter that explained the nature and procedure of the study, and they gave their passive informed consent on the participation of their child(ren). The data of the preadolescent children were compared with those of the 24 young adults (8 male, mean age 22.0 years, ranging from 18.4 to 29.9 years) who gave their informed consent prior to the study. The study was approved by the ethics committee of the Faculty of Behavioral Sciences of the University of Twente. Children and young adults were tested respectively at their school and in our lab.

2.2. Apparatus

Stimulus presentation, timing, and data registration were controlled by E-Prime© 2.0 software. The program ran on a Pentium IV computer with all unnecessary Windows XP services switched off to allow accurate time measurement. The task was performed on a standard desktop computer keyboard.

2.3. Task and procedure

At the start of the experiment, participants received a written instruction regarding the task, which was orally extended by the experimenter if participants had any questions. Participants placed their left and right ring, middle and index fingers on the d, f, g, j, k, and l keys of a computer keyboard. Six black horizontally aligned square stimulus placeholders were displayed against a white background. Between the third and fourth placeholder a small gap appeared with the letter 'H' in the middle to mimic the keyboard lay-out. When a placeholder was filled with green, participants depressed the spatially corresponding key. Directly after pressing the correct key, the next stimulus in the sequence was presented by filling another placeholder with green.

Each participant performed two sequences: They were presented one sequence of three stimuli (S_1-S_3) and one sequence of six stimuli (S_1-S_6). Correctly pressing the corresponding keys resulted in a fixed 3-key sequence of responses R_1-R_3 and a fixed 6-key sequence of responses R_1-R_6. The time between onset of the presentation of a stimulus and the response to that stimulus is indicated by T_n (e.g., T_2 denotes the response time to the second stimulus S_2 in a sequence).

Before each sequence the six empty placeholders were presented for 1000 ms, after which the first stimulus of the sequence was displayed. Directly after depressing the correct key, the next stimulus of the sequence appeared. Following a correctly executed sequence the display was erased white for 2000 ms to indicate completion of the sequence. Pressing a false key resulted in an error message for 500 ms. The ongoing sequence was then aborted, and followed by a 1,000 ms empty screen after which the next sequence started.

For half of the participants, the 6-key sequence in the practice phase contained a pause between R_3 and S_4 (i.e., the *prestructured group*) to impose a segmentation structure onto the sequence (e.g., Verwey, 1996). This pause consisted of a non-aging interval of at least 300 ms (with a maximum of 2000 ms), preventing the participants from gradually increasing their expectation for the next stimulus as the interval lasts longer (Gottsdanker, Perkins, & Aftab, 1986). Importantly, the pause was removed in the test phase. For the other half of the participants in each age group their 6-key sequence did not include a pause and the next stimulus of a sequence was thus presented as soon as the correct key was depressed (i.e., the *unstructured group*).

Across all participants, keys (and therewith fingers) were counterbalanced across sequential positions so that each of the six fingers on the keyboard contributed as much to the response times at each sequential position. For example, one participant practiced the sequences KFGDJL and FKL, the next participant practiced LGJFKD and GLD, and so on. Participants practiced their sequences during six practice blocks. Each block included the presentation (in random order) of 24 3-key sequences and 24 6-key sequences. In total, participants thus practiced each sequence 144 times. Halfway through each block there was a short pause of 40s. At the end of each block a participant's mean reaction time and error percentage were displayed. Before starting the next block, there was a rest period of 4 min.

After the practice phase, participants filled out the awareness questionnaire so that their explicit knowledge of the sequences could be assessed. In the recall test, participants were asked to write down the sequences that they had practiced by using the letters of the keys they had pressed during the experiment. The positions of the six keys on the keyboard (including the 'H' marked in the center position) were printed in the questionnaire as a reminder of the keyboard lay-out. In the recognition test, participants were asked to select their 6-key sequence from a list of 12 alternatives, and their 3-key sequence from another list of 12 alternatives.

In the test phase participants completed three blocks that each involved a distinct experimental condition. In the *familiar condition* the same key-specific stimuli were presented to participants as in the practice phase. In the *single-stimulus condition* only the first stimulus of a familiar sequence was presented, after which each key press was followed by the concurrent filling of all placeholders. When a key was pressed, the placeholders briefly turned white and then were filled with green again. The *unfamiliar condition* involved the presentation of one new 3-key and one new 6-key sequence. The order of the three test blocks was counterbalanced across participants and the blocks were separated by a 40s pause. All blocks involved the presentation (in random order) of 12 trials of both the 3-key and 6-key sequence. Like in the practice phase, an error message was displayed when a false key was pressed and the sequence was then aborted. After completion of each block participants were shown their mean reaction time and error percentage. The duration of the experiment was approximately 1 hour.

2.4. Data analysis

We calculated mean response times (RTs) per key press for the prestructured and unstructured sequences for every participant in each block of the practice and the test phase. RT was defined as the time between stimulus presentation and depression of the appropriate response key. Sequences in which one or more errors had been made were omitted from the RT analyses, with 5% and 13% of the sequences being omitted on average for the young adults and preadolescent children, respectively. This is within the typical range for DSP studies (cf. De Kleine & Verwey, 2009; Verwey, 1999; 2010; Verwey et al., 2011). These error percentages are separately described, analyzed and interpreted in more detail below in the results and discussion sections. In addition, sequences were omitted from the RT analyses when the total execution time exceeded more than 2.5 standard deviations from the mean across participants in a particular age group. This was done separately for the 3- and 6-key sequences per block in the practice phase, and per condition in the test phase, and resulted in the removal of less than 1% of the sequences.

For the practice phase, RTs of the 3-key and 6-key sequences were subjected to separate mixed factorial analyses of variance (ANOVAs) with Block (6) and Key position within the sequence (3 or 6; hereafter referred to as Key) as repeated measures and Age group (2: children vs. young adults) as between-subject variable. For the 6-key sequences Pause (2: pause between R_3 and S_4 vs. no pause) was an additional between-subject variable. Analysis of RTs in the test phase also involved ANOVAs on RTs of the familiar and unfamiliar 3-key and 6-key sequences, but in the single-stimulus condition the number of correctly produced sequences was our variable of main interest. When appropriate, planned comparisons were performed to specifically address our hypotheses stated above in the Introduction. Finally, proportions of errors were calculated for every participant. For the practice phase, this was done per block for each key press of the 3-key and 6-key sequences. In the test phase, we calculated proportions of errors for each key press of the 3-key and 6-key sequences per condition. The error data were then subjected to ANOVAs in a similar way as the RT data.

3. RESULTS AND DISCUSSION

3.1. Practice Phase

For the 3-key sequence, results of the Age group (2) × Block (6) × Key (3) ANOVA showed that children were generally slower than young adults (432 vs. 259 ms), $F(1,46)=57.01$, $p<.001$, $\eta_p^2=.55$. Figure 5.1 shows that mean RTs decreased across blocks, $F(5,230)=126.70$, $p<.001$, $\eta_p^2=.73$, but this reduction did not differ between the age groups, $p>.28$. A main effect of Key showed that RTs reduced with key position in the sequence, $F(2,92)=106.18$, $p<.001$, $\eta_p^2=.69$. Furthermore, a Key × Block interaction was indicative of an increasing T_1 versus T_2T_3 difference across blocks, $F(10,460)=38.11$, $p<.001$, $\eta_p^2=.45$. Planned comparisons confirmed that in both age groups the T_1 versus T_2T_3 difference increased across Blocks 1-6, $Fs(1,46)>69.84$, $ps<.001$, $\eta_p^2s>.60$. The increase did not differ between the groups (p=.14).

Results of the 6-key sequence version of the above ANOVA—now including the between-subject Pause (2) variable—again showed that children were slower than young adults (418 vs. 250 ms), $F(1,44)=52.93$, $p<.001$, $\eta_p^2=.54$. A Key × Pause interaction indicated that key presses differed between the prestructured and unstructured group, $F(5,220)=3.59$, $p<.01$, $\eta_p^2=.08$. Planned comparisons confirmed our expectation that the difference between T4 and other key presses within the sequence was larger in the prestructured sequence than in the unstructured sequence, $F(1,44)=12.58$, $p<.001$, $\eta_p^2=.22$, which is in line with the idea that participants in the prestructured group segmented their sequence systematically at the position of the pause. Figure 5.1 shows that mean RTs decreased across blocks, $F(5,220)=206.27$, $p<.001$, $\eta_p^2=.82$, and a Block × Age interaction suggested that this reduction was larger for the children than for the adults (275 vs. 205 ms), $F(5,220)=4.02$, $p<.05$, $\eta_p^2=.08$. An additional Block × Key × Age interaction, $F(25,1100)=2.91$, $p<.01$, $\eta_p^2=.06$, suggested that the difference between T_1 and the mean of $T_{2\text{-}6}$ developed differently over blocks for the children and the young adults. This seems to mainly be caused by an initial difference between the age groups in Block 1 (T_1 vs. $T_{2\text{-}6}$ difference: -10 ms for children, 87 ms for young adults), whereas in the final practice block this difference between T_1 and $T_{2\text{-}6}$ was similar for both age groups (261 ms for children vs. 277 ms for young adults; p=.19).

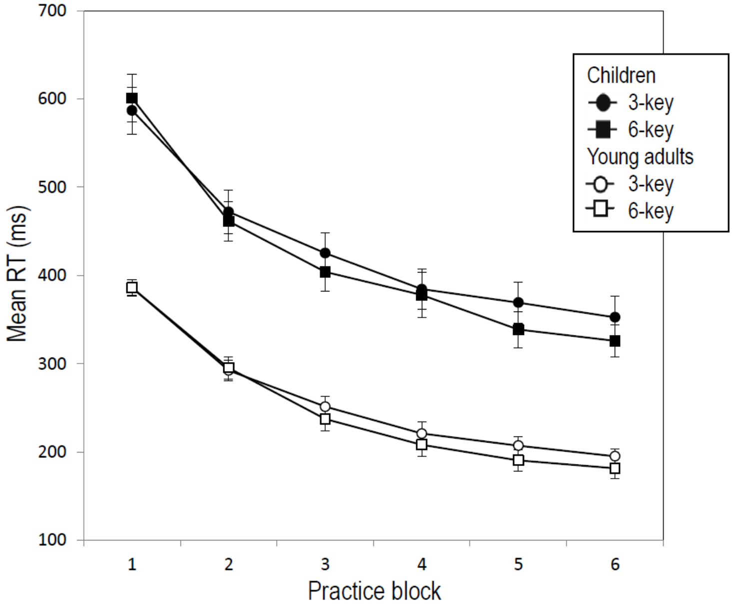

Figure 5.1 Mean RTs across all responses within the 3-key and 6-key sequences per practice block as a function of age group. Error bars represent standard errors.

Previous studies have shown that in unstructured sequences segmentation patterns differ across participants, and that individual differences may be concealed when individual RTs are averaged over participants (e.g., Bo & Seidler, 2009; Kennerley, Sakai, & Rushworth, 2004; Verwey, 2003; Verwey et al., 2009; Verwey & Eikelboom, 2003). In order to examine whether such individual segmentation patterns were present in the final practice block, we determined transition points for each participant who practiced the unstructured sequence. A transition point was defined as a key press that was significantly longer than both its preceding and succeeding key press (cf. Bo & Seidler, 2009; Kennerley et al., 2004). For every participant, we performed one-tailed paired t-tests ($p<.05$) on RTs of the third, fourth and fifth key press of each sequence to evaluate whether they could be classified as a transition point. The first, second and sixth key presses were not included in the analysis, as we assumed that the first key press was always the beginning of the first segment, and that the second and sixth key press were always within the first or last segments. Transition points were found for ten participants (5 in each age group), indicative of sequence segmentation. Interestingly, as Figure 5.2 shows, the difference between the transition points and other key presses within a sequence (not including T_1) was much larger for the children than for the young adults (346 vs. 105 ms, respectively), $t(8)=2.20$, $p<.05$, $d=1.55$. This suggests that the spontaneous transition between two segments of a

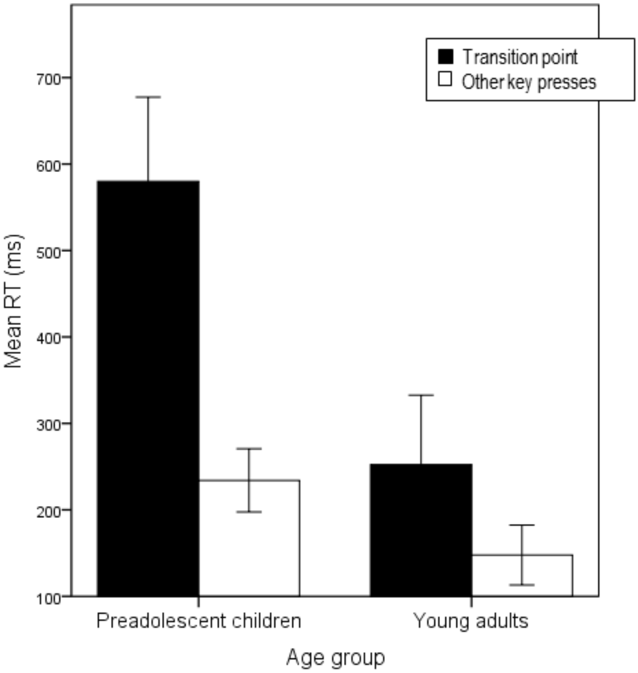

Figure 5.2 Mean RTs of the transition point and other key presses (not including T_1) in the unstructured 6-key sequences in final practice block per age group. Error bars represent standard errors.

sequence is slower in children, possibly due to the inability of automatizing this process.

Finally, error percentages per key position within the 3-key and 6-key sequences were analyzed via Age group (2) × Block (6) × Key (3) and Age group (2) × Block (6) × Key (6) × Pause (2) ANOVAs, respectively. Results showed that mean error percentages per key were similar for preadolescent children and young adults (3.1% vs. 2.2% for the 3-key sequence, p=.12, and 3.0% vs. 2.1% for the 6-key sequence, p=.09). The 3-key ANOVA further showed a main effect of Key, $F(2,92)=30.99$, $p<.001$, $\eta_p^2=.40$, which interacted with Age group, $F(2,92)=8.53$, $p<.01$, $\eta_p^2=.16$, indicating that children's errors differed more between keys (1.5% vs. 5.6% vs. 2.2% for R_1, R_2 and R_3, respectively) than those of the young adults (0.3% vs. 3.1% vs. 3.3%).

In summary, the results of the practice phase showed that children were generally slower at executing their sequences than young adults. There was no indication for a speed-accuracy trade-off, as children also made more errors in absolute terms. As hypothesized, sequencing performance improved with practice in both age groups, as indicated by the RT decrease across the practice blocks as well as an increase in the difference between the first and subsequent key presses of a sequence with practice. Analysis of individual differences in segmentation patterns of the unstructured sequence suggested that the transition between successive segments in that sequence was slower for children than young adults.

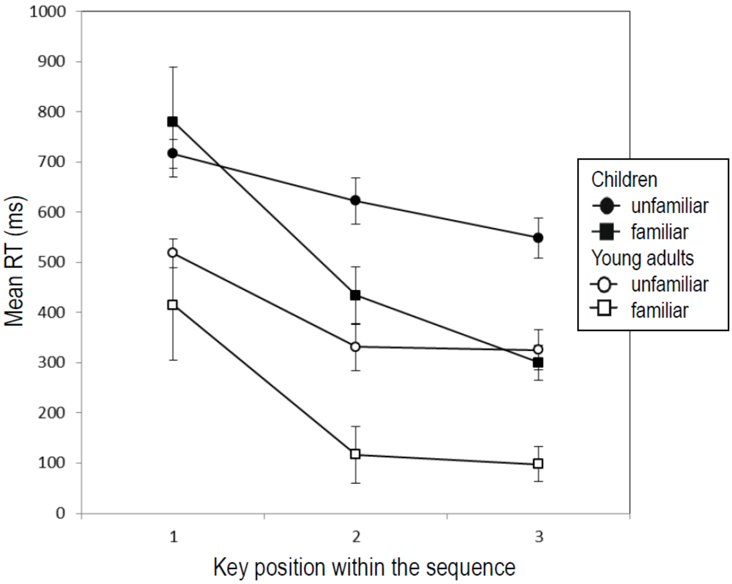

Figure 5.3 Mean RTs per key position in the familiar and unfamiliar 3-key sequences in the test phase per age group. Error bars represent standard errors.

3.2. Test phase

Familiar and unfamiliar sequences

Mean RTs of the 3-key sequence were analyzed with a mixed Age group (2) × Familiarity (2; familiar vs. unfamiliar sequence) × Key (3) ANOVA. Figure 5.3 shows that children were generally slower than young adults (567 vs. 301 ms), $F(1,46)=19.94$, $p<.001$, $\eta_p^2=.30$. In addition, RTs reduced with key position in the sequence, $F(2,92)=58.26$, $p<.001$, $\eta_p^2=.56$. The familiar sequences were executed faster than the unfamiliar sequences (357 vs. 511 ms), $F(1,46)=22.18$, $p<.001$, $\eta_p^2=.33$. Furthermore, a Key × Familiarity interaction supported the notion that the difference between T_1 versus T_2T_3 was larger for the familiar than the unfamiliar sequences, $F(2,92)=6.98$, $p<.01$, $\eta_p^2=.13$. Planned comparisons confirmed sequence-specific performance gains for both age groups, as the T_1 versus T_2T_3 difference was larger in the familiar than unfamiliar sequences, $Fs(1,46)>9.39$, $ps<.001$, $\eta_p^2s>.17$. Performance gains were similar in both age groups ($p=.30$).

Figure 5.4 shows the mean RTs of the 6-key sequences. Results of a mixed Age group (2) × Familiarity (2) × Key (6) × Pause (2) ANOVA once again showed that children were slower than adults (536 vs. 299 ms), $F(1,44)=23.70$, $p<.001$, $\eta_p^2=.35$, and that familiar sequences were executed faster than unfamiliar sequences (311 vs. 524 ms), $F(1,44)=43.77$, $p<.001$, $\eta_p^2=.50$. A Key × Familiarity interaction was in line with the notion from Figure 5.4 that the difference between T_1 versus $T_{2\text{-}6}$ was larger in the familiar than unfamiliar sequences, $F(5,220)=3.61$, $p<.01$, $\eta_p^2=.08$, and planned comparisons further confirmed that this applied to both age groups, $Fs(1,44)>14.72$, $ps<.001$, $\eta_p^2s>.25$. There was no difference between the age groups in this respect ($p=.79$).

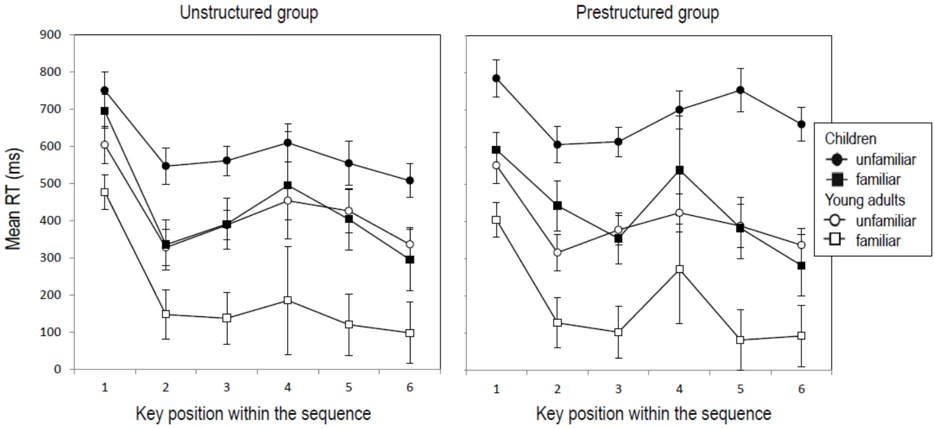

Figure 5.4 Mean RTs per key position in the familiar and unfamiliar 6-key sequences for the prestructured and unstructured groups in the test phase per age group. Error bars represent standard errors.

As expected, planned comparisons showed that in both prestructured age groups T_4 was longer than $T_2T_3T_5T_6$, $Fs(1,44)>4.25$, $ps<.05$, $\eta_p^2s>.09$. This suggests that the sequence was indeed systematically divided into two separated 3-key segments. For each age group, the T_4 versus $T_2T_3T_5T_6$ difference was larger in the familiar than the unfamiliar sequence, $Fs(1,44)>38.52$, $ps<.001$, $\eta_p^2s>.47$. There were no differences between the two age groups ($ps>.45$).

Error percentages of the 3-key and 6-key sequences were submitted to an Age group (2) × Familiarity (2) × Key (3) and an Age group (2) × Familiarity (2) × Key (6) × Pause (2) ANOVA, respectively. Results showed that error percentages were generally higher for the preadolescent children than for the young adults in the 3-key sequence (4.6% vs. 2.1 %), $F(1,46)=5.69$, $p<.05$, $\eta_p^2=.11$, but not in the 6-key sequence (5.3% vs. 4.6%, $p=.54$). The 3-key ANOVA further showed a main effect of Key, $F(2,92)=5.88$, $p<.01$, $\eta_p^2=.11$, which interacted with Age group, $F(2,92)=3.30$, $p<.05$, $\eta_p^2=.07$, indicating that the preadolescent children's errors differed more between keys (3.8% vs. 7.0% vs. 3.0% for R_1, R_2 and R_3, respectively) than those of the young adults (0.7% vs. 2.8% vs. 2.8%). Results of the 6-key ANOVA showed that error percentages were lower in the familiar than unfamiliar condition (3.4% vs. 6.5%), $F(1,44)=18.42$, $p<.001$, $\eta_p^2=.29$. Like in the 3-key ANOVA, results showed a main effect of Key, $F(5,220)=10.69$, $p<.001$, $\eta_p^2=.19$, with errors increasing from R_1 to R_4 (1.0% to 8.5%) and then decreasing again to R_6 (3.9%).

Summarizing, the results showed that in both age groups the difference between the first key press of a sequence and the subsequent key presses was larger for familiar than for unfamiliar sequences. Both age groups showed a relatively slow response at T_4 in the familiar prestructured sequence when the pause was removed, confirming that the pause had induced a transition point for both children and young adults on this position in the sequence.

The single-stimulus condition

For the single-stimulus condition the variable of main interest was the number of correctly performed sequences. Figure 5.5 suggests that children depended more on external stimuli for the execution of familiar sequence than young adults, in that they executed fewer sequences correctly in the single-stimulus condition. A Kruskal-Wallis ANOVA showed that the number of correctly executed 3-key sequences did not differ for preadolescent children and young adults ($p=.65$). However, a similar ANOVA confirmed that the number of correctly executed 6-key sequences was lower for the preadolescent children than for the young adults, $H(1)=8.35$, $p<.01$, $r=.42$.

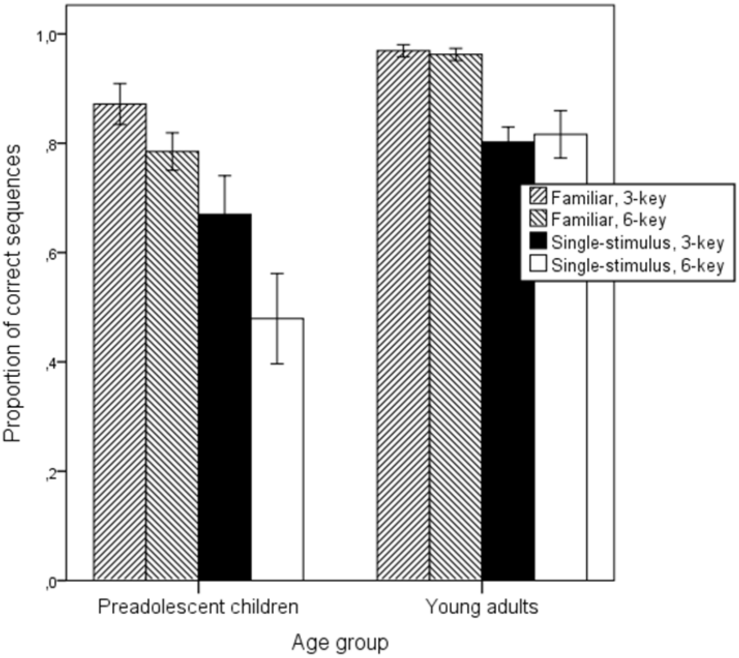

Figure 5.5 The mean proportions of correctly executed sequences per age group in the familiar and single-stimulus conditions of the test phase as a function of sequence length. Error bars represent standard errors.

To analyze the RTs across participants who executed their 3-key sequence at least once in the single-stimulus condition (22 children, 24 young adults), we performed an Age group (2) x Test condition (3; familiar vs. unfamiliar vs. single-stimulus) × Key (3) ANOVA. Results showed that children were generally slower across the conditions than young adults (627 vs. 295 ms), $F(1,44)=30.72$, $p<.001$, $\eta_p^2=.41$. A Key × Test condition × Age group interaction, $F(4,176)=4.07$, $p<.05$, $\eta_p^2=.09$, suggested that the RT patterns of individual key presses differed between the sequence conditions for the children and the young adults. RTs of both the children and young adults reduced with key position in the sequence in the familiar and unfamiliar conditions. However, while RTs of the young adults showed a similar pattern in the single-stimulus condition, children's RTs in this condition actually increased from T_1 to T_2 and then sharply decreased again to T_3. This suggests that the children quickly responded to the first stimulus, but then needed to identify and prepare the sequence resulting in a slower second key press, whereas young adults were able to do so during the first key press. The 6-key version of the above ANOVA also showed that the 16 children who had executed at least one sequence in the single-stimulus condition correctly were slower than the 24 young adults (503 vs. 296 ms), $F(1,38)=23.94$, $p<.001$, $\eta_p^2=.39$. Results further showed a Test condition × Age group interaction, $F(2,72)=3.68$, $p=.05$, $\eta_p^2=.09$, suggesting that the RT difference between age groups varied across the test conditions. Detailed analysis showed that although preadolescent children were generally slower than young adults, the difference between age groups was larger in the single-stimulus condition than in the familiar condition (326 ms vs. 173 ms), $F(1,36)=7.07$, $p<.05$, $\eta_p^2=.16$.

In summary, children executed fewer 6-key sequences correctly in the single-stimulus condition than the young adults, suggesting that they had relied more on the external stimuli for the execution of this sequence in the familiar condition. The number of correctly executed 3-key sequences did not differ between age groups. Children who were able to correctly execute at least one sequence in the single-stimulus condition did so more slowly than the young adults. For the 6-key sequence, this difference between age groups was larger than in the familiar condition.

3.3. Explicit sequence knowledge

Analyses of the awareness questionnaire showed that fewer children than young adults correctly wrote down their 3-key sequence, $\chi^2(1)=9.60$, $p<.01$, $\varphi=.45$ (see Table 5.1). There was no difference between the age groups in recall of the 6-key sequence, $p=.24$. Young adults were better at recognizing both their 3-key and 6-key sequences from a set of 12 alternatives, $\chi^2s(1)>4.00$, $ps<.05$, $\varphi s>.29$. Overall, children seem to have had less explicit knowledge of their familiar sequences than the young adults.

We examined whether execution of the first three responses of the familiar sequences correlated with explicit knowledge (i.e., number of correctly recalled sequences). As RTs are known to rapidly decrease from the first response to ensuing responses in familiar sequences, and awareness is mainly involved in the first few responses, we calculated for each participant the T_1 versus T_2T_3 difference for the 3-key and 6-key sequences. For the 3-key sequence, this difference did not correlate with explicit knowledge of that sequence in either age group ($ps>.14$). For the 6-key sequence the T_1 versus T_2T_3 difference correlated

Table 5.1 The numbers and the corresponding percentages of participants (out of 2 × 24) who correctly wrote down the familiar sequences immediately following the practice phase ('recall' columns), and recognized their sequences from sets of 12 alternatives ('recognition' columns).

	Recall		Recognition	
	3-key	6-key	3-key	6-key
Preadolescent children	16 (67%)	12 (50%)	15 (63%)	15 (63%)
Young adults	24 (100%)	16 (67%)	24 (100%)	21 (88%)

with explicit knowledge of that sequence for the preadolescent children, *r*(24)=.53, *p*<.01, but not for young adults (*p*>.14). When analyzing performance in the single-stimulus condition, results showed that for children the T_1 versus T_2T_3 difference in both the 3-key and 6-key sequences correlated with explicit knowledge of those sequences, *rs*(22)>.42, *ps*<.05. For young adults, however, correlations were not significant (*ps*>.43). It thus seems that children make more use of their explicit knowledge for sequencing performance than young adults do.

3.4. Developmental differences

Although the main goal of the present work was to investigate to what extent preadolescent children, like young adults, learn to perform motor sequences in an automated fashion, we also examined whether there were developmental differences in sequencing performance within the group of preadolescent children. To that end, we compared sequencing performance of 10-11 year old children (*n*=16) with that of 12-13 year old children (*n*=8). Results of ANOVAs on RTs in the 3-key and 6-key sequences in the familiar and unfamiliar test conditions showed no differences between these two groups (*ps*>.11). In addition, the number of correctly performed 3-key and 6-key sequences did not differ between the groups for any of the test conditions (*ps*>.32). The groups did not differ in the amount of explicit knowledge, in that recall and recognition of both the 3-key and 6-key sequences were similar for both groups (*ps*>.22). Overall, then, no indications were found that our group of preadolescent children was heterogeneous in nature with respect to sequence performance. Still, future studies should explicitly address this issue.

4. GENERAL DISCUSSION

The present study examined to what extent preadolescent children, like young adults, perform 3-key and 6-key sequences in the discrete sequence production (DSP) task in an automatic fashion. As predicted on the basis of previous studies (cf. Dorfberger et al., 2007, 2012; Gabbard et al., 2011; Thomas & Nelson, 2001; Thomas et al., 2004; Savion-Lemieux et al., 2009), the results demonstrated that both age groups showed sequence-specific performance gains, as familiar sequences were executed faster than unfamiliar sequences and the difference between the first key press and subsequent key presses was larger for familiar than unfamiliar sequences. The first impression that derives from the RT data (Figs. 5.3 and 5.4) is that preadolescent children perform very similar to the young adults, though they are generally slower (while no indications for a speed-accuracy trade-off were observed since children also produced more errors overall). However, we actually believe that the overall slowing is characteristic of a slower and/or limited development of automaticity in preadolescent children as compared to young adults, and this notion is supported by marked differences between the two age groups across three additional indicators for automaticity in motor sequences. Below we elaborate on this.

First, rapid execution of particular key presses (i.e., the ones after chunk initiation), an indication of automatization (Verwey, 2010), was less pronounced in preadolescent children than in young adults. That is, the children always remained much slower than young adults, and responses beyond the first remained within the range of what could be expected for a typical choice RT task in which performance remains based on S-R translations. For example, in a study by Thomas and Nelson (2001), 10-year old children performed a key press task with spatially corresponding S-R mapping and showed average RTs of around 400 ms when stimuli were presented in random order. Similarly, a group of 13-year old children (the control group) in the study by Deroost et al. (2010) also showed average RTs of around 450 ms under such conditions (i.e., the random blocks of the sequence learning task). From the notion that motor chunking would be expected to generate equally fast responses for children and adults, the slower performance in preadolescent children may be interpreted as performance remaining largely dependent on the workings of a (well-trained) cognitive processor (possibly including advance preparation of future key presses based on sequence knowledge) that selects and loads single key presses into the buffer of the motor processor—as opposed to motor chunks as with young adults.

Secondly, this suggestion is supported by the influence of explicit knowledge during sequence execution—a feature that is assumed to be typical of a dominant cognitive processor and that does not fit well with the notion of motor chunking. For both the familiar and single-stimulus conditions of the test phase, we observed that for preadolescent children—but not for young adults[2]—the difference in RT between the first versus the second/third key press was correlated with explicit sequence knowledge (with exception of the 3-key sequence in the familiar condition): Children with more awareness showed a larger difference. According to the dual processor model, the difference should not be related to explicit knowledge when performance is based on the cognitive processor loading a motor chunk (i.e., representing a series of key presses) into a motor buffer that is subsequently executed by the motor processor as if it were a single response (Verwey et al., 2010). Hence, as a second indication from this study, preadolescent children seem to remain more reliant on explicit knowledge for sequence execution than young adults—which fits the notion that their performance remains largely dependent on the effortful processes of the cognitive processor (i.e., loading and executing key presses one-by-one) for a longer time than in case of young adults. This is further corroborated by the observation that error percentages of the 3-key sequence showed more variation for preadolescent children than for young adults, both in the practice phase and the familiar test condition.

As performance based on motor chunks executed by the motor processor would predict relatively stable error percentages *within* such an integrated representation (cf. Rosenbaum, Kenny, & Derr, 1983), the relatively large variation in preadolescent children fits better with the notion that their performance was largely based on the cognitive processor selecting and loading single key presses.

Thirdly, we examined whether preadolescent children and young adults could perform their sequences without the guidance of external stimuli in the single-stimulus condition. Previous studies have shown that young adults are quite good at this, and from the dual processor model it could be predicted that this is due to motor chunking (and thus automatization): The need for actively using stimuli decreases with practice due to the motor processor autonomously executing motor chunks, and the first stimulus of a sequence suffices for proper preparation and execution of that sequence. The current results show that the number of correctly performed 3-key sequences was similar for both age groups. However, compared to young adults, children completed fewer 6-key sequence correctly in the single-stimulus condition. This suggests that they depend more on external stimuli—that is, on the direct one-by-one S-R translation processes of the cognitive processor—for the execution of this sequence, while young adults could enhance performance in the single-stimulus condition through relying on their motor chunks. Moreover, whereas the drop in RT in young adults was relatively small in the single-stimulus condition, children showed larger RT drops and even seemed to use different RT patterns for sequence execution in the single stimulus condition than in the familiar condition. This further suggests that children used stimulus information across the whole sequence in the practice phase and the familiar test block, and did not engage in motor chunking.

Fourthly, we observed that children who segmented their unstructured sequence needed more time for the transition from one segment to the next compared to young adults. This suggests that the transition between sequence segments is not as quickly automated as it is in young adults (Verwey et al., 2010; Verwey et al., 2013). However, in the prestructured sequence this transition did not differ between both age groups, which suggests that children benefit from prestructured sequences in that the artificial pre-segmentation results in smoother (and possibly more automatic) transitions between segments.

Altogether, these findings suggest that preadolescent children automatize the processes underlying—especially longer—movement sequences to a lesser extent than is the case for young adults. It seems that for children the cognitive processor (and S-R translation) remains dominant in sequence execution even after substantial practice, while for young adults the motor processor (and motor chunking) gradually takes over control with this same amount of practice. It may be suggested that cognitive processor efforts in preadolescent children are based on explicit sequence knowledge, given that awareness was related to the difference between the first and following key presses of a sequence. Additionally, the observation that children completed fewer 6-key sequences in the single-stimulus condition suggests that the cognitive processor continues to be engaged in S-R translations. One could even argue that the cognitive processor uses explicit knowledge in the beginning of the sequence, and then later in the sequence switches to S-R translations as explicit knowledge of later key-presses does not come to mind as readily. Detailed inspection of the awareness questionnaire indeed showed that out of the 12 children who could not reproduce all elements of their 6-key sequence correctly, 2 children recalled none of the sequence elements. The remaining 10 children reproduced at least the first element correctly, up to a maximum of four successive correctly recalled sequence elements. Finally, we would like to point out that the notion that sequencing performance in children—but not young adults—strongly relies on explicit knowledge was recently supported by Weiermann and Meier (2012). They demonstrated that children's sequencing performance in an implicit sequence learning task was largely conditional upon the development of explicit knowledge, with little indication for purely implicit sequence learning in children. These findings are in line with the present results that sequencing performance remains more cognitively controlled—and less automated—in preadolescent children than is the case for young adults.

The differential degree of automaticity in sequential movement skill between preadolescent children and young adults could be related to the involvement of brain structures that may still be maturing in children. During the learning of new motor sequences in young adults, the prefrontal cortex and cerebellum are activated (Doyon & Benali, 2005; Jueptner, Frith, Brooks, Frackowiak, & Passingham, 1997a; Jueptner, Stephan, Frith, Brooks, Frackowiak, & Passingham, 1997b). These areas are mainly responsible for the generation of quick and accurate responses (Hikosaka et al., 1999). The basal ganglia are also involved in sequential motor skill (Doyon & Benali, 2005; Jueptner et al., 1997b). Besides their role in the acquisition of new sequences, they are involved in motor chunking (Boyd et al., 2009; Graybiel, 1998; Hayes, Davidson, Keele, & Rafal, 1998; Penhune & Steele, 2012; Sakai et al., 2003; Tremblay et al., 2010) and may be involved—in close interaction with the prefrontal cortex—in the initiation of individual motor chunks of familiar sequences (Verwey, Lammens, & van Honk, 2002; Wymbs, Bassett, Mucha, Porter, & Grafton, 2012).

From these three main structures, the basal ganglia are thought to mature relatively early compared to the prefrontal cortex and cerebellum (Diamond, 2000; Østby et al., 2009; Sowell, Delis, Stiles, & Jernigan, 2001; Sowell, Trauner, Gamst, & Jernigan, 2002). More specifically, the basal ganglia have been found to change relatively little between people of 8 to 30 years of age (e.g., Østby et al., 2009), whereas prefrontal areas and the cerebellum are known to still develop well into adolescence (e.g., Sowell et al., 2001; 2002). Wymbs et al. (2012) recently showed that a frontoparietal network may be involved in the explicit segmentation of movement sequences. It could be speculated that preadolescent children are less efficient in the stable segmentation of their sequences, and that this results in slower development of motor chunks. However, in the prestructured sequence the segmentation pattern was induced by means of a pause halfway the sequence, and while this should have facilitated stable segmentation we still did not observe the performance rate one would expect on the basis of motor chunking. Another possibility is that the use of motor chunks—rather than the development of such chunks—differs between the two age groups in the current study. Specifically, the study of Verwey (2003) indicates that the initiation of motor chunks is an intentional and goal-directed process, and it may be that these processes—which are among others related to the prefrontal cortex—are less developed and/or efficient in preadolescent children. Admittedly, however, these ideas are highly speculative, and future studies are required to clarify the link with brain structures.

Finally, along with developmental changes in the brain, there are also age-related changes in cognitive abilities. For example, information processing speed (e.g., Kail, 1991; 2000) and working memory capacity (which is related to the prefrontal cortex; e.g., Luciana & Nelson, 1998) in children are less developed than in adults. These factors have been found to be interrelated, in that developmental changes in processing speed have been found to mediate the increase of working memory capacity with age (Fry & Hale, 1996). Various studies have suggested that working memory is related to chunking (Bo, Borza, & Seidler, 2009; Bo & Seidler, 2009; Verwey, 1999, 2010; Verwey et al., 2011). Verwey (1999) proposed that the motor buffer, in which (elements of) motor chunks are loaded before execution, can be viewed as a part of working memory. This may imply that the loading of the motor buffer is less efficient when working memory capacity is limited, which could explain slower transitions between segments of longer sequences in preadolescent children.

In conclusion, the present findings suggest that preadolescent children automatize the execution of longer movement sequences to a lesser extent than young adults. Although both age groups show sequence-specific performance gains with practice, we argue that the relative contributions to sequencing skill of the cognitive and motor processors differ. In preadolescent children, the cognitive processor seems to remain dominant in the execution of longer movement sequences, while for young adults practice leads to clear motor chunking that is dominated by an autonomous motor processor. In all, the present findings are in line with the notion that there are several mechanisms that underlie the execution of familiar movement sequences, and suggest that the relative contribution of these mechanisms may depend on age. Future studies should validate these ideas within other paradigms, and zoom in on developmental changes with respect to automaticity in sequential motor skill.

Notes

1. Although the age range of the preadolescent children may seem relatively large, this group involved only one 10 year old and one 13 year old participant. Removing these participants from the analyses did not yield a different pattern of results.

2. The absence of a significant correlation between explicit knowledge and execution of the 3-key sequence in the familiar and single-stimulus conditions for young adults may reflect a ceiling effect, as all of the young adults correctly recalled the sequence. We thank an anonymous reviewer for this suggestion. However, this reasoning does not apply to the 6-key sequence, as one-third of the young adults were unable to recall the sequence.

Acknowledgements

We would like to thank Hanna Kulbatzki, Florence Lehnert and Jesse Muller for their assistance with the data collection. We would also like to express our gratitude to the Openbare basisschool Glanerbrug-Noord (Enschede, The Netherlands) and the Openbare basisschool Stegeman (Winterswijk, The Netherlands) for their collaboration.

Chapter 6

The role of the premotor cortex and pre-supplementary motor area in skilled sequential action: A TMS study

Marit F. L. Ruitenberg
Elger L. Abrahamse
Willem B. Verwey

Manuscript in preparation

The dual processor model postulates that the production of discrete movement sequences is regulated by a cognitive processor and a motor processor—the relative contribution of each of the processors depends on the mode in which sequences are being executed. The present study (I) tested the core assumptions of this model at the behavioral level, and the data supported these assumptions. In a next step, (II) we explored the neural substrate that underlies the various functions of the cognitive processor. Specifically, we targeted the pre-supplementary motor area (pre-SMA) and the premotor cortex (PMC) by applying 20 min 1 Hz repetitive transcranial magnetic stimulation before performance in a test phase. With respect to the pre-SMA, we predicted its involvement in the selection and initiation of motor chunks. Results demonstrated that rTMS stimulation of the pre-SMA slowed key presses reflecting chunk initiation, indicating that the pre-SMA is involved in the activation of internal sequence representations from long term memory. With respect to the PMC, we predicted its involvement in externally-guided sequencing performance (i.e., based on stimulus-response translation). The current data did not support this prediction. Overall, then, we provided coherent support for the dual processor model, and for the involvement of pre-SMA in the functions of the cognitive processor.

1. INTRODUCTION

Most of the complex motor actions that people perform in daily life consist of a series of relatively simple movements that are executed in a specific order. In this respect one may think of actions such as playing the piano and lacing a shoe. With practice, the order of movements is learned and the action gradually becomes automated, in the sense that little attention is needed for proper execution—a motor skill has developed. Over the last decades, ample research has been devoted to unraveling the cognitive and motor mechanisms underlying the production of brief, discrete movements sequences (see e.g., Abrahamse, Ruitenberg, De Kleine, & Verwey, 2013). Attention has also been given to the neural substrates that underlie sequencing skill, with studies showing that the involvement of different neural substrates strongly depends on factors such as level of practice, sequence type, and type of learning (for overviews, see Ashby, Turner, & Horvitz, 2010; Penhune & Steele, 2012). The present study contributes to the literature by investigating the neural substrate that underlies the involvement of cognitive processes during the execution of discrete movement sequences. Below, we first introduce a cognitive architecture for the production of such sequences. We will then discuss how this architecture may be implemented in the human brain, specifically addressing the role of two neural structures in sequence execution: the premotor cortex and the pre-supplementary motor area.

1.1. Discrete sequential action

The cognitive processes underlying discrete sequence production have been described by the dual processor model (DPM; Verwey, 2001). The DPM postulates that the production of discrete sequences involves a cognitive processor and a motor processor. The model has been derived from work with the so-called discrete sequence production (DSP) task (Verwey, 1999; see for an overview Abrahamse et al., 2013). In the standard version of this task, participants typically respond to fixed series of two to seven stimuli by means of spatially compatible key presses, and accordingly learn to perform fixed movement (i.e., response) patterns. Participants initially respond to each individual stimulus as they lack strong internal representations of the sequences. In this so-called *reaction mode* performance the cognitive processor is assumed to be responsible for the translation of each stimulus into the appropriate response, which is then carried out by the motor processor. With practice, the sequences are learned—participants can identify the to-be-executed sequence on the basis of just the first sequence-specific stimulus, and can execute the whole sequence without the need for further stimuli. The performance improvement is attributed to the development of *motor chunks*: representations of successive responses (here: key presses) that can be prepared and executed as if they were a single response (e.g., Verwey, 1999). The cognitive processor can select such a motor chunk upon presentation of the first stimulus that corresponds to that motor chunk. It then loads the chunk into a motor buffer, after which the motor processor can execute the elements represented within the motor chunk by reading them from the buffer. With longer sequences, participants spontaneously segment their sequence into multiple motor chunks that are concatenated during execution (Bo & Seidler 2009; Kennerley, Sakai, & Rushworth, 2004; Ruitenberg, Abrahamse, De Kleine, & Verwey, 2012; Sakai, Kitaguchi, & Hikosaka, 2003; Verwey, Abrahamse, & Jiménez, 2009; Verwey & Eikelboom 2003). Executing sequences as one or more motor chunks is here referred to as the *chunking mode*.

The DPM also postulates that, after loading motor chunks into the motor buffer, the cognitive processor can assist the motor processor in executing the elements within these chunks by engaging in direct S-R translations (Verwey et al., 2010; Verwey, Abrahamse, De Kleine, & Ruitenberg, 2013). Consequently, two processes for response generation occur simultaneously: the motor processor triggers responses by reading response-related codes from the motor buffer, and the cognitive processor selects responses on the basis of S-R translations. Recently, Ruitenberg et al. (2012) found indications that when stimuli are absent during actual execution and S-R translations are thus prevented, the cognitive processor can also assist the motor processor by using explicit sequence knowledge. The involvement of both the cognitive processor and motor processor during execution leads to a race between two response generation processes, resulting in the fastest possible responses (i.e., statistical facilitation; Verwey, 2001).

Besides the reaction and the chunking mode, the DPM distinguishes a third, *associative mode* (see Verwey & Abrahamse, 2012). In this mode, performance is still based on – and thus requires – external stimuli that are translated into the correct response by the cognitive processor, but these responses are facilitated through associative learning processes: Because of associations between successive stimulus-response events, forthcoming responses are primed. In contrast to the chunking mode, the associative mode is characterized by performance improvements that are relatively small (i.e., average response times do not typically drop below 250 ms), more or less equally divided response times across all key-presses, and a lasting dependence on stimulus presentation. In retrospect, there are some studies that provide tentative support for the existence of these three modes (Verwey, 2010; Verwey, Abrahamse, Ruitenberg, Jiménez & De Kleine, 2011; Jiménez, Méndez, Pasquali, Abrahamse & Verwey, 2011). A major aim of the current study is to test the feasibility of the DPM by replicating the three-mode division (cf. Verwey & Abrahamse, 2012) and the notion that the cognitive processor assists the motor processor during sequence execution (cf. Verwey et al., 2010; Verwey et al., 2013).

1.2. Neural substrate of the cognitive processor

As outlined above, the relative contributions to sequential action of the cognitive and motor processors differ across the execution modes—the cognitive processor in particular performs a variety of roles across the three modes. In recent years the functions and characteristics of the cognitive processor have been extensively studied (see Abrahamse et al., 2013). For example, Verwey et al. (2013) demonstrated that the resources of the cognitive processor can be distributed across several tasks in a graded manner. While the functional aspects of the cognitive processor are thus relatively well-known, its neural underpinnings are less clear. As a second goal of this study, we examine the neural substrate that may underlie the various roles of the cognitive processor during sequential action as postulated by the DPM.

In the last two decades an increasing number of studies have explored the neural basis of sequential action. Imaging techniques such as positron emission tomography (PET; e.g., Jenkins, Brooks, Nixon, Frackowiak, & Passingham, 1994; Jenkins, Jahanshahi, Jueptner, Passingham, & Brooks, 2000) and functional magnetic resonance imaging (fMRI; e.g., Toni, Krams, Turner, & Passingham, 1998; Wymbs, Bassett, Mucha, Porter, & Grafton, 2012) have been used to study the neural activation underlying sequence learning and performance, and transcranial magnetic stimulation (TMS) has been employed to explore the contribution of several brain areas to sequencing skill (e.g., Kennerley et al., 2003; Verwey et al., 2002). Results demonstrate that various brain structures including motor, prefrontal, and parietal cortices, the basal ganglia, and the cerebellum can form networks that are involved in sequencing skill. Here we specifically focus on two cortical structures that may be related to the various roles that the cognitive processor performs across the three aforementioned execution modes: the pre-supplementary motor area (pre-SMA) and the premotor cortex (PMC).

Activation of the pre-SMA is associated with cognitive aspects of a variety of tasks (see Picard & Strick, 2001) and is anatomically connected to pre-frontal areas that are known to be involved in higher cognition (Luppino, Matelli, Camarda, & Rizzolatti, 1993; Picard & Strick, 1996; Wang, Isoda, Matsuzaka, Shima, & Tanji, 2005). This directly distinguishes the pre-SMA from the more posterior located SMA (or SMA-proper), which both functionally and anatomically can be assumed to be more motor based (He, Dum, & Strick, 1995; Luppino et al., 1993; Picard & Strick, 1996, 2001). These differences in connectivity between SMA and pre-SMA suggest that they have distinct roles in motor control—indeed, studies in the domain of sequencing skill have related these structures to different processes. Specifically, whereas Verwey et al. (2002) observed that all elements within a well-learned DSP sequence were equally slowed following rTMS stimulation of the SMA, Kennerley et al. (2004; Exp. 2) found that rTMS stimulation of the pre-SMA slowed only those key presses that reflected chunk initiation. These findings suggest that the SMA is probably responsible for loading and/or executing individual sequence elements (cf. motor processor), while the pre-SMA may be responsible for retrieving entire motor chunks from memory and/or loading these chunks into the motor buffer (cf. cognitive processor). A direct comparison between the studies of Kennerley et al. (2004) and Verwey et al. (2002) is rather difficult due to methodological differences between the studies—that is, subjects in the study by Kennerley et al. (2004) were briefly trained on a 12-element keying sequence, while subjects in the study by Verwey et al. (2002) extensively practiced two 6-element sequences. In the current study we therefore test the involvement of the pre-SMA (instead of SMA like in Verwey et al., 2002) in chunk-based sequencing performance within the context of the DSP task. Compared to the study by Kennerley et al. (2004) we a) employed substantially more practice and shorter sequences to ensure the development of motor chunks that can be executed in a relatively autonomous manner by the motor processor, and b) employed two (instead of one) sequences to force response selection processes also at the start of the sequence. We hypothesize that the pre-SMA is involved in the more automatic sequencing performance in the chunking mode on the basis of active sequence representations in long term memory (i.e., loading of chunks into the motor buffer by the cognitive processor).

With respect to the PMC, we test the hypothesis that this area is involved in the contribution to sequencing performance that is based on S-R translations by the cognitive processor (such as in the reaction and associative modes). The PMC is typically activated relatively early in learning, while later in training this activation decreases and SMA activity gradually increases (Jenkins et al., 1994; Toni et al., 1998; Wymbs & Grafton, 2013). In line with the notion that sequence execution shifts from being stimulus-based to being representation-based, it is assumed that the PMC underlies skill that is stimulus-based, while the SMA is strongly related to memory-based sequence performance, thus independent of external action cueing (Grafton, Hazeltine, & Ivry, 2002; Halsband, Matsuzaka, & Tanji, 1994; Mushiake, Inase, & Tanji, 1991). For instance, in a study by Mushiake et al. (1991), monkeys performed a sequence that was either visually triggered (i.e., they responded to illuminated stimuli) or internally guided (i.e., they remembered and then executed the sequence). Results demonstrated that the PMC was particularly active during visually-guided behavior, while the SMA was particularly active during memory-based execution. The involvement of the PMC in S-R translations has also been demonstrated in studies on human subjects. For example, Schluter, Rushworth, Passingham and Mills (1998) observed that TMS applied to the PMC delayed the selection of simple movements (i.e., S-R). Furthermore, Wymbs and Grafton (2013) recently demonstrated that TMS stimulation of the dorsal PMC affected performance of moderately but not extensively practiced sequences. Pertaining to the aforementioned three mode framework of discrete sequence production, we thus hypothesize that the PMC is involved in controlled sequence execution by means of S-R translations by the cognitive processor in the reaction and associative modes. In addition, it could be argued that the PMC may also be involved in performance in the chunking mode, as the cognitive processor engages in response selection during sequence execution (i.e., online S-R translations) to assist the motor processor.

1.3. The present study

We employed the aforementioned DSP task to study the involvement of the PMC and pre-SMA during sequential action, as this task allows for the rapid development of sequencing skill in a fast and relatively controlled manner (Abrahamse et al., 2013; Rhodes, Bullock, Verwey, Averbeck, & Page, 2004; Verwey et al., 2010). Participants extensively practiced two discrete keying sequences across eight practice blocks. The two sequences were then performed in four test blocks that address the various assumptions of the DPM. In the familiar condition and the single-stimulus condition, participants performed their learned sequences in the chunking mode. However, in the single-stimulus condition they had to perform the sequences based on only the first key-specific stimulus of that sequence and thus completed the rest of the sequence from memory. In the mixed-familiar condition, participants performed their learned sequences, but in the majority of the sequences the order of key-specific stimuli deviated slightly from what was learned during the practice phase. These latter sequences were expected to trigger execution in the associative mode (Verwey & Abrahamse, 2012). Finally, in the mixed-unfamiliar condition, participants performed novel sequences so that sequences are executed in the reaction mode.

First, at the behavioral level, we expected to replicate the findings of Verwey and Abrahamse (2012). We hypothesized that sequences would be performed fastest in the familiar and single-stimulus test conditions, as these allow for execution in the chunking mode. Performance could be predicted to be somewhat slower in the single-stimulus condition, though, as the absence of stimuli prevents the cognitive processor from engaging in response selection on the basis of direct S-R translations in addition to response triggering by the motor processor (Verwey, 1999). Performance in the mixed-unfamiliar test condition was expected to be slowest, as participants had to translate each stimulus into an appropriate response and could not develop or rely on sequence knowledge. Finally, the sequences without deviants in the mixed-familiar condition were thought to be performed slower than sequences in the familiar and single-stimulus conditions, but faster than those in the mixed-unfamiliar condition due to facilitation by the priming of responses (i.e., associative mode; Verwey & Abrahamse, 2012).

Second, we tested the hypothesis that the PMC and pre-SMA are related to the different roles that the cognitive processor performs across the three modes in which discrete movement sequences can be executed. We tested this by applying low-frequency (1 Hz) rTMS stimulation to either the PMC or the pre-SMA for a period of 20 min. It has been established that such low-frequency rTMS stimulation has inhibitory effects on the stimulated region (cf. Chen et al., 1997; Wassermann et al., 1996; see also Kennerley et al., 2004; Rossi & Rossini, 2004; Verwey et al., 2002). The involvement of the PMC and pre-SMA in a particular process can thus be inferred from the slowing of the responses due to the inhibitory effects of rTMS. We compared the performance of participants receiving rTMS to either the PMC or pre-SMA with that of a control group (sham rTMS). As outlined above, we hypothesized that when sequencing performance is based on S-R translations by the cognitive processor—i.e., in the reaction and associative mode—the PMC is particularly employed. This would be reflected in slowed performance of sequences in the mixed-unfamiliar condition and sequences without deviants in mixed-familiar condition. In contrast, when performance is based on internal sequence representations—i.e., motor chunks in the chunking mode—that are loaded into the motor buffer by the cognitive processor and then executed by the motor processor, the pre-SMA is assumed to be involved. This would result in slowed performance in the single-stimulus and familiar conditions. Specifically, in line with previous findings of Kennerley et al. (2004), we expected that rTMS stimulation of the pre-SMA especially slows the initiation, but not execution, of motor chunks.

2. METHOD

2.1. Participants

Forty-eight students from the University of Twente participated in the study (10 male, 38 female). They were aged between 18 and 28 years (*M*=21). All participants were classified as being right-handed according to Annett's (1970) Handedness Inventory and reported to have good eye sight (corrective glasses or contact lenses were permitted). Exclusion criteria in accordance with TMS guidelines were: history of neurological or hearing disorders, severe medical conditions, pacemaker or other metals located near the head, pregnancy, alcohol/drug consumption 48 hours/2 months prior to the experiment, and smoking history (cf. Rossi et al., 2009). Participants gave their written informed consent and could receive credits they needed to obtain as part of a course requirement. The study was approved by the Medical Ethical Committee of the Medical Spectrum Twente (MST), Enschede, The Netherlands.

2.2. Apparatus

Stimulus presentation and response registration were controlled by the E-prime© 2.0 experimental software package that was programmed on a standard Pentium© IV Windows XP© PC. Windows services that could affect reaction time measurements were shut down. Stimuli were presented on a 17-in Philips 107 T5 display. Responses were given on a standard qwerty-keyboard.

Transcranial magnetic stimulation was delivered using a high power Magstim Rapid 2 Stimulator©, connected to a figure-of-eight air-cooled coil that was held by an industrial robot (Viper s850 Six-Axis robot© from Adept Technology Inc.). The robot was controlled by the Advanced Neuro Technology (ANT) software program SmartMove© and automatically corrected for minor head movements made by the participants, so that the coil was continuously above the target area.

2.3. Discrete Sequence Production task

Participants were instructed to place the little, ring, middle and index fingers of their left hand on the c, v, b and n keys, respectively. Four horizontally aligned black square placeholders were presented on a computer display with a white background, and these stimulus squares spatially corresponded with the alignment of the four response keys. As soon as one of the placeholders was filled with a green color, participants pressed the corresponding key (e.g., c, for the leftmost square). When the correct response was given the color in the square changed back to the white background color for 50 ms[1], after which the next stimulus of the sequence was presented. Once all stimuli of the sequence were presented and correctly responded to, the display was erased white for 1000 ms to indicate completion of the sequence. The placeholders were then presented again for 1000 ms before the first stimulus of the next sequence was displayed. Participants were instructed to respond as fast and accurately as possible. An incorrect response resulted in an error message that was presented for 2000 ms, which was used to motivate participants to prevent errors. The ongoing sequence was then aborted and followed by a 1000 ms white screen, after which the placeholders were presented for 1000 ms and the next sequence started.

In the practice phase participants responded to two series of six stimuli, yielding two 6-key response sequences. In order to prevent finger-specific effects on individual response times, response keys were rotated across sequential positions across all participants. This resulted in four versions of each sequence, namely *ncbncb*, *cvncvn*, *vbcvbc* and *bnvbnv* (i.e., the 2×3 sequence) and *nvbcbv*, *cbnvnb*, *vncbcn* and *bcvnvc* (i.e., the 1×6 sequence, cf. Verwey et al., 2002). The two sequences that a participant practiced never started with the same key press and were presented in random order. Each practice block included 90 trials per sequence. With six practice blocks on the first day of the experiment and two practice blocks on the second day, participants completed 720 trials for each sequence. There was a short 40 s break halfway through each practice block and a 4 min break at the end of each practice block. Before each break, participants received feedback on their mean response time and error percentage.

The test phase included four blocks of 60 trials, each including a different experimental condition. The blocks were separated by 40 s breaks and the order of the four blocks was counterbalanced across the participants. Two test blocks involved the two sequences that participants had performed during the practice phase. In the *familiar condition* participants responded to the same order of key-specific stimuli as during the practice phase. In the *single-stimulus condition*, participants performed their sequences on the basis of only the first sequence-specific stimulus. After presentation of that stimulus, the placeholder remained white and participants had to complete the sequences from memory. In the *mixed-familiar condition*, 75 percent of the trials included one of the familiar sequences in which two of the stimuli at the sequences positions 2-6 were randomly changed. These two deviants never occurred at successive positions, resulting in sequences with deviants as positions 2 and 4, 2 and 5, 2 and 5, 3 and 6, and 4 and 6 (indicated as [24], [25], etc.). The remaining 25 percent of the sequences did not involve such deviants (indicated as [00]) and thus were the sequences that participants had learned during the practice phase. Finally, the *mixed-unfamiliar condition* involved two unfamiliar 6-key sequences that were also taken from the eight versions of the 6-key sequences developed by rotating keys across sequential positions. In this condition, too, 75 percent of the sequences involved two random deviations from the unfamiliar base sequences. Each test block was followed by presentation of feedback regarding mean response time and error percentage.

2.4. Repetitive TMS

After the final practice block on the second day of the experiment, participants were seated in a dental chair that allowed them to sit in a comfortable position for the duration of the rTMS procedure. For each participant we first determined the motor hotspot (i.e., the location on the right primary motor cortex (M1) that evoked 100% responsitivity in the participant's hand) as well as the motor threshold (MT; i.e., the intensity at which the hand or thumb responds—as witnessed by visual inspection—in 50% of the stimulations to the hand area of the motor cortex; e.g., Schutter & Van Honk, 2006; Verwey et al., 2002). To this end, we used the ascending staircase method described by Schutter and Van Honk (2006). First, the M1 of the participant was stimulated with single-pulse TMS at a low intensity. The intensity was slowly increased until visible responses of the hand or thumb

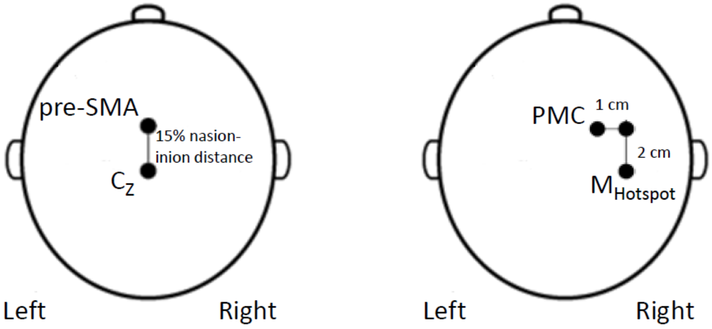

Figure 6.1 Localization of the stimulation site for 1Hz rTMS over the pre-SMA and PMC.

appeared. Second, the intensity was set so that responsitivity was 100% (i.e., each pulse elicited a visible response). Third, the intensity was optimized so that it evoked responses during 50% of the pulses; this intensity is the MT of the individual participant.

Next, the stimulation site was determined for each participant (see Figure 6.1). The pre-SMA was defined as the site 15% of the distance between nasion and inion anterior to Cz on the sagittal midline (cf. Mantovani, Simpson, Fallon, Rossi, & Lisanby, 2010). Hence, we stimulate a more anterior location in comparison to the rTMS-SMA study by Verwey et al. (2002), who targeted the SMA at 10% of the distance between nasion and inion anterior to Cz on the sagittal midline. Across participants in the pre-SMA condition, this procedure yielded a mean coil placement at 5.5 cm anterior to Cz—this distance closely resembles the location of the pre-SMA such as determined by Kennerley et al. (2004). The stimulation site for the right PMC was located 2 cm anterior and 1 cm medial to the motor hotspot (e.g., Bestmann, Baudewig, Siebner, Rothwell, & Frahm, 2005; Bijsterbosch, Lee, Dyson-Suttona, Barker, & Woodruff, 2011; Murase et al., 2005). In line with previous studies, we stimulated PMC contralateral to the hand performing the movements (e.g., Grafton, Hazeltine, & Ivry, 1998; Wymbs & Grafton, 2013). The TMS coil was positioned at the location of stimulation at a 45 degree angle. Participants were then administered 20 minutes of 1Hz rTMS stimulation at an intensity that was set at 90% of each participant's individual MT. Participants assigned to the sham condition were treated as part of one of the experimental conditions, meaning that half of these participants experienced the coil above the pre-SMA and the other half above the PMC region, with the difference that they did not receive the actual stimulation. After the rTMS procedure, there was a 20-minute rest period as the effects of stimulation have been found most pronounced after such a pause (e.g., Verwey et al., 2002).

2.5. Procedure

The experiment consisted of two sessions that took place on two consecutive days. Upon entering the lab on the first day of the experiment, participants filled out the screening questionnaire for TMS candidates (Rossi et al., 2009) and the Handedness Inventory (Annett, 1970) to determine whether they met the requirements for participation in the study. They then signed an informed consent form and received instructions regarding the task. Next, they performed the 6 practice blocks. Finally, participants completed an awareness questionnaire in which they were asked to write down their sequences from memory and to recognize their sequences from a list of 12 alternatives. On the second day of the experiment, participants performed 2 additional practice blocks, after which the rTMS procedure was carried out. The participants then carried out the four blocks of the test phase. The duration of the experiment was about 2 hours per day.

3. RESULTS

We calculated mean response times (RTs) within the 2×3 and 1×6 sequences for every participant in each block of the practice and the test phase. RT was defined as the time between stimulus presentation and depression of the appropriate response key. Sequences in which an error was made—resulting in immediate abortion of the ongoing sequence—and the first two sequences of each (sub-)block were excluded from the RT analyses. RTs deviating more than 2.5 SDs from the mean RT of that sequence for each rTMS group in a particular (sub-)block were also excluded. For one participant in the sham group, the data were outliers in the test phase (i.e., deviating more than 3SD from the group mean) and were therefore not included in the analyses below.

3.1. Practice phase

A mixed ANOVA on RTs with Block (8) and Sequence (2; 2×3 vs. 1×6) as within-subject variables and rTMS group (3; pre-SMA vs. PMC vs. Sham) as between-subject variable showed an effect of Block, $F(7,308)=310.12$, $p<.001$, $\eta_p^2=.87$, indicating that sequencing performance improved with practice (cf. Figure 6.2). The 2×3 sequence was performed faster than the 1×6 sequence (206 ms vs. 214 ms), $F(1,44)=7.01$, $p<.05$, $\eta_p^2=.13$, but as Figure 6.2 illustrates this difference tended to reduce as practice progressed, $F(7,308)=4.65$, $p<.05$, $\eta_p^2=.10$. The absence of any significant effects of rTMS group showed that the later effects of rTMS can not be attributed to group differences (*ps*>.44).

We also analyzed participants' performance in terms of accuracy by means of a mixed ANOVA on proportions of correctly performed sequences with Practice block (8) and

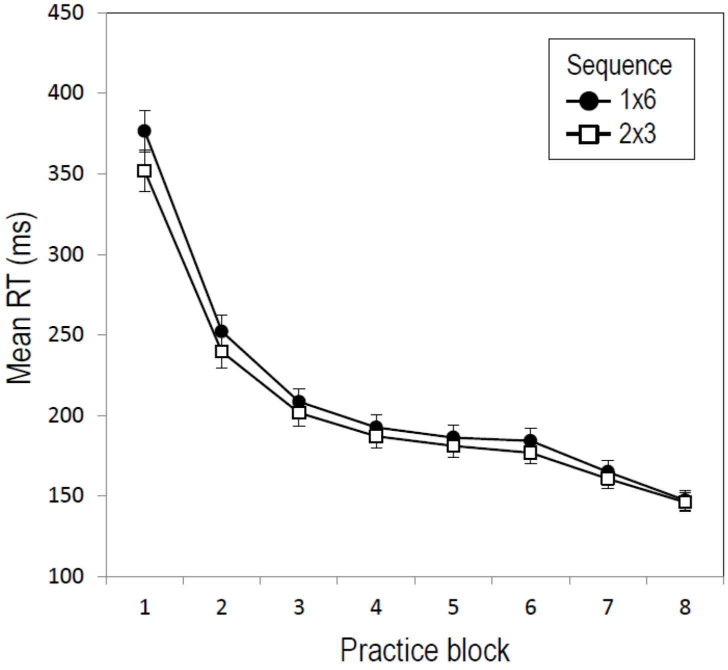

Figure 6.2 Mean RTs (ms) of the 1×6 and 2×3 sequences as a function of practice block. Error bars represent standard errors.

Sequence (2) as within-subject variable and rTMS group (3) as between-subject variable. Results indicated that participants completed more 1×6 sequences than 2×3 sequences (.90 vs. .88), *F*(1,44)=6.81, $p<.05$, $\eta_p^2=.13$. Yet, this pattern was reversed in the first practice block compared to subsequent blocks, *F*(7,308)=2.49, $p<.05$, $\eta_p^2=.05$. Across the practice phase, the mean proportion of correctly completed sequences across participants was never below .84. Like in the RT analysis, there were no main or interaction effects of rTMS group (*ps*>.50).

3.2. Test phase

Overall ANOVA

Results of a mixed ANOVA on RTs with Test condition (4; single-stimulus vs. familiar vs. mixed-familiar [00 sequences] vs. mixed-unfamiliar) and Sequence (2) as within-subject variables and rTMS group (3) as between-subject variable showed that performance in the four test conditions differed substantially, *F*(3,129)=749.20, $p<.001$, $\eta_p^2=.94$ (Figure 6.3). Sequences were performed fastest in the single-stimulus and familiar conditions, which is in line with the notion of rapid performance in the chunking mode. However, sequences were performed slower in the single-stimulus condition than in the familiar condition (192 ms vs. 160 ms, respectively), $F(1,43)=38.23$, $p<.001$, $\eta_p^2=.47$. This is in line with the idea that a race between response selection (i.e., direct S-R translations) and response triggering (i.e., on the basis of response-codes in the motor buffer) speeds up performance: As the response selection process was disabled in the single-stimulus condition, RTs slightly increased. Responses in the mixed-unfamiliar condition were slowest (430 ms), which is in line with purely S-R based performance in the reaction mode. Results further confirmed that sequences without deviants in the mixed-familiar condition were performed in the associative mode (343 ms), as they were performed faster than sequences in the mixed-unfamiliar condition, $F(1,29)=273.35$, $p<.001$, $\eta_p^2=.86$, yet slower than sequences in the single-stimulus and familiar conditions, $Fs>246.29$, $ps<.001$, $\eta_p^2s>.85$. These findings nicely replicate the findings of Verwey and Abrahamse (2012) that discrete movement sequences can be executed in three different execution modes.

Results further showed that the 2×3 sequence was performed faster than the 1×6 sequence (277 ms vs. 286 ms), $F(1,43)=11.49$, $p<.01$, $\eta_p^2=.21$. However, a Sequence × rTMS condition suggested that this difference between the 1×6 and 2×3 sequences varied for the three rTMS groups, $F(2,43)=6.65$, $p<.05$, $\eta_p^2=.23$. Furthermore, a Sequence × rTMS group × Test condition interaction suggested that this in turn depended on test condition, $F(6,129)=2.56$, $p<.05$, $\eta_p^2=.10$. To further investigate these interactions, we performed separate ANOVAs per rTMS group with Test condition (4) and Sequence (2) as within-

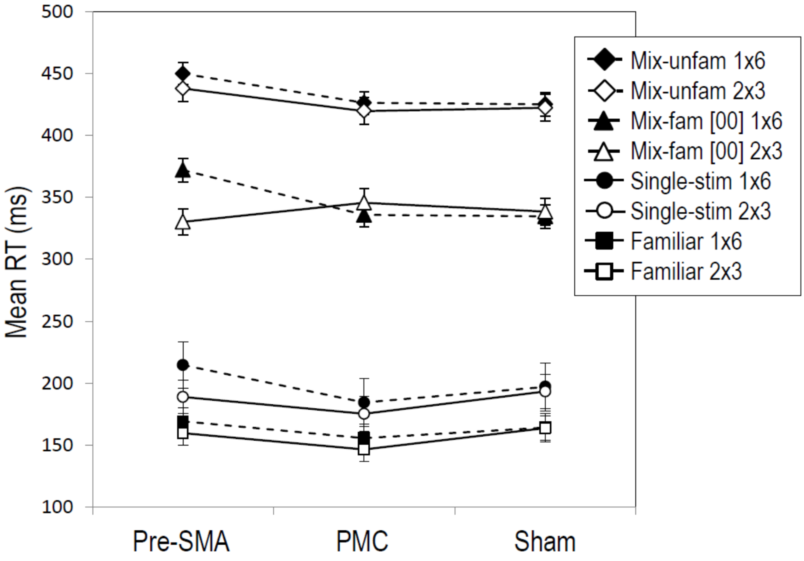

Figure 6.3 Mean RTs (ms) of the 1×6 and 2×3 sequences as a function of test condition for the pre-SMA, PMC and sham groups. Error bars represent standard errors.

subject variables. Results of the PMC and sham groups showed no main or interaction effects of sequence, *ps*>.34. However, results of the pre-SMA group revealed that the 1×6 sequence was performed slower than the 2×3 sequence (301 ms vs. 279 ms), *F*(1,15)=16.33, *p*<.01, η_p^2=.52. In addition, there was a strong trend towards a Test condition × Sequence interaction, *F*(3,45)=3.02, *p*=.06, η_p^2=.16, suggesting that the difference between the sequences varied between test conditions. Detailed analyses showed that the 1×6 sequence was performed slower than the 2×3 sequence in the single-stimulus, mixed-familiar and mixed-unfamiliar conditions, *ts*>2.45, *ps*<.05, but not the familiar condition (*p*=.16).

Testing hypotheses from the DPM

In this section we present a number of planned comparisons that aim to test the tentative neural implementation of the DPM's cognitive processor as described in the introduction (see also Abrahamse et al., 2013). First, we proposed on the basis of Kennerley et al. (2004) that the pre-SMA is involved in the loading of motor chunks into the motor buffer when sequences are performed in the chunking mode (i.e., in the familiar and single-stimulus test conditions). To explore whether the initiation and execution of motor chunks differed amongst the rTMS groups, we first examined whether participants segmented their sequences into multiple motor chunks in the final practice block. We assumed that the first key press always reflects initiation of the first motor chunk. Initiation of subsequent chunks is reflected in a key presses within the sequence that is slower than both the preceding and succeeding key presses (see Bo & Seidler, 2009; Kennerley et al., 2004; Ruitenberg et al., 2012). We ran one-tailed paired t-tests (*p*<.05) on RTs of the third, fourth and fifth key press of each sequence to evaluate whether the RT on a particular position in the sequence was significantly longer than the previous and subsequent RTs. The second and sixth key presses were not evaluated as such, because we assumed that they are always included in the first and last motor chunk, respectively. As chunking patterns are likely to differ for the two sequences that a participant performed, we analyzed the 1×6 and 2×3 sequences separately.

This procedure revealed that 27 (of the 47) participants segmented their 1×6 sequence and 39 participants segmented their 2×3 sequence into multiple motor chunks. RTs of key presses that were classified as being the first key press of a motor chunk (i.e., the first key press and chunk points) were averaged to compute the mean initiation RT per participant per sequence. The RTs of the remaining key presses were averaged to compute the mean execution RT. We subjected these RTs to a mixed ANOVA with Test condition (2; single-stimulus vs. familiar), Sequence (2) and Phase (2; chunk initiation vs. execution of other key presses) as within-subject variables and rTMS group (3) as between-subject variable.

In addition to the effects of Test condition and Sequence found in the earlier analysis, results showed that initiating motor chunks took longer than executing other key presses within the chunks (305ms vs. 113ms), $F(1,43)=568.12$, $p<.001$, $\eta_p^2=.93$. Moreover, a Phase × rTMS group interaction indicated a differential involvement of the pre-SMA and PMC in initiation and execution, $F(2,43)=3.57$, $p<.05$, $\eta_p^2=.14$. Planned comparisons revealed that initiation differed between rTMS groups, $F(2,43)=3.42$, $p<.05$, $\eta_p^2=.13$, while execution did not ($p=.40$). As the results of the ANOVA also showed a Test condition × Phase × rTMS group interaction, $F(2,43)=3.94$, $p<.05$, $\eta_p^2=.15$, we examined the effect of rTMS on the initiation phase in each test condition.

Results revealed that motor chunk initiation in the single-stimulus test condition was different for the various rTMS conditions, $F(2,43)=3.43$, $p<.05$, $\eta_p^2=.14$ (see Figure 6.4). As expected, motor chunk initiation was slowed by rTMS stimulation of the pre-SMA compared to the sham group, $F(1,29)=3.02$, $p<.05$, $\eta_p^2=.09$ (one-tailed), as well as the PMC group, $F(1,29)=5.22$, $p<.05$, $\eta_p^2=.15$. Initiation was not affected by rTMS stimulation of the PMC compared to the sham group ($p=.39$). With regard to the familiar condition, there was an almost significant tendency for initiation to be affected by the rTMS group, $F(2,45)=3.09$, $p=.058$, $\eta_p^2=.12$. Although initiation was quantitatively slower in the pre-SMA group than in the sham group, this difference was not significant ($p=.25$). Like in the single-stimulus condition, initiation in the pre-SMA group was slower than initiation in the PMC group, $F(1,30)=5.35$, $p<.05$, $\eta_p^2=.15$. Initiation in the PMC and sham groups did

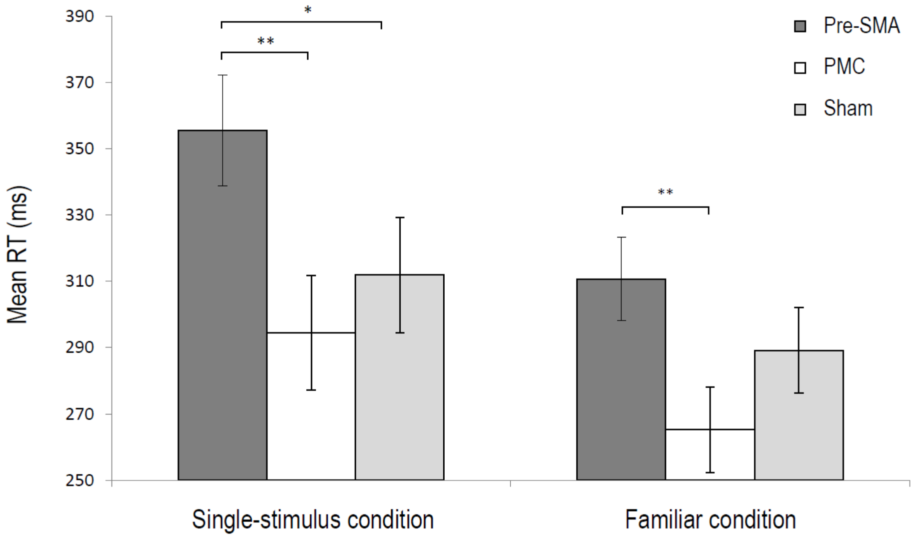

Figure 6.4 Mean RTs (ms) for motor chunk initiation in the single-stimulus and familiar test conditions as a function of rTMS group. (** = $p<.05$ and * = $p<.05$ when tested one-sided). Error bars represent standard errors.

not differ (*p*=.18). So, like in Kennerley et al. (2004), the results suggest that the initiation of motor chunks—but not the execution of elements within motor chunks—is impaired when rTMS was applied to the pre-SMA.

As noted in the introduction, we further predicted that the PMC may be involved in the production of sequences on the basis of S-R translations by the cognitive processor. Such S-R translations occur both with unfamiliar sequences in the reaction mode (i.e., mixed-unfamiliar condition), and with familiar sequences that are performed in the associative mode (i.e., mixed-familiar [00 sequences] condition). We performed a Sequence (2) × rTMS group (3) ANOVA on RTs in the mixed-unfamiliar condition to specifically examine the involvement of the PMC in the reaction mode. RTs of first key press of each sequence were excluded from the analysis, as the first key press may also reflect other factors such as time uncertainty. Results showed no main or interaction effects of rTMS group (*ps*>.32). A similar ANOVA on RTs in the mixed-familiar condition showed an interaction between Sequence and rTMS group, $F(2,44)=4.72$, $p<.05$, $\eta_p^2=.17$. This interaction reflected the previously reported finding that the 1×6 sequence was performed slower than the 2×3 sequence in the pre-SMA group, $F(1,15)=11.35$, $p<.01$, $\eta_p^2=.43$, while the sequences did not differ in the other groups (*ps*>.73). There was no main effect of rTMS group (*p*=.58). These results offer no support for the notion that the PMC is involved in S-R based performance.

Accuracy

The mean proportion of correctly performed sequences was .84 in the single-stimulus condition, .86 in the familiar condition, .81 in the mixed-familiar condition and .84 in the mixed-unfamiliar condition. Results of a mixed ANOVA on these proportions with Test condition (4) and Sequence (2) as within-subject variables and rTMS group (3) as between-subject variable showed there was a marginal tendency for accuracy to differ between the test conditions, $F(3,132)=2.62$, $p=.08$, $\eta_p^2=.05$. There were no other main or interaction effects (*ps*>.15).

3.3. Explicit sequence knowledge

Analyses of the awareness questionnaire showed no differences in recall or recognition of the 1×6 and 2×3 sequences between the rTMS groups ($\chi^2 s(2)<1.4$, *ps*>.38; see Table 6.1). This indicates that the observed performance differences cannot be attributed to group differences with regard to explicit sequence knowledge. To examine the contribution of explicit sequence knowledge to sequencing performance in the test conditions, we calculated correlations per rTMS group between the amount of explicit knowledge

Table 6.1 The numbers and the corresponding percentages of participants per rTMS group who correctly wrote down their 1×6 and 2×3 sequences immediately following the practice phase on the first day of the experiment ('recall' columns), and recognized their sequences from a set of 12 alternatives ('recognition' columns).

	Recall		Recognition	
	1×6	2×3	1×6	2×3
Pre-SMA	13 (81%)	13 (81%)	15 (94%)	15 (94%)
PMC	10 (63%)	12 (75%)	15 (94%)	15 (94%)
Sham	11 (73%)	14 (93%)	15 (100%)	15 (100%)

(i.e., recall plus recognition score) and participants' mean RT in each test condition. For participants in the pre-SMA and sham groups, results showed no significant correlations between explicit knowledge and performance of the 1×6 and 2×3 sequences in any of the test conditions (*ps*>.22). For participants in the PMC group, explicit sequence knowledge of the 1×6 sequence correlated with performance of that sequence in the familiar and single-stimulus conditions, *rs*(16)<-.61, *ps*<.05, in that more explicit knowledge was related to faster performance. Explicit knowledge of the 2×3 sequence tended to correlate with performance in the familiar condition, *r*(16)=-.47, *p*=.06. When more specifically studying motor chunk initiation and execution in the familiar and single-stimulus conditions, results showed that for participants in the PMC group the execution of motor chunks of both the 1×6 and 2×3 sequence in the familiar condition was related to the number of correctly recalled sequence elements and recognition performance, *rs*(16)<-.58, *ps*<.05. This indicates that participants with more explicit knowledge were faster at performing elements *within* their chunks.

4. Discussion

The present study tested the merits of the dual processor model (DPM), which postulates that a cognitive and motor processor are differently involved in the production of discrete movements in three sequence execution modes (Verwey & Abrahamse, 2012). In addition, we explored the neural substrate that may underlie the different roles of the DPM's cognitive processor. Specifically, we studied whether the pre-SMA and PMC could be related to the various functions that the cognitive processor performs during sequence execution in the reaction, associative and chunking modes. To that end, we applied 20 min 1 Hz rTMS to either the pre-SMA or PMC and compared sequencing performance between these two groups and a control group in the ensuing test phase. The current results confirmed (a) that discrete movement sequences can be performed in three execution modes (cf. Verwey & Abrahamse, 2012), and that key-specific stimuli still support execution of familiar movement sequences (cf. Verwey et al., 2010; Verwey et al., 2013). Furthermore, we observed (b) that rTMS stimulation of the pre-SMA disrupted motor chunk initiation in the chunking mode (cf. Kennerley et al., 2004). Finally, results showed (c) that rTMS stimulation of the pre-SMA especially affected performance of 1×6 sequences more than the 2×3 sequences. We observed no performance impairments after rTMS stimulation of the PMC, but found indications that this neural structure may be responsible for the online S-R translations in the chunking mode. Below, we will discuss these findings in more detail.

4.1. Three modes of sequence execution

The current results support the notion that there are three distinct execution modes in which movement sequences can be performed (cf. Verwey & Abrahamse, 2012). The observation that execution was slowest in the mixed-unfamiliar condition is in line with the idea that with little or no practice sequences are performed in the slow reaction mode, on the basis of direct S-R translations by the cognitive processor. With more practice, sequence representations start to develop and can be used for performance, so the need for processing external stimulus information reduces and RTs decrease. Indeed, sequence execution was fastest when performance could be based on motor chunks in the familiar and single-stimulus conditions, which is indicative for performance in the chunking mode. Furthermore, the finding that performance was slower in the single-stimulus condition than in the familiar condition is in line with the DPM's notion that a race between two response generation processes—i.e., response triggering based on motor chunks read from the motor buffer by the motor processor and response selection via direct S-R translations by the cognitive processor—facilitates performance (cf. Verwey et al., 2010; Verwey et al., 2013). Finally, when the chunking mode was prevented by presenting both sequences with deviants in the mixed-familiar condition, performance of the occasionally unchanged familiar sequences dropped but was still better than performance in the mixed-unfamiliar sequences. This confirms that the development of associations between successive responses can enhance sequence execution in the associative mode, so that performance—although still reliant on external stimulus information—is better than in the reaction mode.

In the introduction we hypothesized that the pre-SMA would be particularly involved in the production of well-learned sequences that are executed on the basis of sequence representations that are loaded into the motor buffer. In line with this notion, we observed that rTMS stimulation of the pre-SMA impaired motor chunk initiation. Furthermore, we proposed that the PMC would be mainly involved in S-R based sequencing performance in the reaction and associative modes. The current results offered no support for this latter hypothesis. In the next sections, we will zoom in on the respective roles of the pre-SMA and PMC in relationship to the functions of the cognitive processor during sequencing performance in the three execution modes.

4.2. The neural substrate of the cognitive processor: the pre-SMA

As outlined in the introduction, the pre-SMA is thought to be increasingly involved in the production of sequential action as the sequence becomes more familiar. The current observation that the initiation—but not execution—of familiar motor chunks was slowed in the pre-SMA condition is in line with the notion that this area may be specifically involved in the loading of sequence representations (e.g., motor chunks) into the buffer when sequences are performed in the chunking mode (Halsband & Lange, 2006; Kennerley et al., 2004). In combination with the findings of Verwey et al. (2002) that rTMS stimulation of the SMA slowed all elements of a discrete keying sequence, it could be argued that the SMA is involved in the execution of individual sequence elements, while the pre-SMA operates at an hierarchically higher level and is involved in the loading of motor chunks into the buffer. Such a divide in functionality fits well with anatomical findings, that the SMA is connected to motor areas, while the pre-SMA is connected to frontal areas (see e.g., Picard & Strick, 2001). Overall, the present findings are in line with the idea that at advanced skill levels the pre-SMA activates the relevant long-term memory representations (i.e., load the motor buffer), after which sequence and/or chunk execution may be controlled by more posterior motor regions such as the SMA and the primary motor cortex (M1; e.g., Abrahamse et al., 2013; Karni et al., 1998; Kennerley et al., 2004; Ungerleider, Doyon, & Karni, 2002).

We observed that rTMS stimulation of the pre-SMA impaired performance of the 1×6 but not the 2×3 sequence. This is in line with previous findings that activation in this area is greater for complex than for relatively simple sequences (Boecker et al., 1998; Gerloff, Corwell, Chen, Hallett, & Chen, 1997; Grafton et al., 1998). Interestingly, the effect was observed across all three modes of sequence execution—that is, in the mixed-unfamiliar, mixed-familiar and single-stimulus conditions. The pre-SMA may thus contribute to sequential action across all levels of performance, but its specific role differs amongst the three execution modes. The slowed performance of the 1×6 sequence in the reaction mode could possibly reflect the difficulty of the transformation process by the pre-SMA during initial sequence learning. It has been suggested that the pre-SMA is involved in the transformation of spatial to motor codes (Dayan & Cohen, 2011; Hikosaka, Nakamura, Sakai, & Nakahara, 2002), and therewith the organization of longer movement sequences into manageable chunks (Kennerley et al., 2004). The development of motor codes may have been more difficult for 1×6 than for 2×3 sequences in the mixed-unfamiliar condition, because the regularities within the complex sequence were harder to detect.

Hikosaka et al. (1999) further proposed that the pre-SMA may also have a coordinating role between the spatial and motor sequence mechanisms. That is, when the two mechanisms generate inconsistent signals, the pre-SMA suppresses one mechanism (often the motor mechanism, as it is more desirable to rely on the spatial mechanism). Such conflict between spatial and motoric output may especially apply to the associative mode: The motor mechanism passes on information (i.e., a sequence representation) that would be appropriate for [00] sequences, but that cannot be used for the majority of the sequences as they include deviants. Consequently, in these latter sequences the pre-SMA has to suppress the output of the motor system, so that responses can be based on the spatial information that is presented. In the present study, this may have been more difficult for 1×6 than for 2×3 sequences, as in the former two different chunks needed to be inhibited. Finally, research suggests that the pre-SMA is increasingly involved in the explicit retrieval of sequences of greater complexity (Grafton et al., 1998). One could argue that retrieval is more explicit during performance in the single-stimulus condition than during performance in the familiar condition (as the latter also allows for S-R translations), so that effects of complexity were observed in the single-stimulus but not the familiar condition—even though sequences in both conditions are assumed to be performed in the chunking mode.

4.3. The role of the PMC

The current results showed no effect of rTMS stimulation of the PMC on the sequence execution in the mixed-unfamiliar and mixed-familiar conditions ([00] sequences), and thus did not support our hypothesis that the PMC is related to sequencing performance based on S-R translations by the cognitive processor (i.e., reaction and associative modes). With respect to the reaction mode, an explanation may be that response-selection during the execution of completely novel sequences is more prefrontally controlled (cf. Dayan & Cohen, 2011; Schumacher & D'Esposito, 2002). In the associative mode, execution of the sequences without deviants may already be related to the activation of a sequence representation by the pre-SMA. Moreover, Wymbs and Grafton (2013) recently showed that the PMC is particularly active during the performance of moderately practiced sequences. The present study did not involve such a condition, as participants performed either completely novel sequences in the mixed-unfamiliar and the mixed-familiar conditions (i.e., the sequences with deviants), or very well-practiced sequences in the mixed-familiar (i.e., the [00] sequences), familiar and single-stimulus conditions. Participants thus did not perform moderately practiced sequences, which may explain why we did not observe effects of rTMS stimulation of the PMC on sequencing performance.

As outlined in the introduction, the DPM postulates that the cognitive processor can enhance sequence execution by the motor processor, by engaging in direct S-R translations during sequencing performance in the chunking mode. In addition, Ruitenberg et al. (2012) recently found indications that the cognitive processor might also use explicit sequence knowledge for response selection when response-specific stimuli are absent. Based on the observed correlations between explicit knowledge and sequencing performance in the chunking mode after rTMS stimulation of the PMC, we propose that the PMC may be responsible for the online S-R translations made by the cognitive processor to assist the motor processor. It could be argued that in the familiar condition, online S-R translations were hindered in the PMC group, but participants with more explicit sequence knowledge were able to compensate for the reduced online involvement of the PMC as the sequence knowledge still allowed a race between two response generation processes. As a result, their performance was better than that of participants who lacked explicit sequence knowledge. Furthermore, the observed correlation between explicit knowledge and performance in the single-stimulus condition confirms the notion that the cognitive processor may assist the motor processor in response selection by means of explicit sequence knowledge (cf. Ruitenberg et al., 2012).

One may argue that the absence of clear behavioral effects of rTMS stimulation of the PMC casts doubt on the targeting of this area. Admittedly, we have no anatomical evidence (e.g., fMRI data) that the PMC was correctly localized. Furthermore, there are indications that when the non-dominant hand is used for performance—like in the present study—the bilateral or even ipsilateral PMC is active (e.g., Grafton et al., 2002; Gu et al., 2003). It could be argued that the non-targeted PMC may have been able to (partly or completely) compensate for the functionality of the PMC that received rTMS stimulation, as the left PMC may be dominant for movement selection (Schluter et al., 1998). Future studies should further address the issues of hand- and hemisphere-dominance to increase our understanding of the PMC in sequential action.

4.4. Conclusions

Overall, the present study is in line with the DPM's notion that a cognitive processor and a motor processor are involved in the production of discrete movement sequences, and our results replicate the behavioral findings of Verwey and Abrahamse (2012) that sequences may be executed in three different modes: the reaction mode, the associative mode, and the chunking mode. The current results further indicate that the pre-SMA is involved in the activation of a sequence representation (e.g., motor chunk) from long term memory when familiar movement sequences are performed in the chunking mode (cf. Kennerley et al., 2004). During actual sequence execution in this mode, a race between a) response selection by means of S-R translation, b) response triggering by reading from the motor buffer, and c) response generation on the basis of explicit sequence knowledge occurs so that the fastest possible responses are generated.

Note

1. The response-to-stimulus interval (RSI) of 50 ms differs from that in a typical DSP task, in which an RSI of 0 ms is employed. The here employed RSI allowed participants to perceive an occasional repetition of the same stimulus location in case of random deviants in the mixed-familiar and- unfamiliar conditions of the test phase.

Acknowledgements

We would like to thank Sandra Tillmann for her assistance in running the experiment. We are grateful to Michel van Putten, Esther ter Braack, Cindy Lammertink, Wim Leppink and Dennis Schutter for their practical support in this project.

Summary and conclusions

Chapter 7

Based in part on

Elger L. Abrahamse
Marit F. L. Ruitenberg
Elian De Kleine
Willem B. Verwey

Frontiers in Human Neuroscience, 7 (2013)

The ability to acquire and execute movement sequences is a fundamental aspect of human behavior, as most of the complex actions we perform in daily life consist of series of simpler movements. To study the cognitive mechanisms underlying the production of such sequencing skill, the studies presented in this dissertation employed the discrete sequence production (DSP) task. In this task, participants respond to fixed series of stimuli by means of key presses, and thus learn to perform brief, discrete keying sequences. The DSP task is well-suited for studying cognitive control of sequence production, as the relatively simple key presses do not demand much motor control so that inferences on cognitive processes can be made on the basis of response times (RTs), and the motor chunks that develop with practice are representative for the building blocks that make up our everyday actions. This dissertation focused on the cognitive, perceptual and neural underpinnings of sequential motor skill. Below, the contributions of chapters 2-4 to our understanding of the role of perception in sequential motor skills will first be discussed. Based on the empirical work presented in this dissertation, we will then work towards a general cognitive architecture of motor skill performance. It is discussed how factors such as age may affect the degree to which a skill can be performed automatically.

While sequencing skill is clearly motoric in nature, there is also a role for perception in the learning and performance of sequential actions, as indicated by the notion of context-dependent skill. In chapter 2, we explored the feasibility of a novel form of context-dependence by examining whether people can learn to ignore irrelevant perceptual information in order to achieve optimal sequencing performance. Participants learned to perform sequences of key presses by responding to relevant visual-spatial cues, while at the same time ignoring irrelevant visual-spatial cues (i.e., the context). The relevant and irrelevant cues were consistently paired throughout practice. Results showed that changing the locations of the contextual cues—but not the removal of such cues—had a detrimental effect on performance. We refer to this as context-dependent filtering and propose that when irrelevant information, which people had learned to ignore, is changed, this hinders performance as the developed filter can no longer be used. Interestingly, the effect was observed only after limited practice, but not after extensive practice. We propose that the gradual development with practice from stimulus-driven sequence execution to representation-driven sequence execution on the basis of motor chunks (see below for a more detailed discussion) underlies this effect.

In chapters 3 and 4 we studied whether memory-based sequencing skill would be sensitive to contextual changes, too. We employed the more classical implementation of context-dependence, namely context-dependent retrieval, which is thought to rely on the development of associations between the task (here: sequence) and contextual features, due to which the latter become integrated in the task-representation (e.g., Healy et al., 2005; Wright & Shea, 1991). The results of chapters 3 and 4 demonstrate that sequencing performance can be affected by perceptual changes, even when the sequences are performed from memory and thus in the absence of actual perceptual input. Moreover, the observation in chapter 4 that the preparation—but not execution—of highly practiced motor chunks was affected by contextual changes suggests that perception especially relates to higher cognitive processes. This fits with the notion of the DPM that cognitive processor operations, but not motor processor operations, would be sensitive to perceptual changes as the cognitive processor is responsible for processing external stimulus information. It can be assumed that the associations between the task and the context strengthen with practice, so that the representation becomes more comprehensive. This would explain the observation in chapter 4 that context-dependent retrieval increases with practice.

In all, chapters 2-4 demonstrate that discrete sequencing skill involves not only cognitive and motoric processes, but also perceptual processes – even when sequences are performed from memory in the absence of perceptual input. Specifically, changes in perceptual information may primarily affect higher cognitive processes. At a practical level, the findings on perceptual processing and specifically context-dependent sequencing skill may have important consequences for designing training programs (see also Abrahamse & Noordzij, 2011). The present results suggest that the extent of training as well as the nature of the perceptual context—that is, within the relevant stimulus-dimension (chapter 2) versus within the relevant stimulus itself (chapters 3 and 4)—should be taken into consideration in order to achieve optimal transfer of the learned skill to new contexts (e.g., from a simulator to the real world).

As outlined in the introduction chapter of this dissertation, the dual processor model (DPM) describes how movement sequences are produced in terms of cognitive and motor processes. In addition, three modes for sequence execution were put forward: the reaction, chunking, and associative mode. Here we will try to integrate the efforts of the cognitive and motor processors from the DPM with sequencing performance in these modes. The reaction and chunking modes can be easily accounted for by the DPM (see below). The theoretical challenges concern the implementation of the associative mode, especially with respect to the representational level. It is generally accepted that representing sequential information may involve coding across the perceptual, cognitive and response-based/motor levels (e.g., Abrahamse et al., 2010; Goschke & Bolte, 2012; Hikosaka et al., 1999; Keele et al., 2003). The chunking mode would mostly depend on associations at the motor level from which motor chunks can develop. Conversely, the associative mode could be tentatively linked to various types of visuo-spatial associations—in line with the SRT literature (Abrahamse et al., 2010). However, the possibility cannot be excluded that the associative mode derives directly from the same associations that underlie the chunking mode: Rather than being just static propositions waiting to be used for the chunking mode, motor chunks may continuously influence ongoing processing (Cleeremans, 2008). They may, for example, prime the selection of individual responses. To comply with the notion of distributed coding (cf. Abrahamse et al., 2010; Hikosaka et al., 1999), we assume an event-based sequence representation—where event refers to a specific S-R episode—that potentially involves associations at both the visuo-spatial (e.g., between successive stimuli or response locations) and motor level. Its precise features will probably depend on the task requirements, the context, and the amount of practice.

Figure 7.1 depicts a simple cognitive architecture for the skilled production of movement sequences. It shows how, on basis of stimulus input (S_n), a response (R_n) is generated by the concerted action of the cognitive processor and the motor processor. These processors may use a motor buffer that can temporarily hold representations that concern a limited number of responses. In the reaction mode, which is dominant with unfamiliar or random sequences, the cognitive processor processes sensory input and selects the appropriate response separately for each particular stimulus. Next, it puts the motor processor to work for the actual execution of the response. With repeated execution of the same sequence of events, associations develop between successive events. The resulting representation allows for response selection processes to be primed when they are executed in a familiar order on the basis of preceding events (associative mode). Moreover, when the representation becomes sufficiently strong at the motor level, it allows for the temporary activation of a short series of movements (i.e., a motor chunk) as if they are loaded in a single step into a motor buffer. Next, the motor buffer content is read and executed by the motor processor. Because the motor buffer capacity is limited, the number of simultaneously prepared and executed responses is limited. Finally, the independence of the cognitive processor and motor processor allows a race between response-generation processes, in that the cognitive processor selects responses at the cognitive ('response selection') level, and the motor processor triggers responses from the motor buffer ('response triggering') so that the fastest possible responses are generated. When response-specific stimuli are present during execution, the cognitive processor can engage in direct S-R translations. In addition, results from chapter 3 of this dissertation suggest that, in the absence of such stimuli, the cognitive processor may also assist the motor processor by voluntarily generating the sequence elements from memory—that is, by racing on the basis of explicit sequence knowledge.

The results of chapter 5 suggest that the relative contributions of the cognitive and mo-

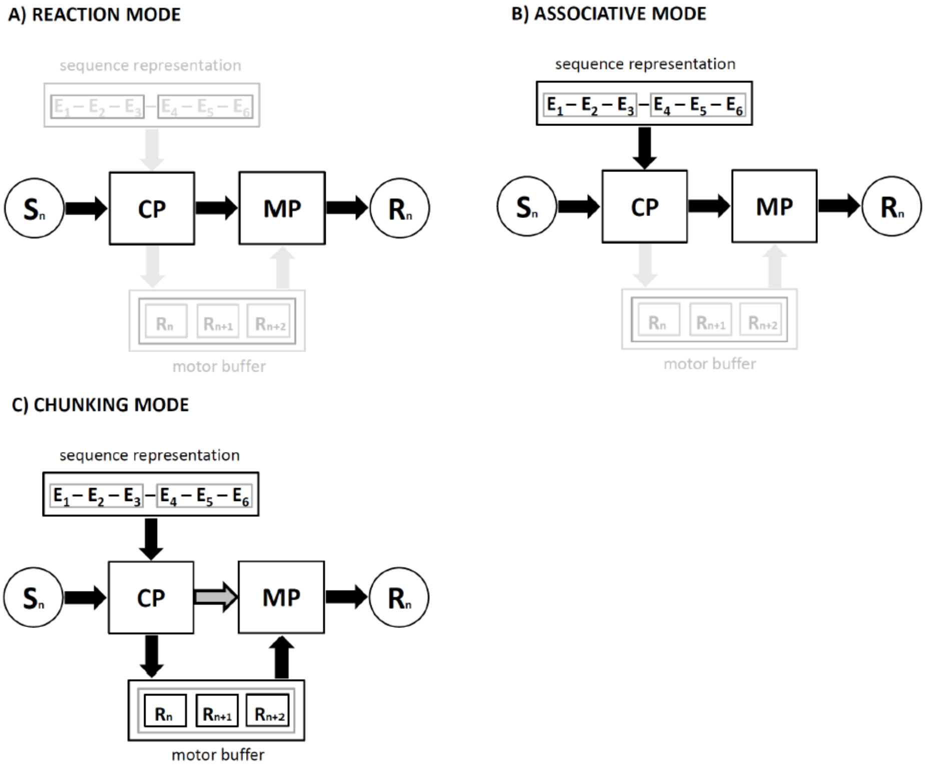

Figure 7.1 The dual processor model (DPM) involves a cognitive processor (CP) and a motor processor (MP) that together drive three distinct modes of sequence execution, through long-term sequential knowledge and the temporary storage in a motor buffer (in the case of motor chunking). Black arrows and boxes denote the relevant processing routes, while light grey arrows and boxes denote processing routes that are not relevant for that particular mode. Panel A: In the reaction mode, responses are selected by the CP on the basis of S-R translations. Panel B: Ongoing response selection by the CP is facilitated by the first, still weak, sequence knowledge that develops. Panel C: Motor chunks have developed, and the CP selects these motor chunks, loads them in the motor buffer, from where the MP can execute them. Please note that panel C also depicts the assumption of the DPM that there can be a race between two response processes: the triggering of responses by the MP reading response related codes from the motor buffer, and response selection by the CP on basis of continued S-R translation or explicit sequence knowledge (dark grey arrow with black lining).

tor processors for sequence production differ between preadolescent children and young adults. Specifically, our findings indicate that the performance of longer movement sequences relies more on cognitive processor efforts in children, while it relies more on motor processor efforts in young adults. This suggests that the mechanisms underlying sequencing skill change with age. Support for this notion comes from findings that elderly do not use motor chunks for in discrete keying sequences (Verwey, 2010; Verwey et al., 2011). This could be related to age-related changes in brain areas that are involved in sequence skill. For example, it has been suggested that the prefrontal cortex involved in the segmentation of longer movement sequences into multiple smaller chunks (e.g., Pammi et al., 2012). This area may be still maturing in children (Sowell et al., 2001; 2002), but is also known to reduce in function with older age (Raz et al., 2005; Resnick et al., 2003).

In chapter 6, we tentatively related two neural structures to the functions of the DPM's cognitive processor during sequencing performance in each of the three aforementioned execution modes. It was proposed that the PMC would be mainly involved in S-R based sequence execution, such as in the reaction and associative modes. Conversely, the pre-SMA was assumed to be involved in execution on the basis of sequence representations (e.g., motor chunks) that are loaded into the motor buffer by the cognitive processor in the chunking mode. We used 20 min low-frequency (1 Hz) rTMS to depress excitability of respectively the PMC and pre-SMA, after which participants performed discrete movement sequences in each of the three execution modes. Results supported the notion of pre-SMA involvement in the initiation—but not execution—of motor chunks, and suggest that the pre-SMA may be responsible for activating relevant sequence representations from memory (which are then executed by the SMA and primary motor cortex). We also found a rather indirect indication that the PMC might be responsible for online S-R translations made by the cognitive processor during sequence execution in the chunking mode. However, results were not in line with involvement of the PMC in the reaction and associative modes. Possibly, execution in these modes is more prefrontally controlled. Future studies should further investigate the neural substrate of the cognitive processor in these modes.

The findings of this dissertation suggest that automaticity in sequential motor skill may develop across several levels. With regard to perception, people may learn to ignore irrelevant contextual information in order to achieve optimal performance. In addition, they may learn to associate perceptual features of a sequence with the movements within that sequence, so that the perceptual information is included in the sequence representation. At the cognitive level, the need for guidance by external information reduces with practice, so that sequence execution shifts from being stimulus-driven towards being representation-driven. This is due to the development of sequence representations in the form of motor chunks – which can be loaded into a motor buffer by the cognitive processor before sequence execution. At the motor level, then, the sequences can be performed very fast, as the motor processor executes these motor chunks in a relatively automatic—that is, autonomous—fashion (i.e., without the need for cognitive involvement once initiated). Furthermore, several studies indicate that even the transition between motor chunks may automatize when the chunks are always performed in the same succession (Verwey et al., 2010; Verwey et al., 2013).

In summary, the work presented in the current dissertation examined the perceptual, cognitive and neural mechanisms underlying skilled sequential action. The results of chapters 2-4 fit well with the idea that perception and action are strongly linked. Specifically, sequencing performance may be hindered when perceptual information that was present during skill acquisition is changed during execution. This is even the case when sequencing skill is memory-based and actual perceptual information thus is absent during performance. The results further suggest that cognitive processes in particular are sensitive to perceptual changes—more so than motor processes. The relative contribution of the cognitive and motor processes to the production of sequential action seem to vary with age (chapter 5 of this dissertation; Verwey, 2010; Verwey et al., 2011). Overall, it may be concluded that automaticity in sequential action is witnessed in perceptual, cognitive and motor processes. The results of chapter 6 suggest that the neural substrate of sequencing performance varies across the three execution modes, and that each involves a different contribution of the DPM's cognitive and motor processors.

References

Abrahamse, E. L., Jiménez, J., Verwey, W. B., & Clegg, B. A. (2010). Representing serial action and perception. *Psychonomic Bulletin and Review, 17*, 603-623.

Abrahamse, E. L., & Noordzij, M. L. (2011). Designing training programs for perceptual-motor skills: Practical implications from the serial reaction time task. *Revue Europeenne de Psychologie Appliquee, 61*, 65-76.

Abrahamse, E. L., Ruitenberg, M. F. L., De Kleine, E., & Verwey, W. B. (2013). Control of automated behaviour: Insights from the Discrete Sequence Production task. *Frontiers in Human Neuroscience*, *7. doi: 10.3389/fnhum.2013.00082.*

Abrahamse, E. L., & Verwey, W. B. (2008). Context dependent learning in the serial RT task. *Psychological Research, 72*, 397-404.

Anderson, T., Wright, D. L., & Immink, M. A. (1998). Contextual dependencies during perceptual-motor skill performance: Influence of task difficulty. *Memory, 6*, 207-221.

Annett, M. (1970). A classification of hand preference by association analysis. *British Journal of Psychology, 61*, 303-321.

Ashby, F. G., Turner, B. O., & Horvitz, J. C. (2010). Cortical and basal ganglia contributions to habit learning and automaticity. *Trends in Cognitive Science, 14*, 208-215.

Averbeck, B. B., Sohn, J. W., & Lee, D. (2006). Activity in prefrontal cortex during dynamic selection of action sequences. *Nature Neuroscience, 9*, 276-282.

Badan, M., Hauert, C.-A., & Mounoud, P. (2000). Sequential pointing in children and adults. *Journal of Experimental Child Psychology, 75*, 43-69.

Bargh, J. A. (1992). The ecology of automaticity: toward establishing the conditions needed to produce automatic processing effects. *American Journal of Psychology, 105*, 181-199.

Bestmann, S., Baudewig, J., Siebner, H. R., Rothwell, J. C., & Frahm, J. (2005). BOLD MRI responses to repetitive TMS over human dorsal premotor cortex. *NeuroImage, 28*, 22-29.

Bijsterbosch, J. D., Lee, K.-H., Dyson-Sutton, W., Barker, A. T., & Woodruff, P. W. R. (2011). Continuous theta burst stimulation over the left pre-motor cortex affects sensorimotor timing accuracy and supraliminal error correction. *Brain Research, 1410*, 101-111.

Bischoff-Grethe, A., Goedert, K. M., Willingham, D. T., & Grafton, S. T. (2004). Neural substrates of response-based sequence learning using fMRI. *Journal of Cognitive Neuroscience, 16*, 127-138.

Bo, J., Borza, V., & Seidler, R. D. (2009). Age-related declines in visuospatial working memory correlate with deficits in explicit motor sequence learning. *Journal of Neurophysiology, 102*, 2744-2754.

Bo, J., & Seidler, R. D. (2009). Visuospatial working memory capacity predicts the organization of acquired explicit motor sequences. *Journal of Neurophysiology, 101*, 3116-3125.

Boecker, H., Dagher, A., Ceballos-Baumann, O., Passingham, R. E., Samuel, M., Friston, K. J., et al. (1998). Role of the human rostral supplementary motor area and the basal ganglia in motor sequence control: Investigations with $H_2{}^{15}O$ PET. *Journal of Neurophysiology, 79*, 1070-1080.

Book, W. F. (1908). *The Psychology of Skill*. Missoula: Montana Press.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review, 108*, 624-652.

Boyd, L. A., Edwards, J. D., Siengsukon, C. S., Vidoni, E. D., Wessel, B. D., & Linsdell, M. A. (2009). Motor sequence chunking is impaired by basal ganglia stroke. *Neurobiology of Learning and Memory, 92*, 35-44.

Brown, T. L., & Carr, T. H. (1989). Automaticity in skill acquisition: Mechanisms for reducing interference in concurrent performance. *Journal of Experimental Psychology: Human Perception and Performance, 15*, 686-700.

Brown, S. D., & Heathcote, A. J. (2008). The simplest complete model of choice reaction time: Linear ballistic accumulation. *Cognitive Psychology, 57*, 153-178.

Canic, M. J., & Franks I. M. (1989). Response preparation and latency in patterns of tapping movements. *Human Movement Science, 8*, 123-139.

Chen, R., Classen, J., Gerloff, C., Celnik, P., Wassermann, E. M., Hallett, M., & Cohen, L. G. (1997). Depression of motor cortex excitability by low-frequency transcranial magnetic stimulation. *Neurology, 48*, 1398-1403.

Cleeremans, A. (2008). Consciousness: The radical plasticity thesis. In R. Banerjee & B. K. Chakrabarti (Eds.), *Progress in Brain Science,* Amsterdam: Elsevier, pp. 19-33.

Cleeremans, A., & Jiménez, L. (2002). Implicit learning and consciousness: A graded, dynamic perspective. In R. M. French & A. Cleeremans (Eds.), *Implicit Learning and Consciousness*, Hove, UK: Psychology Press, pp. 1-40.

Cock, J. J., Berry, D. C., & Buchner, A. (2002). Negative priming and sequence learning. *European Journal of Cognitive Psychology, 14*, 24-48.

Cowan, N. (2000). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral Brain Science, 24*, 87-114.

D'Angelo, M. C., Milliken, B., Jiménez, L., & Lupiáñez, J. (2013). Implementing flexibility in automaticity: Evidence from context-specific implicit sequence learning. *Conscious and Cognition, 22*, 64-81.

Dassonville, P., Lewis, S. M., Zhu, X. H., Ugurbil, K., Kim, S. G., & Ashe, J. (2001). The effect of stimulus–response compatibility on cortical motor activation. *NeuroImage, 13*, 1-14.

Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron, 72*, 443-454.

De Kleine, E., & Van der Lubbe, R. H. J. (2011). Decreased load on general motor preparation and visual-working memory while preparing familiar as compared to unfamiliar movement sequences. *Brain and Cognition, 75*, 126-134.

De Kleine, E., & Verwey, W. B. (2009a). Representations underlying skill in the discrete sequence production task: Effect of hand-based and hand position. *Psychological Research, 73*, 685-694.

De Kleine, E., & Verwey, W. B. (2009b). Motor learning and chunking in dyslexia. *Journal of Motor Behavior, 41*, 331-337.

Deroost, N., Zeischka, P., Coomans, D., Bouazza, S., Depessemier, P., & Soetens, E. (2010). Intact first- and second-order implicit sequence learning in secondary-school-aged children with developmental dyslexia. *Journal of Clinical and Experimental Neuropsychology, 32*, 561-572.

Deroost, N., Zeischka, P., & Soetens, E. (2008). Negative priming in the SRT task: Learning of irrelevant sequences is enhanced by concurrent learning of relevant sequences. *European Journal of Cognitive Psychology, 20*, 47-68.

Destrebecqz, A., & Cleeremans, A. (2001). Can sequence learning be implicit? New evidence with the Process Dissociation Procedure. *Psychonomic Bulletin and Review, 8*, 343-350.

Dienes, Z., & Scott, R. (2005). Measuring unconscious knowledge: distinguishing structural knowledge and judgment knowledge. *Psychological Research, 69*, 338-351.

Dorfberger, S., Adi-Japha, E., & Karni, A. (2007). Reduced susceptibility to interference in the consolidation of motor memory before adolescence. *PLoS ONE, 2*, e240. doi:10.1371/journal.pone.0000240

Dorfberger, S., Adi-Japha, E., & Karni, A. (2012). Sequence specific motor performance gains after memory consolidation in children and adolescents. *PLoS ONE, 7*, e28673. doi:10.1371/journal.pone.0028673

Doyon, J., & Benali, H. (2005). Reorganization and plasticity in the adult brain during learning of motor skills. *Current Opinion in Neurobiology, 15*, 161-167.

Eich, J. E. (1980). The cue-dependent nature of state-dependent retrieval. *Memory and Cognition, 8*, 157-173.

Eysenck, H. J., & Frith, C. D. (1977). *Reminiscence, motivation, and personality. A case study in experimental psychology*. New York: Plenum.

Fitts, P. M., & Posner, M. I. (1967). *Learning and skilled performance in human performance*. Belmont, CA: Brock-Cole.

Fox, E. (1995). Negative priming from ignored distractors in visual selection: A review. *Psychonomic Bulletin & Review, 2*, 145-173.

Fry, A. F., & Hale, S. (1996). Processing speed, working memory, and fluid intelligence: Evidence for a developmental cascade. *Psychological Science, 7*, 237-241.

Gabbard, C., Caçola, P., & Bobbio, T. (2011). Examining age-related movement representations for sequential (fine-motor) finger movements. *Brain and Cognition, 77*, 459-463.

Gallistel, C. R. (1980). *The organization of action: a new synthesis*. Hillsdale, NJ: Erlbaum.

Gerloff, C., Corwell, B., Chen, R., Hallett, M., & Chen, L. G. (1997). Stimulation over the human supplementary motor area interferes with the organization of future elements in complex motor sequences. *Brain, 120*, 1587-1602.

Girelli, L., Lucangeli, D., & Butterworth, B. (2000). The development of automaticity in accessing number magnitude. *Journal of Experimental Child Psychology, 76*, 104-122.

Godden, D. R., & Baddeley, A. D. (1975). Context-dependent memory in two natural environments: On land and underwater. *British Journal of Psychology, 66*, 325-331.

Goschke, T., & Bolte, A. (2012). On the modularity of implicit sequence learning: Independent acquisition of spatial, symbolic, and manual sequences. *Cognitive Psychology, 65*, 284-320.

Gottsdanker, R., Perkins, T., & Aftab, J. (1986). Studying reaction time with nonaging intervals: An effective procedure. *Behavior Research Methods, Instruments, & Computers, 18*, 287-292.

Grafton, S. T., Hazeltine, E., & Ivry, R. B. (1998). Abstract and effector-specific representations of motor sequences identified with PET. *The Journal of Neuroscience, 18*, 9420-9428.

Grafton, S. T., Hazeltine, E., & Ivry, R. B. (2002). Motor sequence learning with the non-dominant left hand. A PET functional imaging study. *Experimental Brain Research, 146*, 369-378.

Gu, Y., Zang, Y., Weng, X., Jia, F., Li, E., & Wang, J. (2003). Involvement of secondary motor areas in externally-triggered single-finger movements of dominant and non-dominant hands. *Chinese Science Bulletin, 48*, 1569-1575.

Haaland, K. Y., Elsinger, C. L., Mayer, A. R., Durgerian, S., & Rao, S.M. (2004). Motor sequence complexity and performing hand produce differential patterns of hemispheric lateralization. *Journal of Cognitive Neuroscience, 16*, 621-636.

Haider, H., & Frensch, P. A. (2005). The generation of conscious awareness in an incidental learning situation. *Psychological Research, 69*, 399-411.

Halsband, U., & Lange, R. K. (2006). Motor learning in man: A review of functional and clinical studies. *Journal of Physiology (Paris), 99*, 414-424.

Halsband, U., Matsuzaka, Y., & Tanji, J. (1994). Neuronal activity in the primate supplementary, pre-supplementary and premotor cortex during externally and internally instructed sequential movements. *Neuroscience Research, 20*, 149-155.

Hayes, A. E., Davidson, M. C., Keele, S. W., & Rafal, R. D. (1998). Toward a functional analysis of the basal ganglia. *Journal of Cognitive Neuroscience, 10*, 178-198.

He, S. Q., Dum, R. P., & Strick, P. L. (1995). Topographic organization of corticospinal projections from the frontal lobe: Motor areas on the medial surface of the hemisphere. *Journal of Neuroscience, 15*, 3284-3306.

Healy, A. F., Wohldmann, E. L., Parker, J. T., & Bourne, L. E., Jr. (2005). Skill training, retention, and transfer: The effects of a concurrent secondary task. *Memory & Cognition, 33*, 1457-1470.

Hikosaka, O., Nakahara, H., Rand, M. K., Sakai, K., Lu, X. F., Nakamura, K., et al. (1999). Parallel neural networks for learning sequential procedures. *Trends in Neurosciences, 22*, 464-471.

Hikosaka, O., Nakamura, K., Sakai, K., & Nakahara, H. (2002). Central mechanisms of motor skill learning. *Current Opinion in Neurobiology, 12*, 217-222.

Hommel, B. (2000). The prepared reflex: Automaticity and control in stimulus-response translation. In S. Monsell & J. Driver (Eds.), *Control of Cognitive Processes: Attention and Performance XVIII*, Cambridge, MA: MIT Press, pp. 247-273.

Hommel, B. (2004). Event files: feature binding in and across perception and action. *Trends in Cognitive Sciences, 8*, 494-500.

Hommel, B. (2007). Feature integration across perception and action: event files affect response choice. *Psychological Research, 71*, 42-63.

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences, 24*, 849-937.

Hulstijn, W., & Van Galen, G. P. (1983). Programming in handwriting: Reaction time and movement time as a function of sequence length. *Acta Psychologica, 54*, 23-49.

Iacoboni, M., Woods, R. P., & Mazziotta, J. C. (1996). Brain-behavior relationships: Evidence from practice effects in spatial stimulus–response compatibility. *Journal of Neurophysiology, 76*, 321-331.

Jankowski, J., Scheef, L., Hüppe, C., & Boecker, H. (2009). Distinct striatal regions for planning and executing novel and automated movement sequences. *Neuroimage, 44*, 369-1379.

Jenkins, I. H., Brooks, D. J., Nixon, P. D., Frackowiak, R. S., & Passingham, R. E. (1994). Motor sequence learning: a study with positron emission tomography. *Journal of Neuroscience, 14*, 3775-3790.

Jenkins, I. H., Jahanshahi, M., Jueptner, M., Passingham, R. E., & Brooks, D. J. (2000). Self-initiated versus externally triggered movements. II. The effect of movement predictability on regional cerebral blood flow. *Brain, 123*, 1216-1228.

Jiang, Y., & Kanwisher, N. (2003). Common neural substrates for response selection across modalities and mapping paradigms. *Journal of Cognitive Neuroscience, 15*, 1080-1094.

Jiménez, L., Méndez, A., Pasquali, A., Abrahamse, E. L., & Verwey, W. B. (2011). Chunking by colors: Assessing discrete learning in a continuous serial reaction-time task. *Acta Psychologica, 137*, 318-329.

Jueptner, M., Frith, C. D., Brooks, D. J., Frackowiak, R. S. J., & Passingham, R. E. (1997a). Anatomy of motor learning. II. Subcortical structures and learning by trial and error. *Journal of Neurophysiology, 77*, 1325-1337.

Jueptner, M., Stephan, K. M., Frith, C. D., Brooks, D. J., Frackowiak, R. S. J., & Passingham, R. E. (1997b). Anatomy of motor learning. I. Frontal cortex and attention to action. *Journal of Neurophysiology, 77*, 1313-1324.

Kail, R. (1991). Developmental change in speed of processing during childhood and adolescence. *Psychological Bulletin, 109*, 490-501.

Kail, R. (2000). Speed of information processing: developmental change and links to intelligence. *Journal of School Psychology, 38*, 51-61.

Karni, A., Meyer, G., Rey-Hipolito, C., Jezzard, P., Adams, M. M., Turner, R., & Ungerleider, L. G. (1998). The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. *Proceedings of the National Academy of Science USA, 95*, 861-868.

Keele, S. W., Ivry, R., Mayr, U., Hazeltine, E., & Heuer, H. (2003). The cognitive and neural architecture of sequence representation. *Psychological Review, 110*, 316-339.

Kennerley, S. W., Sakai, K., & Rushworth, M. F. S. (2004). Organization of action sequences and the role of the pre-SMA. *Journal of Neurophysiology, 91*, 978-993.

Klapp, S. T. (1995). Motor response programming during simple and choice-reaction time: the role of practice. *Journal of Experimental Psychology: Human Perception and Performance, 21*, 1015-1027.

Kornbrot, D. E. (1989). Organisation of keying skills: The effect of motor complexity and number of units. *Acta Psychologica, 70*, 19-41.

Kozak, J. J., Hancock, P. A., Arthur, E. J., & Chrysler, S. T. (1993). Transfer of training from virtual reality. *Ergonomics, 36*, 777-784.

Kuhtz-Buschbeck, J. P., Stolze, H., Jöhnk, K., Boczek-Funcke, A., & Illert, M. (1998). Development of prehension movements in children: a kinematic study. *Experimental Brain Research, 122*, 424-432.

Luciana, M., & Nelson, C. A. (1998). The functional emergence of prefrontally-guided working memory systems in four- to eight-year-old children. *Neuropsychologia, 36*, 273-293.

Luppino, G., Matelli, M., Camarda, R., & Rizzolatti, G. (1993). Corticocortical connections of area F3 (SMA-proper) and area F6 (pre-SMA) in the macaque monkey. *Journal of Comparative Neurology, 338*, 114-140.

MacKay, D. G. (1982). The problems of flexibility, fluency, and speed-accuracy trade-off in skilled behavior. *Psychological Review, 89*, 483-506.

Magnuson, C. E., Wright, D. L., & Verwey, W. B. (2004). Changes in the incidental context impacts search but not loading of the motor buffer. *Quarterly Journal of Experimental Psychology, 57A*, 935-951.

Mantovani, A., Simpson, H. B., Fallon, B. A., Rossi, S., & Lisanby, S. H. (2010). Randomized sham-controlled trial of repetitive transcranial magnetic stimulation in treatment-resistant obsessive-compulsive disorder. *The International Journal of Neuropsychopharmacology, 13*, 217-227.

Merriam, E. P., Colby, C. L., Thulborn, K. R., Luna, B., Olson, C. R., & Sweeney, J. A. (2001). Stimulus-response incompatibility activates cortex proximate to three eye fields. *Neuroimage, 13*, 794-800.

Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review, 63*, 81-97.

Miller, G. A., Galanter, E., & Pribram, K. H. (1960). *Plans and the Structure of Behavior*. New York: H. Holt & Co.

Miyachi, S., Hikosaka, O., & Lu, X. (2002). Differential activation of monkey striatal neurons in the early and late stages of procedural learning. *Experimental Brain Research, 146*, 122-126.

Miyachi, S., Hikosaka, O, Miyashita, K., Karadi, Z., & Rand, M. K. (1997). Differential roles of monkey striatum in learning of sequential hand movement. *Experimental Brain Research, 115*, 1-5.

Murase, N., Rothwell, J. C., Kaji, R., Urushihara, R. Nakamura, K., Murayama, K. et al.

(2005). Subthreshold low-frequency repetitive transcranial magnetic stimulation over the premotor cortex modulates writer's cramp. *Brain, 128*, 104-115.

Mushiake, H., Inase, M., & Tanji, J. (1991). Neuronal activity in the primate premotor, supplementary, and precentral motor cortex during visually guided and internally determined sequential movements. *Journal of Neurophysiology, 66*, 705-718.

Newell, A., & Rosenbloom, P. (1981). Mechanisms of skill acquisition and the law of practice. In J. A. Anderson (Ed.), *Cognitive Skills and their Acquisition*, Hillsdale, NJ: Erlbaum, pp. 1-55.

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology, 19*, 1-32.

Østby, Y., Tamnes, C. K., Fjell, A. M., Westlye, L. T., Due-Tønnessen, P., & Walhovd, K. B. (2009). Heterogeneity in subcortical brain development: A structural magnetic resonance imaging study of brain maturation from 8 to 30 years. *The Journal of Neuroscience, 29*, 11772-11782.

Paillard, J. (1960). Neurophysiology. In H. W. Magoun (Ed.), *Handbook of Physiology*, Washington, D.C.: American Physiological Society, pp. 1679-1708.

Pammi, V. S. C., Miyapuram, K. P., Samejima, K., Bapi, R. S., & Doya, K. (2012). Changing the structure of complex visuo-motor sequences selectively activates the fronto-parietal network. *Neuroimage, 59*, 1180-1189.

Park, J. H., & Shea, C. H. (2005). Sequence learning: response structure and effector transfer. *Quarterly Journal of Experimental Psychology, 58A*, 387-419.

Park, J.-H., Wilde, H., & Shea, C. H. (2004). Part-whole practice of movement sequences. *Journal of Motor Behavior, 36*, 51-61.

Penhune, V. B., & Steele, C. J. (2012). Parallel contributions of cerebellar, striatal and M1 mechanisms to motor sequence learning. *Behavioural Brain Research, 226*, 579-591.

Pew, R. W. (1966). Acquisition of hierarchical control over the temporal organization of a skill. *Journal of Experimental Psychology, 71*, 764-771.

Picard, N., & Strick, P. L. (1996). Medial wall motor areas: A review of their location and functional activation. *Cerebral Cortex, 6*, 342-353.

Picard, N., & Strick, P. L. (2001). Imaging the premotor areas. *Current Opinion in Neurobiology, 11*, 663-672.

Piek, J. P., Glencross, D. J., Barrett, N. C., & Love, G. L. (1993). The effect of temporal and force changes on the patterning of sequential movements. *Psychological Research, 55*, 116-123.

Pollard, R. (2008). Home advantage in football: A current review of an unsolved puzzle. *The Open Sports Sciences Journal, 1*, 12-14.

Povel, D. J., & Collard, R. F. (1982). Structural factors in patterned finger tapping. *Acta Psychologica, 52*, 107-123.

Raz, N., Lindenberger, U., Rodrigue, K. M., Kennedy, K. M., Head, D., Williamson, A., et al. (2005). Regional brain changes in aging healthy adults: General trends, individual differences, and modifiers. *Cerebral Cortex, 15*, 1676-1689.

Resnick, S. M., Pham, D. L., Kraut, M. A., Zonderman, A. B., & Davatzikos, C. (2003). Longitudinal magnetic resonance imaging studies of older adults: a shrinking brain. *Journal of Neuroscience, 23*, 3295-3301.

Rhodes, B. J., Bullock, D., Verwey, W. B., Averbeck, B. B., & Page, M. P. A. (2004). Learning and production of movement sequences: Behavioral, neurophysiological, and modeling perspectives. *Human Movement Science, 23*, 699-746.

Rosenbaum, D. A., Hindroff, V., & Munro, E. M. (1987). Scheduling and programming of rapid finger sequences: Tests and elaborations of the hierarchical editor model. *Journal of Experimental Psychology: Human Perception and Performance, 13*, 193-203.

Rosenbaum, D. A., Kenny, S. B., & Derr, M. A. (1983). Hierarchical control of rapid movement sequences. *Journal of Experimental Psychology: Human Perception and Performance, 9*, 86-102.

Rossi, S., Hallet, M., Rossini, P. M., Pascual-Leone, A., & the safety of TMS consensus group. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology, 120*, 2008-2039.

Rossi, S., & Rossini, P. M. (2004). TMS in cognitive plasticity and the potential for rehabilitation. *TRENDS in Cognitive Sciences, 8*, 273-279.

Ruitenberg, M. F. L., Abrahamse, E. L., De Kleine, E., & Verwey, W. B. (2012a). Context-dependent motor skill: Perceptual processing in memory-based sequence production. *Experimental Brain Research, 222*, 31-40.

Ruitenberg, M. F. L., De Kleine, E., Van der Lubbe, R. H. J., Verwey, W. B., & Abrahamse,

E. L. (2012b). Context-dependent motor skill and the role of practice. *Psychological Research, 76*, 812-820.

Rünger, D., & Frensch, P. A. (2010). Defining consciousness in the context of incidental sequence learning: Theoretical considerations and empirical implications. *Psychological Research, 74*, 121-137.

Sakai, K., Kitagucki, K., & Hikosaka, O. (2003). Chunking during human visuomotor sequence learning. *Experimental Brain Research, 152*, 229-242.

Saling, L. L., & Phillips, J. G. (2007). Automatic behaviour: Efficient not mindless. *Brain Research Bulletin, 73*, 1-20.

Savion-Lemieux, T., Bailey, J. A., & Penhune, V. B. (2009). Developmental contributions to motor sequence learning. *Experimental Brain Research, 195*, 293-306.

Schluter, N. D., Rushworth, M. F. S., Passingham, R. E., & Mills, K. R. (1998). Temporary interference in human lateral premotor cortex suggests dominance for the selection of movements. A study using transcranial magnetic stimulation. *Brain, 121*, 785-799.

Schumacher, E. H., Cole, M. W., & D'Esposito, M. (2007). Selection and maintenance of stimulus-response rules during preparation and performance of a spatial choice reaction task. *Brain Research, 1136*, 77-87.

Schumacher, E. H., & D'Esposito, M. (2002). Neural implementation of response selection in humans as revealed by localized effects of stimulus-response compatibility on brain activation. *Human Brain Mapping, 17*, 193-201.

Schumacher, E. H., Elston, P. A., & D'Esposito, M. (2003). Neural evidence for representation-specific response selection. *Journal of Cognitive Neuroscience, 15*, 1111-1121.

Schumacher, E. H., Hendricks M. J., & D'Esposito, M. (2005). Sustained involvement of a frontal-parietal network for spatial response selection with practice of a spatial choice-reaction task. *Neuropsychologia, 43*, 1444-1455.

Schutter, D. J. L. G., & van Honk, J. (2006). A standardized motor threshold estimation procedure for transcranial magnetic stimulation research. *Journal of ECT, 22*, 176-178.

Schvaneveldt, R. W., & Gomez, R. L. (1998). Attention and probabilistic sequence learning. *Psychological Research, 61*, 175-190.

Seger, C. A. (2006). The basal ganglia in human learning. *Neuroscientist, 12*, 285-290.

Seger, C. A. (2008). How do the basal ganglia contribute to categorization? Their roles in generalization, response selection, and learning via feedback. *Neuroscience and Biobehavioral Reviews, 32*, 265-278.

Semjen, A., & Gottsdanker, R. (1990). Rapid serial movements: Relation between the planning of sequential structure and effector selection. In M. Jeannerod (Ed.), *Attention and Performance XIII*, Hillsdale, NJ: Lawrence Erlbaum, pp. 409-427.

Shea, C. H., & Wright, D. L. (1995). Contextual dependencies: Influence on response latency. *Memory, 3*, 81-95.

Smith, S. M. (1985). Background music and context-dependent memory. *The American Journal of Psychology, 98*, 591-603.

Smith, S. M., & Vela, E. (2001). Environmental context-dependent memory: A review and meta-analysis. *Psychonomic Bulletin and Review, 8*, 203-220.

Smits-Engelsman, B. C. M., Sugden, D., & Duysens, J. (2006). Developmental trends in speed accuracy trade-off in 6 to 10-year-old children performing rapid reciprocal and discrete aiming movements. *Human Movement Science, 25*, 37-49.

Sowell, E. R., Delis, D., Stiles, J., & Jernigan, T. L. (2001). Improved memory functioning and frontal lobe maturation between childhood and adolescence: A structural MRI study. *Journal of the International Neuropsychological Society, 7*, 312-322.

Sowell, E. R., Trauner, D. A., Gamst, A., & Jernigan, T. L. (2002). Development of cortical and subcortical brain structures in childhood and adolescence: a structural MRI study. *Developmental Medicine & Child Neurology, 44*, 4-16.

Spironelli, C., & Angrilli, A. (2009). Developmental aspects of automatic word processing: Language lateralization of early ERP components in children, young adults and middle-aged subjects. *Biological Psychology, 80*, 35-45.

Sternberg, S., Knoll, R. L., Monsell, S., & Wright, C. E. (1988). Motor programs and hierarchical organization in the control of rapid speech. *Phonetica, 45*, 175-197.

Sternberg, S., Monsell, S., Knoll, R. L., & Wright, C. E. (1978). The latency and duration of rapid movement sequences: Comparisons of speech and typewriting. In G. E. Stelmach (Ed.), *Information Processing in Motor Control and Learning*, Academic Press: New York, pp. 117-152.

Stocco, A., Lebiere, C., & Anderson, J. R. (2010). Conditional routing of information to the cortex: A model of the basal ganglia's role in cognitive coordination. *Psychological*

Review, 117, 541-574.

Thomas, K. M., Hunt, R., Vizueta, N., Sommer, T., Durston, S., Yang, Y., & Worden, M. S. (2004). Evidence of developmental differences in implicit sequence learning: an fMRI study in children and adults. *Journal of Cognitive Neuroscience, 16*, 1339-1351.

Thomas, K. M., & Nelson, C. A. (2001). Serial reaction time learning in preschool- and school-age children. *Journal of Experimental Child Psychology, 79*, 364-387.

Toni, I., Krams, M., Turner, R., & Passingham, R. E. (1998). The time course of changes during motor sequence learning: a whole-brain fMRI study. *Neuroimage, 8*, 50-61.

Tremblay, P.-L., Bedard, M.-A., Langlois, D., Blanche, P. J., Lemay, M., & Parent, M. (2002). Movement chunking during sequence learning is a dopamine-dependant process: a study conducted in Parkinson's disease. *Experimental Brain Research, 205*, 375-385.

Tubau, E., Hommel, B., & López-Moliner, J. (2007). Modes of executive control in sequence learning: From stimulus-based to plan-based control. *Journal of Experimental Psychology: General, 136*, 43-63.

Tulving, E., & Thompson, D. M. (1973). Encoding specificity and retrieval processes in episodic memory. *Psychological Review, 80*, 352-373.

Tzelgov, J. (1997). Specifying the relations between automaticity and conscious: A theoretical note. *Consciousness & Cognition, 6*, 441-451.

Ungerleider, L. G., Doyon, J., & Karni, A. (2002). Imaging brain plasticity during motor skill learning. *Neurobiology of Learning and Memory, 78*, 553-564.

Verhaeghen, P., & Salthouse, T. A. (1997). Meta-analyses of age-cognition relations in adulthood: Estimates of linear and nonlinear age effects and structural models. *Psychological Bulletin, 122*, 231-249.

Verwey, W. B. (1995). A forthcoming key press can be selected while earlier ones are executed. *Journal of Motor Behavior, 27*, 275-284.

Verwey, W. B. (1996). Buffer loading and chunking in sequential keypressing. *Journal of Experimental Psychology: Human Perception and Performance, 22*, 544-562.

Verwey, W. B. (1999). Evidence for a multi-stage model of practice in a sequential movement task. *Journal of Experimental Psychology: Human Perception and Performance, 25*, 1693-1708.

Verwey, W. B. (2001). Concatenating familiar movement sequences: The versatile cognitive processor. *Acta Psychologica, 106*, 69-95.

Verwey, W. B. (2003a). Effect of sequence length on executing familiar keying sequences: Lasting segmentation and preparation? *Journal of Motor Behavior, 35*, 343-354.

Verwey, W. B. (2003b). Processing modes and parallel processors in producing familiar keying sequences. *Psychological Research, 67*, 106-122.

Verwey, W. B. (2010). Diminished motor skill development in elderly: Indications for limited motor chunk use. *Acta Psychologica, 134*, 206-214.

Verwey, W. B., & Abrahamse, E. L. (2012). Distinct modes of executing movement sequences: Reacting, associating, and chunking. *Acta Psychologica, 140*, 274-282.

Verwey, W. B., Abrahamse, E. L., & De Kleine, E. (2010). Cognitive processing in new and practiced discrete keying sequences. *Frontiers in Psychology, 1*, 1-13.

Verwey, W. B., Abrahamse, E. L., De Kleine, E., & Ruitenberg, M. F. L. (2013). Evidence for graded central processing resources in a sequential movement task. *Psychological Research, doi 10.1007/s00426-013-0484-x.*

Verwey, W. B., Abrahamse, E. L., & Jiménez, L. (2009). Segmentation of relatively short keying sequences does not transfer to other sequences. *Human Movement Science, 28*, 348-361.

Verwey, W. B., Abrahamse, E. L., Ruitenberg, M. F. L., Jiménez, L., & De Kleine, E. (2011). Motor skill learning in the middle-aged: limited development of motor chunks and explicit sequence knowledge. *Psychological Research, 75*, 406-422.

Verwey, W. B., & Eikelboom, T. (2003). Evidence for lasting sequence segmentation in the discrete sequence-production task. *Journal of Motor Behavior, 35*, 171-181.

Verwey, W. B., Lammens, R., & Van Honk, J. (2002). On the role of the SMA in the discrete sequence production task: A TMS study. *Neuropsychologia, 40*, 1268-1276.

Wang, Y., Isoda, M., Matsuzaka, Y., Shima, K., & Tanji, J. (2005). Prefrontal cortical cells projecting to the supplementary eye field and presupplementary motor area in the monkey. *Neuroscience Research, 53*, 1-7.

Wassermann, E. M., Grafman, J., Berry, C., Hollnagel, C., Wild, K., Clark, K., & Hallett, M. (1996). Use and safety of a new repetitive transcranial magnetic stimulator. *Electroencephalography and Clinical Neurophysiology, 101*, 412-417.

Weiermann, B., & Meier, B. (2012). Incidental sequence learning across the lifespan. *Cognition, 123*, 380-391.

Whitall, J. (1991). The developmental effect of concurrent cognitive and locomotor skills: Time-sharing from a dynamical perspective. *Journal of Experimental Child Psychology, 51*, 245-266.

Williams, Z. M., & Eskandar, E. N. (2006). Selective enhancement of associative learning by microstimulation of the anterior caudate. *Nature Neuroscience, 9*, 562-568.

Wright, D. L., & Shea, C. H. (1991). Contextual dependencies in motor skills. *Memory & Cognition, 19*, 361-370.

Wright, D. L., Shea, C. H., Li, Y., & Whitacre, C. (1996). Contextual dependencies during perceptual-motor skill acquisition: gone but not forgotten! *Memory, 4*, 91-108.

Wymbs, N. F., Bassett, D. S., Mucha, P. J., Porter, M. A., & Grafton, S. T. (2012). Differential recruitment of the sensorimotor putamen and frontoparietal cortex during motor chunking in humans. *Neuron, 74*, 936-946.

Wymbs, N. F., & Grafton, S. T. (2013). Contributions from the left PMd and the SMA during sequence retrieval as determined by depth of training. *Experimental Brain Research, 224*, 49-58.

Samenvatting

Het aanleren en uitvoeren van verschillende series van handelingen is een fundamenteel aspect van menselijk gedrag, aangezien de complexe acties die we in het dagelijks leven verrichten over het algemeen bestaan uit series van simpelere bewegingen: dit noemen we bewegingssequenties. Om de cognitieve mechanismen die betrokken zijn bij de productie van dergelijke sequentiële vaardigheden te onderzoeken, is in de studies in dit proefschrift gebruik gemaakt van de *discrete sequence production* (DSP) taak. In deze taak reageren proefpersonen door middel van het aanslaan van toetsen op stimuli die in een vaste volgorde worden gepresenteerd. Op deze manier leren ze korte, discrete series van toetsaanslagen uit te voeren. De DSP taak is zeer geschikt voor het bestuderen van cognitieve controle gedurende de uitvoer van bewegingssequenties omdat de relatief simpele toetsaanslagen niet veel motorische controle vergen, waardoor op basis van reactietijden (RTs) uitspraken gedaan kunnen worden over de cognitieve processen. Bovendien zijn de motor chunks die zich ontwikkelen met meer oefening representatief voor de bouwstenen van onze alledaagse acties. Dit proefschrift richt zich op de cognitieve, perceptuele en neurale basis van motorische vaardigheden. Hieronder zullen eerst de bevindingen over de rol van waarneming (‘perceptie’) uit hoofdstukken 2-4 besproken worden. Op basis van de empirische studies die in dit proefschrift zijn opgenomen zal dan toegewerkt worden naar een algemene cognitieve architectuur voor het uitvoeren van motorische vaardigheden. Er wordt besproken hoe factoren zoals leeftijd invloed kunnen hebben op de mate waarin een bewegingssequentie automatisch uitgevoerd kan worden.

Hoewel bewegingssequenties duidelijk motorisch van aard zijn, is tijdens het leren en uitvoeren van zulke handelingen ook een rol weggelegd voor perceptie. Dit blijkt uit het concept van context-afhankelijk leren, waarbij het uitvoeren van een bepaalde vaardigheid beter verloopt naarmate de omgeving (‘context’) waarin dit gebeurt meer lijkt op de omgeving waarin de vaardigheid aangeleerd werd. In hoofdstuk 2 hebben we een nieuwe vorm van context-afhankelijkheid onderzocht, waarbij bestudeerd is of mensen kunnen leren irrelevante perceptuele informatie te negeren om daardoor zo goed mogelijk te presteren bij het uitvoeren van een motorische sequentie. Proefpersonen leerden een serie toetsaanslagen uit te voeren door te reageren op relevante visueel-spatiële stimuli, terwijl ze irrelevante visueel-spatiële stimuli (dat wil zeggen, de context) moesten negeren. De relevante en irrelevante stimuli werden tijdens het oefenen steeds in paren aangeboden. De resultaten lieten zien dat het veranderen van de locaties van de contextuele stimuli—maar niet het verwijderen van dergelijke stimuli—een negatief effect had op de prestatie. Wij duiden dit aan als context-afhankelijk filteren en denken dat het veranderen van irrelevante informatie, die mensen hebben geleerd te negeren, de prestatie verslechtert omdat de ontwikkelde filter niet langer bruikbaar is. Dit effect werd alleen gevonden na relatief weinig oefening, maar niet na uitgebreide oefening. We veronderstellen dat dit komt doordat het uitvoeren van bewegingssequenties tijdens het oefenen geleidelijk verschuift van stimulus-gedreven naar representatie-gedreven dankzij de ontwikkeling van *motor chunks* (verderop wordt hier verder op ingegaan).

In de hoofdstukken 3 en 4 hebben we onderzocht of het uitvoeren van bewegingssequenties vanuit het geheugen ook gevoelig zou zijn voor contextuele veranderingen. We hebben hier de meer klassieke vorm van context-afhankelijkheid bestudeerd, namelijk context-afhankelijk herinneren, waarvan wordt aangenomen dat het te maken heeft met het ontstaan van associaties tussen de taak (hier: sequentie) en contextuele kenmerken, waardoor deze worden geïntegreerd in de taak-representatie (e.g., Healy et al., 2005; Wright & Shea, 1991). De resultaten van hoofdstuk 3 en 4 tonen aan dat het uitvoeren van een bewegingssequentie kan worden beïnvloed door perceptuele veranderingen, zelfs wanneer de sequenties worden uitgevoerd vanuit het geheugen en dus in afwezigheid van daadwerkelijke perceptuele input. De bevinding in hoofdstuk 4, dat het voorbereiden—maar niet daadwerkelijk uitvoeren—van zeer goed geoefende *motor chunks* werd beïnvloed door contextuele veranderingen, lijkt bovendien aan te duiden dat perceptie met name invloed heeft op hogere cognitieve processen. Dit sluit aan bij het idee van het DPM dat bewerkingen door de cognitieve processor, maar niet de motor processor, gevoelig zouden zijn voor perceptuele veranderingen aangezien de cognitieve processor betrokken is bij het verwerken van externe stimulus informatie. Het kan worden aangenomen dat de associaties tussen de taak en de context versterken naarmate er meer geoefend is, zodat de representatie vollediger wordt. Dit zou kunnen verklaren waarom in hoofdstuk 4 werd gevonden dat context-afhankelijk herinneren toeneemt naarmate er meer oefening heeft plaatsgevonden.

Gezamenlijk tonen de resultaten van hoofdstukken 2-4 aan dat discrete bewegingssequenties niet alleen cognitieve en motorische processen omvatten, maar ook waarnemingsprocessen—zelfs wanneer sequenties worden uitgevoerd uit het geheugen in afwezigheid van perceptuele informatie. Veranderingen in de perceptuele informatie lijken voornamelijk van invloed te zijn op hogere cognitieve processen. Op een praktisch niveau kunnen de bevindingen over perceptuele verwerking en met name context-afhankelijke vaardigheden belangrijke gevolgen hebben voor het ontwerpen van trainingsprogramma's (zie ook Abrahamse & Noordzij, 2011). De huidige resultaten wijzen erop dat rekening moet worden gehouden met zowel de mate van training als ook de aard van de perceptuele context—dat wil zeggen, binnen de relevante stimulus-dimensie (hoofdstuk 2) versus binnen de relevante stimulus zelf (hoofdstuk 3 en 4)—om een optimale overdracht van de geleerde vaardigheden naar nieuwe contexten te bereiken (bijvoorbeeld van een simulator naar de echte wereld).

Zoals beschreven in het inleidende hoofdstuk van dit proefschrift beschrijft het zogeheten *dual processor model* (DPM) de cognitieve en motorische processen die betrokken zijn bij de productie van bewegingssequenties. Daarnaast zijn drie modi voor het uitvoeren van een sequentie geïntroduceerd: de reactieve, chunking en associatieve modus. Hier zullen we proberen om de taken van de cognitieve en motorische processoren van het DPM te integreren met het uitvoeren van een sequentie in elk van deze modi. De reactieve en chunking modi kunnen gemakkelijk worden verklaard door het DPM (zie hieronder). De theoretische uitdagingen betreffen het implementeren van de associatieve modus, vooral met betrekking tot het representatieve niveau. Het is algemeen aanvaard dat sequentiële informatie gerepresenteerd kan worden op perceptuele, cognitieve en response-gebaseerde /motorische niveaus (e.g., Abrahamse et al., 2010; Goschke & Bolte, 2012; Hikosaka et al., 1999; Keele et al., 2003). De chunking modus zal vooral associaties op het motorisch niveau bevatten, van waaruit de *motor chunks* kunnen ontwikkelen. Omgekeerd zou de associatieve modus gekoppeld kunnen worden aan verschillende vormen van visueel-spatiële associaties—in overeenstemming met de SRT literatuur (Abrahamse et al., 2010). Echter, het kan niet worden uitgesloten dat de associatieve modus rechtstreeks voortvloeit uit de dezelfde associaties die aan de chunking modus ten grondslag liggen: mogelijk zouden *motor chunks* continu de lopende processen kunnen beïnvloeden (Cleeremans, 2008). Zij zouden bijvoorbeeld de selectie van individuele responses kunnen faciliteren. Om aan te sluiten bij het concept van gedistribueerde codering (cf. Abrahamse et al., 2010; Hikosaka et al., 1999) gaan we uit van een sequentie representatie die berust op individuele gebeurtenissen—waarbij gebeurtenis verwijst naar een specifieke S-R omzetting—die mogelijk associaties bevatten op zowel het visueel-spatiële (bijvoorbeeld tussen opeenvolgende stimuli of respons-locaties) als het motorische niveau. De precieze kenmerken zullen waarschijnlijk afhangen van de taakeisen, de context, en de hoeveelheid oefening.

Figuur 7.1 (zie hoofdstuk 7, “Summary and conclusions”) toont een eenvoudige cognitieve architectuur voor de productie van bewegingssequenties. Het illustreert hoe op basis van stimulus input (S_n), een respons (R_n) wordt gegenereerd door de onderlinge afstemming van de cognitieve processor en de motor processor. Deze processoren kunnen gebruik maken van een motor buffer die tijdelijk representaties kan vasthouden die betrekking hebben op een beperkt aantal reacties. In de reactieve modus, die dominant is bij onbekende of willekeurige series, verwerkt de cognitieve processor zintuiglijke input en selecteert deze de juiste respons voor elke afzonderlijke stimulus. Vervolgens voert de motor processor de daadwerkelijke respons uit. Dankzij de herhaalde uitvoering van dezelfde reeks gebeurtenissen ontstaan associaties tussen deze achtereenvolgende gebeurtenissen. De resulterende representatie zorgt ervoor dat response selectieprocessen gefaciliteerd worden wanneer zij in een bekende volgorde worden uitgevoerd op basis van voorafgaande gebeurtenissen (associatieve modus). Wanneer de representatie sterk genoeg is op het motorische niveau, kan een korte reeks van bewegingen (bijv. een *motor chunk*) bovendien tijdelijk geactiveerd worden zodat deze in één enkele stap in een motor buffer kan worden geladen. Vervolgens wordt de inhoud van deze motor buffer gelezen en uitgevoerd door de motor processor. Omdat de capaciteit van de motor buffer beperkt is, is het aantal gelijktijdig voorbereide en uitgevoerde reacties beperkt. Ten slotte veroorzaakt de onafhankelijkheid van de cognitieve processor en motor processor een race tussen verschillende respons-generatie processen, omdat de cognitieve processor de reacties op het cognitieve ('response selectie') niveau selecteert, en de motor processor de reacties vanuit de motor buffer leest, zodat de snelst mogelijke antwoorden worden gegenereerd. Als reactie-specifieke stimuli aanwezig zijn tijdens de uitvoering, kan de cognitieve processor zich bezighouden met directe S-R omzettingen. Bovendien wijzen de resultaten van hoofdstuk 3 van dit proefschrift erop dat, bij afwezigheid van dergelijke stimuli, de cognitieve processor ook de motor processor ondersteunt door het genereren van de sequentie-elementen uit het geheugen—dat wil zeggen, door te racen op basis van expliciete kennis.

De resultaten van hoofdstuk 5 duiden aan dat de relatieve bijdrage van de cognitieve en motorische processoren aan het uitvoeren van een sequentie anders is bij preadolescente kinderen dan bij jongvolwassenen. Onze bevindingen wijzen erop dat het uitvoeren van langere bewegingssequenties bij kinderen meer leunt op de werking van de cognitieve processor, terwijl het bij jongvolwassenen meer berust op de werking van de motor processor. Dit laat zien dat de onderliggende mechanismen van sequentiële vaardigheden veranderen met leeftijd. Dit idee wordt gesteund door bevindingen dat ouderen geen *motor chunks* gebruiken voor het uitvoeren van discrete sequenties van toetsaanslagen (Verwey, 2010; Verwey et al., 2011). Dit kan worden gerelateerd aan de leeftijdsgebonden veranderingen in hersengebieden die betrokken zijn bij sequentiële vaardigheden. Zo lijkt de prefrontale cortex bijvoorbeeld betrokken te zijn bij het opdelen van langere bewegingssequenties in meerdere kleine chunks (e.g., Pammi et al., 2012). Dit hersengebied is bij kinderen nog in ontwikkeling (Sowell et al., 2001; 2002), maar neemt af in functionaliteit naarmate mensen ouder worden (Raz et al., 2005; Resnick et al., 2003).

In hoofdstuk 6 hebben we getracht twee neurale structuren te relateren aan de functies die de cognitieve processor heeft tijdens het uitvoeren van sequenties in elk van de drie bovengenoemde modi. Er werd verondersteld dat de PMC voornamelijk betrokken zou zijn bij S-R gebaseerde uitvoering, zoals in de reactieve en associatieve modi. Daarnaast werd verondersteld dat de pre-SMA betrokken zou zijn bij uitvoering op basis van sequentie representaties (e.g., *motor chunks*) die door de cognitieve processor in de motor buffer worden geladen in chunking mode. We gebruikten 20 minuten rTMS stimulatie op lage frequentie (1 Hz) om de gevoeligheid van respectievelijk de PMC en pre-SMA tijdelijk te verminderen, waarna deelnemers discrete bewegingssequenties uitvoerden in elk van de drie uitvoeringsmodi. De resultaten waren in overeenstemming met het idee dat de pre-SMA betrokken is bij het initiëren—maar niet uitvoeren—van *motor chunks*, en duiden aan dat de pre-SMA verantwoordelijk zou kunnen zijn voor het activeren van relevante sequentie representaties uit het lange termijn geheugen (welke vervolgens worden uitgevoerd door de SMA en primaire motor cortex). We vonden ook een indirecte aanwijzing dat de PMC betrokken zou kunnen zijn bij de online S-R vertalingen die de cognitieve processor maakt tijdens het uitvoeren van sequenties in de chunking modus. Echter, de resultaten waren niet in overeenstemming met de betrokkenheid van de PMC in de reactieve en associatieve modi. Mogelijk wordt de uitvoering in deze modi meer prefrontaal gecontroleerd. Toekomstige studies zullen het neurale substraat van de cognitieve processor in deze modi nader moeten onderzoeken.

De bevindingen in dit proefschrift duiden aan dat automatismen in sequentiële motorische vaardigheden zich op verschillende niveaus kunnen ontwikkelen. Met betrekking tot perceptie kunnen mensen leren om irrelevante contextuele informatie te negeren om zo een optimale prestatie te bereiken. Daarnaast kunnen ze leren perceptuele kenmerken van een sequentie te associëren met de bewegingen binnen die sequentie, zodat de perceptuele informatie opgenomen wordt in de representatie. Op cognitief niveau vermindert de noodzaak tot het gebruiken van externe informatie naarmate er meer geoefend is, zodat het uitvoeren van de bewegingssequentie verschuift van zijnde stimulus-gedreven naar representatie-gedreven. Dit heeft te maken met de ontwikkeling van sequentie representaties in de vorm van *motor chunks*—deze kunnen voorafgaand aan het uitvoeren van de sequentie door de cognitieve processor in een motor buffer worden geladen. Op motorisch niveau kunnen de sequenties vervolgens zeer snel worden uitgevoerd, doordat de motor processor deze motor chunks op een automatische—dat wil zeggen autonome—manier uitvoert (i.e., zonder cognitieve inbreng wanneer eenmaal met de uitvoering is begonnen). Daarnaast zijn in verschillende studies aanwijzingen gevonden dat zelfs de overgang tussen *motor chunks* kan automatiseren, wanneer deze steeds in dezelfde volgorde worden uitgevoerd (Verwey et al., 2010; Verwey et al., 2013).

Samengevat hebben de studies in dit proefschrift zich gericht op de perceptuele, cognitieve en neurale mechanismen die ten grondslag liggen aan sequentiële motorische vaardigheden. De resultaten van hoofdstukken 2-4 zijn in overeenstemming met het idee dat perceptie en actie sterk met elkaar verbonden zijn. Meer specifiek gezegd is het zo dat een seriële handeling gehinderd kan worden wanneer de perceptuele informatie die aanwezig was tijdens het aanleren van die handeling veranderd wordt tijdens het uitvoeren ervan.

Dit gebeurt zelfs wanneer de sequentiële handeling vanuit het geheugen wordt uitgevoerd, en de daadwerkelijke perceptuele informatie dus afwezig is tijdens het uitvoeren. Voorts lijken de resultaten erop te duiden dat met name de cognitieve processor gevoelig is voor perceptuele veranderingen—meer gevoelig dan de motor processor. De relatieve bijdrage van de cognitieve en motor processen aan de productie van sequentiële bewegingen lijken afhankelijk van leeftijd te variëren (hoofdstuk 5 van dit proefschrift; Verwey, 2010; Verwey et al., 2011). In het algemeen kan worden geconcludeerd dat automatisme in sequentiële vaardigheden geobserveerd kan worden in zowel perceptuele, cognitieve als motorische processen. De resultaten van hoofdstuk 6 geven aan dat het neurale substraat dat betrokken is bij het uitvoeren van bewegingssequenties varieert tussen de drie uitvoer modi, en dat elke modus een andere bijdrage vergt van de cognitieve en motor processoren van het DPM.

DANKWOORD

Na vier jaar met veel plezier onderzoek te hebben gedaan markeert dit proefschrift het einde van mijn promotietraject. Natuurlijk zijn er veel mensen zonder wie dit proefschrift niet tot stand was gekomen, of zonder wie het er misschien wel was gekomen maar zonder wie het traject een stuk minder leuk zou zijn geweest. Deze mensen zou ik dan ook graag bedanken.

Allereerst wil ik mijn promotor Willem Verwey bedanken. Willem, bedankt dat je mij hebt aangenomen op dit project en ik dit promotieonderzoek heb mogen verrichten. Het is niet altijd een gemakkelijk project geweest vanwege exploratieve karakter ervan, maar uiteindelijk hebben we toch een aantal mooie studies gedraaid waaruit ook publicaties zijn voortgekomen. Ik vond het plezierig te weten dat jouw deur altijd open stond.

Uiteraard wil ik ook mijn co-promotor Elger Abrahamse bedanken. Een paar maanden nadat ik met mijn promotieonderzoek was begonnen werd mij gemeld dat ik bij jou op de kamer zou komen te zitten. Je bleek een hele gezellige kamergenoot te zijn, ik kon veel vragen aan je stellen en soms zelfs een vraag van jouw kant beantwoorden (al had je vaak zelf al een antwoord gevonden voordat je de vraag afgemaakt had). Uiteindelijk raakte je steeds meer betrokken bij mijn onderzoek en het was dan ook een logische stap dat je mijn co-promotor zou worden. Je bent altijd heel enthousiast en betrokken geweest, en na elk van onze talloze mailwisselingen en telefoontjes had ik steeds het gevoel weer verder te kunnen met een paper. Ons bezoek aan San Sebastian en Bilbao voor het ESCOP congres was ook een erg leuke ervaring. Ik heb veel van je geleerd en hoop onze samenwerking te kunnen voortzetten.

Alle collega's van CPE wil ik bedanken voor de samenwerking. Een aantal collega's wil ik graag specifiek noemen. Rob, bedankt voor het mede-aanvragen van mijn project en je bijdrage aan het eerste paper dat uit mijn onderzoek voortkwam. Elian, dank voor het meedenken over experimenten en hulp bij het schrijven van papers. Ik vond het erg prettig om met je samen te werken. Daarnaast bedankt voor de gezelligheid, niet alleen de laatste paar maanden als kamergenoot maar zeker ook daarvoor. Teun en Jorian, de afgelopen vier jaar hebben we met zijn drieën zo'n beetje hetzelfde traject doorlopen. Het was leuk om ervaringen te kunnen uitwisselen, samen cursussen te volgen en natuurlijk de Grolsch Veste te bezoeken. Gedurende deze vier jaar heb ik bovendien bij ieder van jullie op een kamer gezeten, wat ik heel gezellig heb gevonden. We hebben regelmatig discussies en gesprekken gehad op wetenschappelijk niveau, maar misschien nog wel meer op een iets minder wetenschappelijk niveau. Bedankt daarvoor!

Naast goede begeleiding is voor mij goede afleiding ook heel belangrijk geweest. Ik ben blij dat ik dit al jaren kan vinden bij de Coornherters. We wonen nogal verspreid over het land (wat volgens mij momenteel vooral door mijn locatie komt…) maar we zien elkaar gelukkig een aantal keer per jaar. Ik vind het iedere keer weer super gezellig en wil jullie bedanken voor jullie continue interesse in mijn onderzoek en Twentse leven in het algemeen.

Binnen Enschede vormt de grootste bron van positieve afleiding de Drienerlose Hockeyclub, in het bijzonder Dames 1. De afgelopen vier jaar heb ik regelmatig moeten verdedigen dat promoveren toch heus wel een echte baan is en ik dus student-af ben. Dankzij jullie kon ik echter nog een beetje in het studentenleven blijven hangen en tijdens de vele gezellige Torenzondagen, borrels en andere spontaan ontstane feestjes op de Toren heb ik me altijd zeer goed vermaakt. De torentosti's, pizza's, vrijgezellen van de week, eindeloze roddels en overwinningsdrankjes zal ik me nog lang herinneren. Bedankt voor jullie interesse in mijn onderzoek en een aantal van jullie ook bedankt voor hun rol als proefpersoon. Eens…Drienerlo!

Ook alle andere vrienden en familie die steeds geïnteresseerd naar mijn onderzoek hebben gevraagd wil ik hiervoor bedanken.

Dan nog een woord van dank voor mijn paranimfen, Anna en Eric. An, hoewel we bij verschillende organisaties werkten hebben we toch veel overeenkomstige ervaringen gehad tijdens onze promoties. Het was leuk en soms ook verhelderend om te horen hoe het er bij jou aan toe ging en ik ben blij dat je mijn paranimf wilt zijn—volgende keer bij jou! Eer, ik heb je de afgelopen jaren niet zo vaak gezien als voorheen. Ondanks dat we een flink eind uit elkaar wonen wilde je toch altijd op de hoogte blijven van mijn onderzoek. Leuk dat je mijn verdediging nu van heel dichtbij kunt zien!

Lieve papa en mama, ik ben heel blij met jullie oneindige interesse, vertrouwen en enthousiasme—niet alleen met betrekking tot mijn onderzoek, maar ook alles daaromheen. Bedankt dat jullie altijd bereid zijn om mee te denken, een eerlijke mening te geven en zelfs mijn concept-proefschrift wilden lezen. Het resultaat is zeker mede aan jullie te danken!

Wouter, mijn allerleukste proefpersoon, je bent altijd positief geweest over mijn promotieonderzoek en hebt me steeds het vertrouwen gegeven dat ik dit kon. Ik ben blij dat we het zo leuk hebben samen en dat ik altijd bij je terecht kan. Heel erg bedankt hiervoor—ik hoop tijdens jouw promotietraject hetzelfde voor jou te kunnen doen!

CURRICULUM VITAE

Marit Ruitenberg werd geboren op 7 april 1985 in Boskoop. In 1997 ging zij naar het Coornhert Gymnasium te Gouda, waar zij in 2003 succesvol het eindexamen aflegde. Daarna begon zij aan de studie Psychologie aan de Universiteit Leiden. Zij rondde in 2006 haar bachelor opleiding af en behaalde daarna in 2007 cum laude haar master diploma in de Sociale en Organisatie Psychologie. Vervolgens volgde zij de master Cognitie, Media en Ergonomie aan de Universiteit Twente, welke zij in 2009 met goed gevolg afrondde. In datzelfde jaar startte Marit haar promotieonderzoek bij de afdeling Cognitieve Psychologie en Ergonomie van de faculteit Gedragswetenschappen aan de Universiteit Twente, begeleid door promotor prof. dr. ing. Willem Verwey en co-promotor dr. Elger Abrahamse. De resultaten van haar onderzoek zijn beschreven in dit proefschrift en in internationaal wetenschappelijke tijdschriften. Tevens zijn verschillende resultaten gepresenteerd op (inter)nationale congressen en symposia. Na haar promotie zal Marit haar werkzaamheden bij de vakgroep Cognitieve Psychologie en Ergonomie voortzetten.