MOTOR PREPARATION CHANGES WITH PRACTICE

by

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Abstract

The goal of this dissertation was to examine how the preparation of a movement changes as a result of practice, in order to gain a better understanding of the learning process. To investigate what aspects of a motor action can be prepared in advance, a startle methodology was used as the presentation of a startling stimulus is thought to cause the release of a pre-programmed response. Limits to pre-programming and changes to preparation as a result of learning were examined through practice of movements of varying complexities. Furthermore, movement preparation during physical practice, imagery and observational practice were examined. The use of startle methodology in a learning paradigm allowed for new information regarding the role of motor preparation processes in the learning of novel motor skills. Six experiments are detailed along with their contribution to the advancement of our understanding of what is learned and what is prepared.

The first four experiments examined the effects of physical practice on motor preparation and involved movements of varying spatial and temporal characteristics. These experiments provided support that practice results in more accurate pre-programming of motor commands, as well as information pertaining to differences in how spatially targeted and temporally defined movements are prepared. For timing based movements, we found evidence for the reliance on an internal timekeeper, of which the pacemaker pulse is affected by activation level. We also examined the effects of extended physical practice on single component and multiple component movements. In support of previous work, we found multiple element movements had a longer reaction time as compared to single element movements, although this difference was minimized with practice. However, because the startling stimulus triggered all movements at short latencies, we suggested that movement...
complexity may be more related to the neural commands necessary to produce the movement, rather than a sequencing requirement. The last two experiments examined preparation during motor imagery and observation. Limited support was found during imagery for motor preparation processes that mirror those of intended movements; however observational benefits appeared to be largely perceptual in nature.
Preface

I, Dana Maslovat, was primarily responsible for the research program, experimental design, manuscript and thesis preparation for all of the included experiments, with input and oversight by my Thesis Committee consisting of Dr. Ian M. Franks (Co-Supervisor), Dr. Nicola J. Hodges (Co-Supervisor) and Dr. Romeo Chua. I was also primarily responsible for all data collection, data analysis, and experimental set-up including programming, participant briefing, data reduction, and statistical analysis. Assistance with physical set-up of the hardware and technical support was provided by Paul Nagelkerke (all experiments) and Dr. Tony Carlsen (Experiment 1 and 2). Assistance with carrying out the experimental protocol and EMG marking was provided by Ryu Ishimoto (Experiment 1) and Chris Forgaard (Experiment 3 and 4). Assistance with fMRI analysis for Appendix B was provided by Dr. Olav Krigolson and Dr. Todd Handy.

Ethical approval was obtained for all the studies included in this dissertation. Listed below are the ethics boards and certificate numbers for the respective experiments:

UBC Behavioural Research Ethics Board - #H09-00632 (Experiments 1-5)

UBC Behavioural Research Ethics Board - #H08-01794 (Experiment 6)

UBC Clinical Research Ethics Board - #H07-00016 (Experiment 6, Appendix B)
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1. General Introduction
The learning of novel motor skills is fundamental to human existence, yet determining the actual process by which learning occurs has provided a considerable challenge. To overcome this challenge researchers often evaluate the production of a motor skill from an information processing perspective, as this can allow for isolation of the various stages of processing that are thought to occur. If we consider a situation where one of a number of possible movements is to be produced in response to the appearance of a “go” stimulus (known as a choice reaction time task), it is thought that a performer must identify the stimulus, select the appropriate response, and prepare the motor commands associated with the selected response (Donders, 1969). Alternately, if the learner knows in advance what movement is required (known as a simple reaction time task), response selection is not required thus simplifying the processing of information. Given that a simple reaction time (RT) task only involves stimulus identification and response programming, we assume that performance improvements are likely due to changes in the response preparation stage. However, complicating this assessment is that response preparation can occur before the “go” stimulus (known as pre-programming), during the RT interval (between the “go” and movement initiation), or once the movement has already begun (known as on-line programming). The purpose of this dissertation was to investigate motor preparation changes that occur during the skill acquisition process and in response to changes in task demands.

Motor Preparation

A number of different methodologies have been employed to examine motor preparation. One avenue has been to examine performance of movements in either a simple or choice RT paradigm to determine how movements are prepared when they are known or unknown in advance. In a seminal study, Henry and Rogers (1960) found an increase in
simple RT with increasing complexity of the required movement. The authors explained this finding via a “memory drum theory”, which suggested that more complex movements (in this case involving programming more action components) required retrieval of more elements from memory, thus increasing reaction time (see also Sternberg, Monsell, Knoll, & Wright, 1978). Expanding on the work by Henry and Rogers, Klapp (1995, 2003) performed a series of studies manipulating response complexity by increasing both the duration and number of response elements. In a simple RT situation, RT did not change for a single component movement of different durations but did increase when extra components of the movement were added. This led Klapp to hypothesize that for simple RT tasks, the internal features of the movement elements could be pre-programmed, while sequencing of movements could not. This was an important distinction as it suggested that not all response preparation needed to occur after the “go” signal and thus information processing was not always performed in the same serial order.

In an attempt to separately examine the preparation of the internal features of the movement and the sequencing of movement elements, a self-select paradigm has been employed (Immink & Wright, 2001; Magnuson, Robin, & Wright, 2008; Magnuson, Wright, & Verwey, 2004; Wright, Black, Immink, Brueckner, & Magnuson, 2004). In this case, the performer is allowed to study the stimulus cue identifying the movement to be performed for as long as deemed necessary to pre-program the response. This interval, known as study time, is thought to represent the time required for the preparation of the internal features of the movement(s). Following the study time interval, a “go” signal is presented, to which the performer reacts as rapidly as possible to perform the movement. This reaction time interval is thought to reflect the time required to sequence the movement. Consistent with Klapp’s
(1995, 2003) theoretical model, increasing movement duration has been shown to produce an increase in study time while increasing the number of movement elements has been shown to produce an increase in reaction time. These effects also confirmed that response preparation can occur in advance of the imperative stimulus.

Other lines of experimentation have also provided evidence that response preparation can occur before the “go” signal. One example of this is the use of a “precue” methodology, whereby participants are put into a choice RT paradigm but are given selected information as to what movement will be required. Using an 8-choice button press task that involved four targets for each of the left and right arm, two in both the forward and backward direction, Rosenbaum (1980) provided a precue that gave information about one or more of the three response dimensions (arm, direction or extent of movement). As more information was provided, RT decreased suggesting advance preparation occurred even when participants only had partial information as to the required response. Evidence for partial advance preparation has also been provided by the examination of brain activation pattern via electroencephalography (EEG) (see Leuthold, Sommer, & Ulrich, 2004 for a review). Two event-related brain potential measures that relate to response preparation are the contingent negative variation (CNV) and lateralized readiness potential (LRP). CNV is a sustained negativity that develops between the warning and “go” signal and is thought to reflect general motor preparation. Using a precueing paradigm, it has been shown that CNV amplitude increases with the number of precues, suggesting that more movement preparation can occur with more advance information (MacKay & Bonnet, 1990; Vidal, Bonnet, & Macar, 1995). LRP allows assessment of the relative activation of the two motor cortex hemispheres, with greater negativity developing contralateral to the required movement. The
development of LRP is thought to represent the preparation of a specific hand action. When the hand is precued in a choice RT task, the LRP onset occurs before the “go” signal, suggesting that response preparation is occurring even though the entire movement is not known (Osman, Moore, & Ulrich, 1995, 2003; Schroter & Leuthold, 2008).

Building on the evidence that a motor response can be partially or fully prepared in advance, more recent methodology has allowed the examination of response preparation through the use of a startling acoustic stimulus. During a simple RT task, replacing the auditory “go” signal with a loud (>124dB) startling stimulus has been shown to elicit the prepared movement at a much shorter latency, with kinematics and EMG configurations largely unchanged (see Carlsen, Maslovat, Lam, Chua, & Franks, in press; Valls-Solé, Kumru, & Kofler, 2008 for reviews). Due to dramatic shortening of premotor reaction times (<70 ms), it has been hypothesized that the startle can act as a trigger for a pre-programmed response, bypassing the usual voluntary processes (Valls-Solé, Rothwell, Goulart, Cossu, & Muñoz, 1999; Carlsen, Chua, Inglis, Sanderson, & Franks, 2004a). Thus the use of a startling stimulus can act as a probe for what is prepared in advance, as pre-programmed movements would be expected to be triggered (with similar movement characteristics) at a shorter latency when compared to control trials.

An advantage of using a startle methodology to examine motor preparation is that, given the short latency of the response, it is unlikely that any cortical processing has occurred in the reaction time interval. In this way the produced movement is likely to be reflective of the pre-programmed motor commands (although some studies have shown increased movement amplitude due to increased activation of the nervous system; e.g., Carlsen et al., 2004a). Startle methodology does not, however, allow for determination of the relative
amount of time required to prepare responses of varying complexities as these measurements are better left to simple, choice and self-select RT paradigms. Rather, the use of a startling stimulus provides a complement to these reaction time results and allows for an assessment as to if, when and how advance preparation occurs.

Motor Preparation and Practice

Although there has been much research examining response preparation processes, comparatively less work has focussed on how this preparation changes with practice. For single component movements that can be fully prepared in advance, improvements due to practice would likely be attributed to more accurate or consistent pre-programming of the motor commands. For example, rapid aiming movements have shown practice-related improvements in the accuracy of the primary movement, which is thought to be prepared in advance (Abrams & Pratt 1993; Pratt & Abrams 1996; Khan, Franks, & Goodman, 1998). For multiple component movements, however, the changes associated with practice are less clear. It has been suggested that with practice, multiple movement elements can somehow be concatenated such that they are eventually controlled by a single representation or motor “chunk” (Keele & Summers, 1976). Evidence was provided for such an organizational hierarchy over one hundred years ago when Bryan and Harter (1899) described acquisition of the telegraph language as a progression from considering individual letters, then words, then phrases. A similar hierarchy was proposed by Johnson (1978, 1973) for the memorization of a sequence of letters. More recently, Klapp (1995) examined changes in RT for single and multiple component key press sequences. Reaction times were initially higher for multiple component responses compared to single component responses (a difference of 62ms), a result attributed to the sequencing requirement which was thought to occur after the “go”
stimulus. However this RT difference was minimized after 8 days of practice (reduced to 2ms), a result that was interpreted as evidence for “chunking” whereby the multiple component movement was eventually recoded into a single element, and could thus be fully prepared in advance.

The notion of movement chunking has been described via a “gear-shift analogy” (Keele & MacKay, cited in Schmidt & Lee, 2005, pp. 422). Early in practice the process of shifting gears in a car may involve numerous separate movement elements that are all individually prepared. With practice the learner eventually blends the separate components into a single movement that is prepared as a single action. While some evidence of chunking with practice has been provided for key-press tasks, research examining more complex movement sequences has been limited and the findings have been disparate. Initial work by Sherwood and Canabal (1998) involving a sequential limb movement found little support for the gear-shift analogy, as the correlation between interlimb components showed little change with practice. Conversely, others have shown evidence for movement chunking with practice. For example, Fischman and Lim (1991) found that the components of a well-learned target-striking task did not provide positive transfer to a novel but similar task, suggesting that the movement was eventually controlled as a single unit that did not allow access to the individual movement elements. Similarly, Gray and Beilock (2007) found that expert golfers showed a decreased ability to inhibit a golf putt during execution as compared to novices. The authors attributed this result to a more encapsulated motor program that could not be easily interrupted once initiated.
Motor Preparation and Alternative Methods of Practice

Physical practice is the most common means to improve performance; however there is evidence that other types of practice can also impact learning. For example, meta-analyses of both mental practice (Feltz & Landers, 2007) and observational practice (Ashford, Bennett, & Davids, 2006) have shown that these processes are capable of producing significant learning benefits. While these alternate forms of practice may assist the learner with strategic information, there is now evidence that the process of imagery and observation involve neurophysiological activation of the motor system, even though no physical movement occurs (see Maslovat, Hayes, Horn, & Hodges, 2010; Rizzolatti & Fabbri-Destro, 2010 for recent reviews). There is a wealth of research providing evidence for motor involvement at the cortical, subcortical, and spinal levels during both imagery and observation. Although it is not clear if this motor activation is reflective of response preparation processes, it is conceivable that preparation changes can occur in the absence of physical practice, although this has received little attention.

Summary

This dissertation details six experiments that were designed to study motor preparation during various types of practice including physical practice, mental imagery and observation. For most studies we employed a simple RT paradigm to isolate response preparation and utilized startle methodology to probe what was pre-programmed. To date, most studies using a startling stimulus have involved relatively simple movements that participants can perform with a high degree of accuracy. In this dissertation, we used this methodology to examine how pre-programming changes during the learning process. The startling stimulus is a valuable tool to examine motor preparation as we assume that if the
response is triggered at short latencies, it reflects what has been prepared in advance by the participant. By examining the response to startle trials at various points in the acquisition process it is possible to determine changes to what is being pre-programmed as learning progresses. That is, the movement preparation changes that occur during practice should be reflected in the triggered movement when a startle stimulus is provided. Thus not only can the limits of advance preparation be examined by startle methodology, we can also gain information as to whether these limits change as a task is practiced.

The studies described herein used different types of upper limb movements of varying complexities including bimanual and unimanual movements, as well as discrete and continuous movements. We also examined various dependent measures including behavioural outcome measures, perceptual measures, electromyographic (EMG) measures and measures of cortical activation levels (functional magnetic resonance imaging or fMRI). In the first four studies motor preparation was examined in terms of changes that occur with physical practice, while the final two studies were concerned with preparation during imagery and observation. Collectively, they provided information regarding the role of practice in the advance preparation of movements contributing to the literature involving examination of the learning process. The six experiments are outlined briefly below with specific hypotheses contained within each section.

1. Experiment 1 used startle methodology in a simple RT paradigm to examine short term learning of an *asymmetrical* bimanual movement, whereby one limb moved to a target twice the amplitude of the other limb. This study validated the use of a startling stimulus within a learning context and provided information as to how an asymmetrical movement is prepared and improved with practice.
2. Experiment 2 also used startle methodology in a simple RT paradigm to examine short term learning of an *asynchronous* bimanual movement, whereby initiation of the second limb was delayed by 100 ms relative to the first limb. This study afforded insight into the preparation process associated with the acquisition of a timed interval during the production of a sequenced movement.

3. Experiment 3 used startle methodology to examine differences in response preparation between spatially and temporally defined unimanual movements, as the results of Experiment 1 and 2 suggested these movements were prepared in a different manner. Although not specifically a learning study, we investigated how the goals of the movement can affect the mechanisms by which the movement is prepared.

4. Experiment 4 used startle methodology in both a simple and choice RT paradigm to examine the effects of extended practice (4 days) on a variety of unimanual movements of different complexities. Investigation of practice-related changes to motor preparation when the required movement was both known in advance and unknown provided results that allowed us to evaluate current theories of motor preparation and determine the aspects of movement complexity that affect response preparation.

5. Experiment 5 examined whether motor preparation occurs during observation and mental imagery and whether the preparation process is similar to that undertaken during physical practice. Through the use of startle methodology, we explored if an observed or imagined movement could be triggered with a startling stimulus.
6. Experiment 6 examined the behavioural, perceptual and neurophysiological changes that occurred during extended observation of a model learning a novel bimanual coordination movement. To determine if motor system involvement could occur for an unpracticed movement, we chose a task that is difficult for observers to extract strategic information. Results from this study provided information pertaining to cognitive mediation models of motor skill learning, as well as possible mechanisms by which observation can provide benefits to motor skill performance.
2. **Experiment 1**

Response Preparation Changes Following Practice of an
Asymmetrical Bimanual Movement$^1$

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Introduction

The examination of how practice affects skill acquisition has provided valuable insight into what factors affect learning; however these experiments are often limited in their evaluation of what is actually learned by the participants. Assessing changes in internal processes that lead to the improvements in the capability to produce a skill can prove to be challenging. One way to explore these internal changes associated with learning is to examine how practice affects the different stages of information processing (i.e. stimulus identification, response selection, response programming). It has been hypothesized that these processing stages develop independently with practice, depending on the type of task and experience of the performer (Verwey, 1999). It would be expected that during practice of a simple reaction time task (where only one movement alternative is performed in response to a stimulus) participants could bypass response selection and primarily focus on response programming (Schmidt & Lee, 2005, pp. 69-74). Response programming is the process by which the response to the stimulus (i.e. the “program”, Young & Schmidt, 1991; Schmidt, Heuer, Ghodsian, & Young, 1997) is prepared prior to initiation. In a simple reaction time task, because the required response is known in advance, response preparation may occur prior to the “go” stimulus (Klapp, 1996). Thus, in the context of learning, improvement in performance of a task in a simple reaction time paradigm may be due to a more accurate response being pre-programmed. The purpose of the current study was to examine the effects of practice on the advance preparation of a movement.

A number of different methodologies have been employed to examine response preparation and its changes with practice. One avenue has examined reaction time changes with practice of a multiple component movement (Fischman & Lim, 1991; Klapp, 1995).
These studies reported a decrease in reaction time with practice, which the authors attributed to a change in response preparation whereby a multiple segment movement could be pre-programmed as a single chunk. Another avenue has examined practice-related changes to the initial, ballistic portion of a rapid aiming movement (Abrams & Pratt, 1993; Pratt & Abrams, 1996; Khan, Franks, & Goodman, 1998). These studies showed an increase in time spent in the initial impulse phase following practice, which is considered to be pre-programmed and initiated without modifications.

The methodology we chose for this experiment involved the implementation of a startling acoustic stimulus (SAS), which has been used to examine movement preparation. During a simple reaction time task, replacing the auditory “go” signal with a loud (>124dB) startling stimulus has been shown to elicit the required action at a much shorter latency, with kinematics and EMG configurations largely unchanged (Valls-Solé, Solé, Valdeoriola, Muñoz, Gonzalez, & Tolosa, 1995; Valls-Solé, Rothwell, Goulart, Cossu, & Muñoz, 1999; Siegmund, Inglis, & Sanderson, 2001; Carslen, Chua, Inglis, Sanderson, & Franks, 2003, 2004a, 2004b; Carlsen, Dakin, Chua, & Franks, 2007; Cressman, Carlsen, Chua, & Franks, 2006; MacKinnon et al., 2007). Due to dramatic shortening of premotor reaction times (<60 ms), it has been hypothesized that the startle can act as a trigger for a pre-programmed response, bypassing the usual voluntary command (Valls-Solé et al., 1999; Carlsen et al., 2004b). This hypothesis has been supported by a number of studies showing that startle effects are distinct from and larger than stimulus intensity effects (Carlsen et al., 2007), and only occur when the participant has prepared the response in advance (Valls-Solé et al., 1999; Carlsen et al., 2004a; Rothwell, 2006).
The startle paradigm has provided valuable information regarding when advance movement preparation occurs. Previous studies have shown that pre-programming may not occur when there is uncertainty with regards to the movement being produced, such as during a choice (Carlsen et al., 2004a) or discrimination reaction time task (Carlsen, Chua, Dakin, Inglis, Sanderson, & Franks, 2008). However, advance knowledge of the to-be-performed task does not guarantee the movement can be fully pre-programmed. Movements involving multiple subcomponents are thought to require a sequencing component which can only be completed following the “go” stimulus (Klapp, 1995, 1996). Indeed, recent evidence has shown that a multiple component unimanual movement is not triggered by a startling stimulus (Carlsen et al., 2008). Thus the use of a SAS can act as a probe for what is pre-programmed, as fully prepared movements would be expected to be triggered at a shorter latency when compared to control trials (with similar movement characteristics).

Furthermore, the startle paradigm can be used as a valuable tool to examine preparation changes during the learning process, and determine if practice related changes are due to a change in pre-programming.

The task we chose was a bimanual asymmetrical movement, whereby each limb moved simultaneously to a target of different amplitude. While there is evidence that this type of task can be performed without extensive training (e.g. Kelso, Southard, & Goodman, 1979; Marteniuk & MacKenzie, 1980; Marteniuk, MacKenzie, & Baba, 1984; Fowler, Duck, Mosher, & Mathieson, 1991; Sherwood, 1991; Sherwood & Nishimura, 1992; Heuer & Klein, 2005, 2006), it has also been shown that participants become more accurate with practice (Sherwood, 1990, 1994; see also Gottlieb, Corcos, Jaric, & Agarwal, 1988). Furthermore, target-directed arm movements produce a consistent and characteristic triphasic
EMG activation pattern (Gottlieb, Corcos, & Agarwal, 1989b; Latash & Gottlieb, 1991) that can be prepared prior to the “go” stimulus (Wadman, Denier van der Gon, Geuze, & Mol, 1979). Although advance preparation has not specifically been examined for this type of task, it has been suggested that amplitude can be individually pre-programmed for bimanual movements (Schmidt, Zelaznik, Hawkins, Franks & Quinn, 1979; Heuer, 1986, 1993). Additionally, bimanually asymmetrical movements are typically performed with a similar start and endpoint in time (Kelso et al., 1979), therefore no sequencing should be required. Thus we predicted that this particular asymmetrical bimanual movement would be treated as a single component movement and fully prepared in advance of the “go” stimulus. This was investigated by comparing control trials to those where the “go” signal was replaced with a SAS, to determine if the startling stimulus triggered a movement with similar characteristics at a shorter latency. We also predicted that performance of the movement would improve with practice, and we could attribute at least some of this improvement to changes in response preparation. This was explored by comparing control and startle trials prior to, and following a number of practice trials. If practice-related changes resulted in a modification of the pre-programmed features (i.e. muscle activation pattern), we would expect that any differences in performance for control trials would also be present in the startle trials.

Method

Participants

Thirteen right-handed volunteers with no obvious upper body abnormalities or sensory or motor dysfunctions participated in the study after giving informed consent. However, only data from ten right-handed volunteers (6 male, 4 female; age 23±3 years) were employed in the final analysis. Three participants did not show activation in the
sternocleidomastoid muscle during any startle trials (which is thought to be the most reliable indicator of a startle response), and thus were excluded from the analysis (see Carlsen et al., 2003, 2004a, 2007 for more detail regarding the exclusion criteria for participants). All participants were naïve to the hypothesis under investigation and this study was conducted in accordance with ethical guidelines established by the University of British Columbia.

Task and Instructions

Participants sat in a height-adjustable chair in front of a 17-inch color monitor (VGA 640 x 480 pixels, 60 Hz refresh) resting on a table. Attached to the table on each side of the monitor were lightweight manipulanda that participants used to perform horizontal flexion-extension movements about the elbow joint. Participants’ arms and hands were secured with velcro straps to the manipulanda with the elbow joint aligned with the axis of rotation and the hands pronated. The home position was a point where the elbow joint approximated 90° for each limb and was defined as 0°. In response to an auditory “go” signal, the participants were asked to rapidly extend the right and left limb to targets on the table located at 20° (right limb) and 10° (left limb) respectively.

Participants were instructed to look straight ahead at the monitor and respond by making a movement “as fast and as accurately as possible” from the starting position and to stop at the final targets. No augmented feedback was provided during the trial; however following each trial terminal feedback was provided for five seconds on the monitor that included reaction time (RT, in ms), movement time (MT, in ms), and movement error (root mean squared error or RMSE, in deg). To further promote performance improvements during the acquisition period (see procedure section below), terminal feedback was also provided regarding details of how the movement was performed. This was presented via Lissajous
feedback superimposed over the correct movement template. Lissajous feedback merges the two limb movements into a single two-dimensional orthogonal movement. Specifically, movements of the right manipulandum produce horizontal movements of the cursor on the screen while movements of the left manipulandum produce vertical movements of the cursor on the screen. Thus the Lissajous template resulted in a diagonal line with a slope of one-half of the screen. At the end of each trial, participants were allowed to examine the final position of their hands, relative to the targets. To encourage fast and accurate responses, a monetary bonus was offered for fast RT, MT and low RMSE scores.

Experimental Design

All trials began with a warning tone consisting of a short beep (82 +/-2 dB, 100 ms, 100 Hz), followed by a random variable foreperiod of two to four seconds, then by the imperative “go” signal. The “go” signal could either consist of a control stimulus (82 +/-2 dB, 100 ms, 1000 Hz) or startling stimulus (124 +/-2 dB, 40 ms, 1000 Hz, <1 ms rise time). All auditory signals were generated by a computer program and were amplified and presented via a loudspeaker placed directly behind the head of the participant. The acoustic stimulus intensities were measured using a sound level meter (Cirrus Research model CR:252B) at a distance of 30 cm from the loudspeaker (approximately the distance to the ears of the participant). Testing consisted of three phases: pre-testing (10 trials), acquisition (6 blocks of 25 trials), and post-testing (10 trials). During both pre-test and post-test conditions, three of the 10 trials included a startling “go” stimulus. These trials were presented in a pseudo-random order. The first trial was always a control trial, and startle trials were never presented consecutively.
Recording Equipment

Surface EMG data were collected from the muscle bellies of the following superficial muscles: right and left lateral head of the triceps brachii (TRI - agonist), right and left long head of the biceps brachii (BIC - antagonist), and left sternocleidomastoid (SCM - startle indicator) using preamplified bipolar Ag/AgCl surface electrodes connected via shielded cabling to an external amplifier system (Therapeutics Unlimited Inc. Model 544). Recording sites were prepared and cleansed in order to decrease electrical impedance. The electrodes were oriented parallel to the muscle fibers, and then attached using double sided adhesive strips. A grounding electrode was placed on the participant’s left lateral malleolus. Arm angular displacement was measured using optical encoders (Dynapar, E20-2500-130) attached to the central axis of the manipulanda. Analog data were digitized in real time (LabMaster PGH) and all data were collected at a rate of 1000 Hz and stored for offline analysis. A custom computer program initiated data collection 100 ms before the presentation of the “go” signal and terminated data collection 1000 ms following the “go” signal.

Data Reduction

Movement onset was defined as the first point when velocity reached and remained above 0 m/s following the “go” stimulus. Final position was defined as the first point at which angular velocity fell below 8 deg/s and remained below this value for 100ms. To calculate velocity, displacement data were passed through a digital, fourth order Butterworth lowpass filter (cutoff frequency of 10 Hz), and then differentiated. Surface EMG burst onsets were defined as the point at which the EMG first began a sustained rise above baseline levels. The location of this point was determined by first displaying the EMG pattern with a superimposed line indicating the point at which activity increased to more than 2 standard
deviations above baseline (mean of 100 ms of EMG activity preceding the go signal). Onset was then verified by visually locating and manually adjusting the onset mark to the point at which the activity first increased. This method allowed for correction of errors due to the strictness of the algorithm. EMG offsets were marked in a similar fashion, with the activity between EMG onset and EMG offset being defined as the duration of a muscle burst. Startle trials in which no detectable startle response (SCM activity) was observed were discarded (total of 3 of 60 trials) (see Carlsen et al., 2003, 2004b, 2007 for a more detailed discussion regarding the use of various startle indicators).

**Dependent Measures and Statistical Analyses**

Kinematic dependent measures included movement time (MT), velocity ratio to peak velocity, and endpoint error (as a percentage of total movement distance). MT was defined as the difference in time between movement onset and final position. Velocity ratio was calculated as the mean ratio of left arm to right arm velocity between movement onset and peak velocity, which typically occurred at approximately 100 ms ($M = 106.5$ ms, $SD = 7.5$ ms). This time frame was chosen to reflect the initial portion of the movement which sensory information is expected to have minimal influence. As the target displacement of the left limb was half that of the right limb, we expected this ratio value to approach 0.5 with practice. Finally we examined absolute error of the final endpoint position for each limb as a measure of movement accuracy. We expressed this error score as a percentage of the target movement amplitude. For example, a 5° error for a 10° movement would represent a 50% movement error and a 5° error for a 20° movement would represent a 25% error. Endpoint error and MT were analyzed via a 2 Time (pre-test, post-test) x 2 Type (control, startle) x 2 Arm (left, right) repeated measures analysis of variance (ANOVA). Velocity ratio was
analyzed via a 2 Time (pre-test, post-test) x 2 Type (control, startle) repeated measures ANOVA.

Previous work involving bimanual movements with asymmetrical amplitudes has shown that the kinematic profiles of the two limbs are relatively consistent with regards to their temporal structure (e.g. reaction time, movement time, peak velocity, peak acceleration); however the force production is different (Kelso et al., 1979; although see also Marteniuk & MacKenzie, 1980; Marteniuk et al., 1984; Fowler et al., 1991). To examine the synchrony of the kinematic profiles, we calculated a correlation coefficient between the velocity profiles of the two limbs from movement onset to movement endpoint for each trial.

To compare EMG patterns, burst onsets and durations were calculated. The onset of the first agonist burst (AG1, TRI) was measured from the time of the “go” stimulus and represented premotor reaction time (PMT). Onset of the antagonist (ANT, BIC) and second agonist burst (AG2, TRI), were calculated as the time from the onset of the AG1, as this allowed for determination of the relative timing of the triphasic EMG pattern. To quantify activation amplitude of the first agonist burst we integrated the rectified raw EMG trace (normalized to the mean peak of control trial values for each participant) for the first 30 ms of the AG1 burst (Q30, Corcos, Gottlieb, & Argawal, 1989; Gottlieb, Corcos, & Argawal, 1989a; Khan, Garry, & Franks, 1999). The Q30 measure represents the initial slope of the agonist burst and is minimally affected by feedback, thus providing insight into pre-programmed agonist EMG activity. Muscle onsets, burst durations and Q30 values were analyzed independently via a 2 Time (pre-test, post-test) x 2 Type (control, startle) x 2 Arm (left, right) repeated measures ANOVA.
The alpha level for the entire experiment was set at .05. Partial eta squared ($\eta^2_p$) values are reported as a measure of effect size. Significant results for the repeated measures ANOVAs were examined via Tukey’s honestly significant difference (HSD) test and simple effects tests to determine the locus of the differences.

Results

A summary of the results for all dependent measures, including mean and standard deviations, are provided in Table 2.1. Figure 2.1 shows limb displacement and EMG data (rectified and smoothed by 20-point averaging) for a representative post-test control trial (top) and startle trial (bottom). During control trials, participants performed temporally symmetrical movements to the targets of different distances. Although each limb moved a different displacement, the timing of the triphasic EMG bursts remained relatively consistent between arms but the relative EMG burst amplitudes were greater for the right arm. During startle trials, participants still produced a temporally synchronous movement to different distances; however they typically overshot both targets. Although EMG activity began at a much shorter latency for startle trials, the temporal pattern was similar to control trials as the EMG timing between limbs remained similar with dissimilar burst amplitudes.
Table 2.1 Experimental results for each stimulus type, arm and testing condition, showing means and standard deviations (bracketed). AG1 = initial agonist burst (triceps), ANT = antagonist burst (biceps), AG2 = second agonist burst (triceps). Note that velocity ratio and correlation coefficients only have one value for both limbs.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control Condition</th>
<th>Startle Condition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Left Arm</td>
<td>Right Arm</td>
</tr>
<tr>
<td></td>
<td>Pre-Test</td>
<td>Post-Test</td>
</tr>
<tr>
<td>Movement Time (ms)</td>
<td>419.9 (59.1)</td>
<td>345.4 (48.7)</td>
</tr>
<tr>
<td>Velocity Ratio</td>
<td>0.74 (0.15)</td>
<td>0.64 (0.16)</td>
</tr>
<tr>
<td>Endpoint Error (%)</td>
<td>35.3 (21.4)</td>
<td>17.7 (7.5)</td>
</tr>
<tr>
<td>Correlation Coefficient</td>
<td>0.913 (0.156)</td>
<td>0.936 (0.080)</td>
</tr>
<tr>
<td>AG1 Onset (ms)</td>
<td>188.9 (52.7)</td>
<td>172.5 (49.1)</td>
</tr>
<tr>
<td>AG1 to ANT Onset (ms)</td>
<td>76.4 (25.5)</td>
<td>59.0 (19.2)</td>
</tr>
<tr>
<td>AG1 to AG2 Onset (ms)</td>
<td>168.1 (40.6)</td>
<td>151.1 (28.5)</td>
</tr>
<tr>
<td>AG1 Duration (ms)</td>
<td>96.6 (22.5)</td>
<td>93.0 (24.4)</td>
</tr>
<tr>
<td>ANT Duration (ms)</td>
<td>95.6 (21.3)</td>
<td>120.4 (23.6)</td>
</tr>
<tr>
<td>AG2 Duration (ms)</td>
<td>81.1 (18.0)</td>
<td>91.2 (18.3)</td>
</tr>
<tr>
<td>Q30 (%peak*ms)</td>
<td>342.0 (158.7)</td>
<td>474.7 (239.4)</td>
</tr>
</tbody>
</table>
Figure 2.1 Limb displacement and EMG data for a representative control (top) and startle (bottom) trial, following acquisition. Note the temporal consistency of EMG activity in both control and startle trials, even though the limbs are moving to different amplitude targets. Also note startle trials are performed with a shortened latency and increased movement amplitude.
Kinematics

Although participants were able to produce asymmetrical movement amplitudes during the pre-test, they did improve their performance with practice. This was shown by a significant main effect for time in the velocity ratio between the limbs ($F(1, 9) = 12.66, p = .006, \eta^2_p = .58$). In the post-test, both limbs moved closer to the required value of 0.5 ($M = 0.67$), as compared to the pre-test ($M = 0.81$). The lack of a main effect for type of stimulus ($p = .111$) provided evidence that there was no significant difference between the velocity ratio for control and startle trials. This result supports our prediction that the movement would be prepared in advance as the SAS triggered a similar movement to that produced in control trials. Furthermore, the lack of time x type interaction ($p = .297$) confirmed that both control and startle trials showed a similar improvement in velocity ratio following practice. This result supports our prediction that practice-related changes could be attributed to an improvement in response preparation, as the response triggered by the SAS was more accurate following the acquisition period.

In addition to becoming more accurate with respect to the relative velocity of the limbs, participants also decreased the duration of the movement. Movement time showed a main effect for time ($F(1, 9) = 19.13, p = .002, \eta^2_p = .68$) due to significantly faster movements ($M = 396$ ms) following practice as compared to pre-test trials ($M = 438$ ms). The effects of practice were also seen in endpoint error, as there was a main effect for time ($F(1, 9) = 5.49, p = .044, \eta^2_p = .38$), arm ($F(1, 9) = 16.15, p = .003, \eta^2_p = .64$), and a significant arm x time interaction ($F(1, 9) = 5.13, p = .050, \eta^2_p = .36$). This interaction was examined by separately analyzing the left and right arm data. This analysis revealed a significant time effect for the left arm ($p = .038$) due to a relatively large decrease in error from pre-test ($M =
43.0%) to post test ($M = 19.9\%$), but no significant time effect for the right arm ($p = .261$) due to a relatively small decrease in error for the right arm from pre-test ($M = 15.9\%$) to post-test ($M = 11.6\%$). Thus the change in performance during acquisition appeared to be due to reducing the error of the smaller movement of the non-dominant arm, while the larger movement of the dominant arm stayed fairly constant. There was also a main effect in endpoint error for type of stimulus ($F(1, 9) = 6.73, p = .029, \eta_p^2 = .43$), with control trials having less overall error ($M = 19.3\%$) when compared to startle trials ($M = 25.9\%$).

As expected, all three kinematic variables improved with practice. To determine when improvement occurred and if participants reached a performance asymptote, we performed a post-hoc examination of performance during the acquisition period. This was done by analyzing participant means for velocity ratio and endpoint error during non-startle trials for the pre-test, the six acquisition blocks and the post-test. Velocity ratio means were subjected to an 8 Block (pre-test, acquisition block 1-6, post-test) repeated measures ANOVA, while endpoint error means were subjected to an 8 Block (pre-test, acquisition block 1-6, post-test) x 2 Arm (left, right) repeated measures ANOVA. Results of the endpoint analysis confirmed a significant hand x block interaction effect ($p = .005$) which a Tukey’s HSD test determined was due to a significant difference for the left hand between the pre-test and all other blocks (with no significant difference occurring after the first acquisition block). Results of the velocity ratio analysis did not produce a significant block effect ($p = .157$), however a similar trend occurred whereby the largest improvement in performance occurred between the pre-test and first acquisition block. Thus, the majority of performance improvements appeared to occur within the first 25 trials, with little change in performance during the rest of the acquisition period. Endpoint error for the left and right arm for control
trials during acquisition, and startle and control trials during pre and post-testing is shown in Figure 2.2.
Figure 2.2 Mean (SEM) endpoint error as a percentage of total movement, during Pre-Test, Acquisition (ACQ) and Post-Test startle and control trials, separated by arm. Note the significant arm by time interaction whereby the left arm decreases error with practice more than the right arm.
In support of previous results (e.g. Kelso et al., 1979), kinematic variables showed a high degree of synchrony. Specifically, correlation coefficients of movement velocity were above 0.90 for all conditions (Table 2.1). However these numbers may be somewhat deceptive, given that the movement would require some degree of coordination between the kinematics of the two limbs. To contrast trials with a high and low correlation coefficient, Figure 2.3 shows kinematic data (displacement, velocity, and acceleration versus time), from one participant, of two consecutive post-test control trials. The left panel (a) depicts one trial with a low velocity correlation between limbs ($r = 0.6245$), whereas the right panel (b) shows a high correlation ($r = 0.9678$). Notice for panel (a) that the peak velocity for the left arm occurs earlier than the right arm, as compared to panel (b) when they occur almost simultaneously.
Figure 2.3 Kinematic profiles showing displacement (top), velocity (middle), and acceleration (bottom), of the two limbs for single trials. Left panel (a) shows a movement with low velocity correlation ($r = 0.6245$) while right panel (b) shows a movement with high velocity correlation ($r = 0.9678$).
The collection of EMG allowed us to determine how participants achieved limb movements of different amplitudes (Figure 2.1). We expected participants would either alter the timing pattern of the triphasic burst, or change the relative EMG amplitude between the arms. EMG boxplots, showing the triphasic burst for both limbs during control and startle trials (collapsed by time), are shown in Figure 2.4, as well as the SCM burst for startle trials. Overall our results support the hypothesis that asymmetrical movement amplitudes were achieved by adjusting the ratio of EMG amplitude while keeping the timing invariant between the limbs. During startle trials EMG latencies were decreased; however the triphasic pattern and amplitude differences between the limbs followed the same pattern as the control trials.
Figure 2.4 Plots of triphasic EMG configurations during startle and control trials, collapsed by time. Boxes represent EMG burst durations with mean (SEM) onsets and offsets with respect to time. AG1 represents the initial agonist (triceps) burst, ANT represents the antagonist (biceps), AG2 represents the second agonist burst, and SCM represents the startle indicator (sternocleidomastoid). Note the consistency of the triphasic burst pattern between limbs (left and right) and conditions (control and startle).
Analysis of AG1 onset confirmed a main effect for type of stimulus ($F(1, 9) = 52.47$, $p < .001$, $\eta^2_p = .85$), whereby startle trials exhibited a significantly shorter PMT ($M = 99$ ms) when compared to control trials ($M = 179$ ms). Although PMT did decrease with practice (pre-test $M = 143$ ms, post-test $M = 133$ms), this result was not statistically significant as there was no main effect for time ($p = .260$). This was not unexpected as the entire movement was likely prepared in advance both prior to, and following practice. Although changes in reaction time have been shown with practice (e.g., Fischman & Lim, 1991), this result is typically found for a multiple component movement that cannot be initially fully pre-programmed (see Klapp, 1995, 1996 for a more detailed description).

The pattern of EMG activity produced was investigated by examining the relative onset of the ANT and AG2 burst, and the three muscle burst durations. Analysis of ANT onset revealed a main effect for arm ($F(1, 9) = 6.46, p = .032, \eta^2_p = .42$), with the onset of the right arm ANT occurring later ($M = 80$ ms) than that of the left arm ($M = 66$ ms). Analysis of the AG2 onset revealed a main effect for time ($F(1, 9) = 5.51, p = .044, \eta^2_p = .38$), with the onset of AG2 occurring earlier in post-testing ($M = 151$ ms) when compared to pre-testing ($M = 168$ ms). This effect likely contributed to the decrease in MT with practice, as earlier AG2 activity would result in the limb stopping at the target sooner. The analysis of duration for all three muscle bursts showed no main effect for time (AG1, $p = .210$; ANT, $p = .210$; AG2, $p = .690$), type (AG1, $p = .826$; ANT, $p = .801$; AG2, $p = .220$), or arm (AG1, $p = .785$; ANT, $p = .151$; AG2, $p = .721$), nor any significant interaction effects. The analysis of the Q30 scores showed a significant effect for arm ($F(1, 9) = 27.52, p = .001, \eta^2_p = .75$), and stimulus type ($F(1, 9) = 26.94, p = .001, \eta^2_p = .75$). This was due to significantly greater EMG activity for the right AG1 ($M = 851$ %peak*ms) versus the left ($M = 642$ %peak*ms),
and greater activity during startle trials ($M = 1002$ %peak*ms) versus control trials ($M = 491$ %peak*ms). Thus while the timing pattern of the triphasic burst remained similar between the limbs, increased EMG activity for the limb moving the greater distance allowed the participants to move the different amplitudes.

**Discussion**

The purpose of this experiment was to examine the effects of practice on the preparation of an asymmetrical bimanual movement. Our results supported the hypothesis that this movement could be prepared in advance both prior to and following practice, as illustrated by similar movement production during startle and control conditions. Not only was there no significant difference between conditions for velocity ratio, the timing of the triphasic EMG pattern (including both durations and relative onset timings) also remained essentially unchanged between control and startle trials. The only significant effect of startle on the performed movement was an increase in endpoint error (from 19.3% to 25.8%) and Q30 values (from 491 %peak*ms to 1002 %peak*ms). Previous research has shown increased peak movement amplitude and increased peak EMG amplitudes associated with startle trials (e.g. Carlsen et al., 2004a), which the authors attributed to increased neural activation associated with the increased stimulus intensity. This explanation seems likely for the current experiment as the difference in endpoint error and agonist EMG amplitude between control and startle trials was consistent for both limbs, before and after practice (Table 2.1).

Although pre-programming of the required movement was possible before and after the acquisition period, we were interested in whether the prepared response changed with practice. Our results indicate that participants did improve at the task, as shown by a decrease
in MT, a more accurate velocity ratio, and lower endpoint error. The post hoc analysis of the acquisition data confirmed that the majority of improvement occurred within the first block of 25 acquisition trials (Figure 2.2). While MT and velocity ratio changed with practice, these changes were also reflected in startle trials, confirming that both types of trials improved following practice. Furthermore, the change in velocity ratio confirmed that practice affected the first 100 ms of the movement, a time frame which is thought to be minimally influenced by sensory feedback. Thus, as we predicted, the practice-related changes appeared to be due to a change in pre-programming, resulting in a more accurately prepared movement.

The arm by time interaction for endpoint error provided insight as to how the improvements in performance occurred. Participants decreased the error of the non-dominant arm moving the smaller distance (Figure 2.2), which is consistent with previous work investigating how asymmetrical bimanual movements change with practice. Poor performance early in acquisition has been attributed to assimilation effects, whereby errors in performance are due to neural crosstalk between the motor commands of the two limbs (Marteniuk et al., 1984; Sherwood, 1990, 1991, 1994; Sherwood & Nishimura, 1992; Spijkers & Heuer, 1995; Spijkers, Heuer, Kleinsorge, & van der Loo, 1997; Heuer, Spijkers, Kleinsorge, van der Loo, & Steglich, 1998). Assimilation effects are more pronounced for the shorter movement as the crosstalk interaction is from a larger amplitude movement, resulting in larger errors. With practice these effects are thought to be either decreased or eliminated, allowing the participant to more accurately perform the asymmetrical movement (Marteniuk et al., 1984; Sherwood, 1990, 1994).
The use of a SAS allowed us to probe preparation changes with practice; however it is necessary to ensure the startling stimulus acted as a trigger for the prepared movement. While the temporal movement characteristics remained unchanged for startle trials, response latencies were much reduced. Specifically, startle trials resulted in a PMT of 99 ms, compared to 179 ms during control trials, which is consistent with previous work involving a SAS with a targeted upper limb movement (e.g. Carlsen et al., 2003, 2004a; Kumru & Valls-Solé, 2006). Although shortened reaction times occur with a more intense stimulus (Piéron, 1920), it has been shown that the use of a SAS can result in a further decrease in reaction time, which is thought to be due to triggering a pre-programmed representation of the movement (Valls-Solé et al., 1999; Carlsen et al., 2004b). The presence of SCM activity prior to the movement, as observed in the current experiment (Figure 2.4), appears to be the most reliable indicator that the participant has indeed been startled (Carlsen et al., 2007). Thus we believe that the SAS acted as a trigger and released the pre-programmed movement, confirming the movement was indeed prepared in advance of the “go” stimulus.

The design of the current experiment allowed investigation into how movement preparation occurs for an asymmetrical bimanual movement. The previous work by Kelso et al. (1979) led to the observation that when two movements of asymmetrical amplitude are combined, the temporal structure of the limbs became synchronous, while the force production varied. Our results support this finding as the temporal structure of both kinematic (Figure 2.3) and EMG (Figure 2.4) data showed remarkable invariance between the limbs. This temporal invariance in EMG pattern between the limbs was also maintained in startle trials, suggesting this pattern was prepared in advance. However, EMG amplitudes of the initial agonist burst differed between the limbs allowing the participants to make movements
of different distances. These results suggest that to perform a bimanual movement of
different amplitudes, we prepare and execute motor commands for the two limbs with a
similar timing structure but different muscle activation levels. This is in contrast to
unimanual limb movements where changes in amplitude are associated with changes in
timing of the triphasic EMG pattern (Wadman et al., 1979; Carlsen et al., 2004b). Therefore
it appears that it is the coupling of the limbs that causes a similar EMG timing structure for
both limbs to be pre-programmed. This is in line with previous bimanual research showing
that different movement amplitudes can easily be specified between the limbs but producing
movements with different durations is more difficult (Schmidt et al., 1979; Heuer, 1986,
1993; Spijkers et al., 1994).

In addition to examining how movement preparation occurs in a bimanual movement,
we also determined how preparation changed with practice. The improvement in performing
the task appeared to result from pre-programming a more accurate ratio of left to right limb
amplitude, rather than a change in the timing of the triphasic muscle activity. This again can
be contrasted to improvements in unimanual targeted movements where changes occur in the
timing pattern of muscle activations (Gabriel & Boucher, 1998, 2000; Liang et al., 2008).
This suggests that during practice of a bimanual movement, it may be easier to modify the
relative EMG activation level rather than timing pattern to adjust the movement amplitude of
one of the limbs.

In conclusion, the results from this study support the notion that we can prepare in
advance an asymmetrical bimanual movement, and that this response preparation changes
with practice. Results also indicate that this movement is performed using similar EMG
timing between limbs, while adjusting the relative ratio of EMG amplitude. Furthermore,
learning of the task appears to be related to the ability to produce the correct asymmetrical
EMG amplitudes, rather than changing the timing of the triphasic pattern. By investigating
the practice-related changes in certain aspects of information processing, we believe we can
begin to gain insight into what is learned during acquisition of this particular skill. The
current results provide additional support that skill acquisition can result from changes in the
process of advance response preparation.
Bridging Summary to Following Chapters

The results of the current experiment validated the use of a startling stimulus as a useful tool to examine practice-related change in response preparation. Improvements in performance as a result of practice were reflected in the movements triggered by the startling stimulus and provided specific information as to how an asymmetrical bimanual movement is prepared. As predicted, the synchronous bimanual movement was fully prepared in advance confirming individual amplitudes can be independently pre-programmed for each limb. Our next question of interest was whether an asynchronous bimanual movement could also be pre-programmed. It has been hypothesized that the sequencing of movements cannot occur in advance (Klapp, 1995, 2003); however this has primarily been tested for unimanual movements. For a bimanual movement, the two movement elements are independent (i.e., do not require the same limb) and may overlap temporally (i.e., the second movement element may start before the first element is complete), which may allow both components of the bimanual movement to be prepared in advance.
3. **Experiment 2**

Response Preparation Changes Following Practice of an

Asynchronous Bimanual Movement

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Introduction

The learning of novel motor skills is an essential part of human existence. Researchers have long examined numerous aspects of skill acquisition, typically examining how a behavioural measure (e.g., time to complete a movement, error score, reaction time) changes with the amount and/or quality of practice undertaken by the learner. While we know that practice is a predominant factor in skill acquisition, determining the actual process by which learning occurs has provided a considerable challenge. One way to simplify the investigation of the learning process is to consider the production of a task from an information processing perspective. For example, if a simple movement is to be produced in response to the appearance of a “go” stimulus, a number of stages are thought to occur, including stimulus identification and recognition, response selection, and response programming (Donders, 1969). The purpose of the current study was to examine response programming changes that occur during acquisition of a movement. More specifically, this experiment was designed to study what aspects of a movement could be prepared in advance (i.e., pre-programmed), and how this preparation changed with practice.

A number of different methodologies have been employed to examine motor preparation. One avenue has used a simple reaction time (RT) paradigm whereby the response to the “go” stimulus is known in advance. In this situation, it has been suggested that response preparation may occur prior to the “go” signal, depending on the nature of the required movement (see Klapp, 1996 for a review). To examine when advance preparation can occur, reaction time is used as a measure of time needed to process information following the “go” signal. It is assumed that an increase in reaction time is due to preparation being performed after the “go” signal. In a series of studies, Klapp (1995, 2003) showed that
a sequenced movement could not initially be pre-programmed. However, with sufficient practice a multiple component movement could be recoded into a single element (i.e., “chunked”), and thus fully prepared in advance (see also Fischman & Lim, 1991; cf. Sherwood & Canabal, 1988).

A more recent methodology used to examine response preparation involves the use of a startling acoustic stimulus (SAS). During a simple reaction time task, replacing the auditory “go” signal with a loud (>124dB) SAS has been shown to elicit the required action at a much shorter latency, with kinematics and EMG configurations largely unchanged (Valls-Solé, Solé, Valdeoriola, Munoz, & Gonzalez, 1995; Valls- Solé, Rothwell, Goulart, Cossu, & Munoz, 1999; Siegmund, Inglis, & Sanderson, 2001; Carslen, Chua, Inglis, Sanderson, & Franks, 2003, 2004a, 2004b; Carlsen, Dakin, Chua & Franks, 2007; Cressman, Carlsen, Chua, & Franks, 2006; MacKinnon et al., 2007). Due to dramatic shortening of premotor reaction times (i.e. premotor RT <60 ms), it has been hypothesized that the startle can bypass the usual voluntary command and act as a trigger for a pre-programmed response (Valls-Solé et al. 1999; Carlsen et al. 2004b). Support for this hypothesis has come from a number of studies that have shown that startle effects are distinct from and larger than stimulus intensity effects (Carlsen et al., 2007), and only occur when the participant has prepared the response in advance (Valls-Solé et al., 1999; Carlsen et al., 2004a; Rothwell, 2006). Alternately, when uncertainty exists regarding what movement is required, such as a discrimination (Carslen, Chua, Inglis, Sanderson, & Franks, 2008) or choice reaction time task (Carlsen et al., 2004a), advance preparation may not occur and thus the startle does not trigger the movement.

The use of a SAS can act as a probe for what is pre-programmed, as fully prepared movements would be expected to be triggered at a shorter latency than control trials, with
similar movement characteristics. In addition, the startle paradigm can also be used as a tool to examine how pre-programming changes during the learning process. By examining the response to startle trials provided at various points in the acquisition process (i.e., early, middle, late) it is possible to determine what is being prepared as learning progresses. We have previously used a startling stimulus to examine preparation changes for a synchronous bimanual movement of asymmetrical amplitudes (Maslovat, Carlsen, Ishimoto, Chua, & Franks, 2008). In response to an auditory “go” signal, participants were required to perform simultaneous elbow extension movements with the right arm to a 20° target and the left arm to a 10° target. Prior to and following practice, startle trials were interspersed with control trials to examine the effects of a SAS on the bimanual movement. The comparison of startle to control trials indicated that a different amplitude movement could indeed be prepared in advance for each limb, and that this preparation improved with practice. In addition, while startle trial reaction times were much faster than control trials, the configuration of the EMG patterns was unchanged. This was taken as evidence for the prepared movement being triggered at an early latency by the startling stimulus.

Our previous work (Maslovat et al., 2008) confirmed that a synchronous bimanual movement of different amplitudes could be prepared in advance. The focus of the current experiment was to extend these findings by examining whether an asynchronous bimanual movement of equal amplitudes could be prepared in advance, and whether this preparation would change as a result of practice. The task we chose was a bimanual elbow extension movement whereby both limbs moved to a 20° target; however initiation of the left limb was required to be delayed by 100 ms relative to initiation of the right limb. A 100 ms delay was chosen to be sufficiently short to promote advance preparation of both arm movements.
(rather than on-line preparation of the second movement), yet long enough that participants could distinguish the difference in arm initiation and thus improve with practice. We were unsure whether this movement could be pre-programmed early in the acquisition period. On the one hand, based on the theoretical model proposed by Klapp (1995, 2003), an asynchronous movement should not be prepared in advance due to a sequencing requirement of the limb movements. This model has been supported by studies involving two-step unimanual movements that have shown that only the first movement is prepared in advance, with the second movement programmed on-line (Adam et al., 2000; Vindras & Viviani, 2005; Khan, Lawrence, Buckolz, & Franks, 2006). However, to our knowledge, this model has not been specifically tested for sequenced bimanual movements. An asynchronous bimanual movement may be prepared in a different manner to a two-step unimanual movement, as the two movement elements are independent (i.e., do not require the same limb) and may overlap temporally (i.e., the second movement element may start before the first element is complete). These differences may allow both components of the bimanual movement to be prepared in advance.

The results of this study should further our knowledge of the preparation process for asynchronous bimanual movements. Additionally, the use of a learning paradigm will allow for examination of how the preparation process changes with practice. If advance preparation is not possible early in acquisition, we would not expect the asynchronous bimanual movement to be triggered by the startling stimulus. However, with practice we would predict that movement “chunking” would occur, thus allowing for advance preparation and triggering by the startling stimulus. Alternatively, if the movement is able to be prepared
early in acquisition, we would predict that as performance changes with practice, the movement triggered by the startling stimulus would reflect these changes.

Method

Participants

Thirteen right-handed volunteers with no obvious upper body abnormalities or sensory or motor dysfunctions participated in the study after giving informed consent. However, only data from ten right-handed volunteers (3 male, 7 female; age 25±5 years) were employed in the final analysis. Three participants did not show activation in the sternocleidomastoid muscle during any startle trials (which is thought to be the most reliable indicator of a startle response), and thus were excluded from the analysis (see Carlsen et al., 2003, 2004a, 2007 for more detail regarding the exclusion criteria for participants). All participants were naïve to the hypothesis under investigation and this study was conducted in accordance with ethical guidelines established by the University of British Columbia.

Task and Experimental Design

Participants sat in a height-adjustable chair in front of a 15-inch color monitor (ADI Microscan A505, 1024 x 768 pixels, 75 Hz refresh) resting on a table. Attached to the table on each side of the monitor were lightweight manipulanda that participants used to perform horizontal flexion-extension movements about the elbow joint. Participants’ arms and hands were secured with Velcro straps to the manipulanda with the elbow joint aligned with the axis of rotation and the hands pronated. The home position for each arm was located such that a 20° extension movement resulted in the arms being straight ahead (i.e., perpendicular to the monitor on the table), and was defined as 0°. Targets were located on the table top at 20° of extension from each home position. In response to an auditory “go” signal, the
participants were asked to rapidly extend the right and left limb to the targets such that the left arm moved from the home position 100 ms after the right arm. Participants were instructed to look straight ahead at the monitor and respond by making a movement “as fast and as accurately as possible” from the starting position and to stop at the final targets.

All trials began with a warning tone consisting of a short beep (80 +/-2 dB, 100 ms, 100 Hz), followed by a random variable foreperiod of 1500ms-2500ms, then by the imperative “go” signal. The “go” signal could either consist of a control stimulus (80 +/-2 dB, 100 ms, 1000 Hz) or startling stimulus (124 +/-2 dB, 40 ms, 1000 Hz, <1 ms rise time). All auditory signals were generated by a customized computer program and were amplified and presented via a loudspeaker placed directly behind the head of the participant. The acoustic stimulus intensities were measured using a sound level meter (Cirrus Research model CR:252B) at a distance of 30 cm from the loudspeaker (approximately the distance to the ears of the participant).

Participants performed a total of 160 trials in a single testing session (approximately 45 minutes), alternating between “testing” and “practice” trials. Participants began with a block of 10 testing trials whereby three trials included a startling “go” stimulus in a pseudo-random order (the first trial was never a startle, and startle trials were never presented consecutively). This was followed by two blocks of 20 practice trials where no startle trials were presented. This pattern was repeated two additional times (testing, practice, testing, practice) and then ended with a final testing block. Thus a total of four testing blocks (10 trials each – seven control, three startle) and six practice blocks (20 trials each) were performed by each participant. No augmented feedback was provided during each trial; however terminal feedback was provided on the monitor for three seconds following the trial
that included reaction time (RT, in ms) and arm delay (practice trials only, in ms). At the end of each trial, participants were allowed to examine the final position of their arms, relative to the targets. To encourage fast and accurate responses, a monetary bonus was offered for fast RT and accurate delay times.

**Recording Equipment**

Surface EMG data were collected from the muscle bellies of the following superficial muscles: right and left lateral head of the triceps brachii (TRI - agonist), right and left long head of the biceps brachii (BIC - antagonist), and left sternocleidomastoid (SCM - startle indicator) using preamplified surface electrodes connected via shielded cabling to an external amplifier system (Delsys Model DS-80). Recording sites were prepared and cleansed in order to decrease electrical impedance. The electrodes were oriented parallel to the muscle fibers, and then attached using double sided adhesive strips. A grounding electrode was placed on the participant’s left lateral malleolus. Arm angular displacement was measured using potentiometers (Precision, MD157) attached to the central axis of the manipulanda. A customized LabView® computer program controlled stimulus and feedback presentation, and initiated data collection at a rate of 1 kHz (National Instruments, PC-MIO-16E-1) 500 ms before the presentation of the “go” signal and terminated data collection 2000 ms following the “go” signal.

**Data Reduction**

Movement onset was defined as the first point when velocity reached and remained above 0 deg/s following the “go” stimulus. Final position was defined as the first point at which angular velocity fell below 8 deg/s and remained below this value for 50ms. Surface EMG burst onsets were defined as the point at which the EMG first began a sustained rise
above baseline levels. The location of this point was determined by first displaying the EMG pattern with a superimposed line indicating the point at which activity increased to more than two standard deviations above baseline (mean of 100 ms of EMG activity preceding the go signal). Onset was then verified by visually locating and manually adjusting the onset mark to the point at which the activity first increased. This method allowed for correction of errors due to the strictness of the algorithm. EMG offsets were marked in a similar fashion, with the activity between EMG onset and EMG offset being defined as the duration of a muscle burst. Startle trials in which no detectable startle response (SCM activity) was observed were discarded (total of 5 of 120 trials - 4%), as were trials when reaction time was longer than 400ms (total of 14 of 1600 trials - <1%) or when movement occurred prior to the “go” signal (total of 12 of 1600 trials - <1%).

Dependent Measures and Statistical Analyses

Premotor reaction time (PMT) was analyzed to examine whether the startling stimulus initiated the movement at latency values that would suggest the movement was prepared in advance and triggered by the startle (Valls-Solé et al., 1999; Carlsen et al., 2004b). PMT was defined as the time difference between the “go” stimulus and the onset of the first agonist burst in the right arm. Kinematic dependent measures included arm delay, movement time (MT), and endpoint constant error (CE). Arm delay was defined as the time interval between movement onset of the right and left arm and was the primary measure used to determine improvements in performance. Endpoint error and MT were used as secondary measures to determine if any changes in speed and accuracy occurred with practice, and for a comparison between startle and control trials to determine if similar movements were produced. MT was defined as the difference in time between movement onset and final
position. Endpoint CE was determined by calculating the mean error of the final endpoint for each limb.

To compare EMG patterns, burst onsets and durations were calculated for each arm. The onset of the first agonist burst (AG1, TRI) was measured from the time of the “go” stimulus while onset of the antagonist (ANT, BIC) and second agonist burst (AG2, TRI), were calculated as the time from the onset of the AG1. This allowed for determination of the relative timing of the triphasic EMG pattern. To quantify activation amplitude of the first agonist burst we integrated the rectified raw EMG trace for the first 30 ms of the AG1 burst (Q30, Corcos, Gottlieb, & Agarwal, 1989; Gottlieb, Corcos, Argawal, 1989; Khan, Garry, & Franks, 1999; Maslovat et al., 2008). The Q30 measure represents the initial slope of the agonist burst and is minimally affected by feedback, thus providing a useful measure of neural activation.

We limited our statistical analysis to the four testing blocks to allow us to directly compare startle and control trials throughout the practice period. PMT and arm delay were independently analyzed via a 4 Block x 2 Stimulus Type (control, startle) repeated measures analysis of variance (ANOVA). All other dependent measures were independently analyzed via a 4 Block x 2 Stimulus Type (control, startle) x 2 Arm (left, right) repeated measures ANOVA. The alpha level for the entire experiment was set at .05. Partial eta squared (ηp²) values are reported as a measure of effect size. Significant results for the repeated measures ANOVAs were examined via Tukey’s honestly significant difference (HSD) test and simple effects tests to determine the locus of the differences.
Results

A summary of the results for all dependent measures, including mean and standard deviations, are provided in Table 3.1. Figure 3.1 shows limb displacement and EMG data (rectified and smoothed by 20-point averaging) for a representative control trial (top) and startle trial (bottom). Overall PMT values during startle trials suggest that the movement was prepared in advance and triggered by the startle throughout the acquisition period. With practice, participants showed improvement at the between-limb timing delay in both control and startle trials; however during startle trials the delay was consistently shorter. Furthermore, startle trials produced faster movements, larger endpoint error, and a within-limb muscle activation pattern that was temporally compressed.
Table 3.1 Experimental results for each stimulus type, arm and testing condition, showing means and standard deviations (bracketed). AG1 = initial agonist burst (triceps), ANT = antagonist burst (biceps), AG2 = second agonist burst (triceps). Note that arm delay only has one value for both limbs. Also note that premotor RT is equivalent to AG1 onset for the right arm.

<table>
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<th>Control Condition</th>
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<tbody>
<tr>
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<td>Arm Delay (ms)</td>
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<tr>
<td>Endpoint CE (deg)</td>
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<td>AG1 Onset (ms)</td>
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<td>AG2 Duration (ms)</td>
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<tr>
<td>AG2 Duration (ms)</td>
<td>82.2 (13.9)</td>
<td>90.9 (10.4)</td>
</tr>
<tr>
<td>Q30 (mV*ms)</td>
<td>2.25 (2.01)</td>
<td>2.25 (2.26)</td>
</tr>
</tbody>
</table>
Figure 3.1 Limb displacement and EMG data (AG = agonist, ANT = antagonist, SCM = sternocleidomastoid) for a representative control (top) and startle (bottom) trial. Note that startle trials were performed with a shortened latency, increased EMG activity and increased peak limb displacement. Also note that during startle trials the within-limb EMG pattern was temporally compressed such that antagonist was activated earlier relative to the agonist onset.
PMT

As predicted, analysis of PMT confirmed a main effect for stimulus type ($F(1, 9) = 54.19, p < .001, \eta^2_p = .86$) whereby startle trials exhibited a significantly shorter PMT ($M = 90$ ms) compared to control trials ($M = 156$ ms). PMT values during startle trials were consistent with previous experiments involving arm movements that have suggested that such short reaction times are due to triggering of the pre-programmed response (i.e., Carlsen et al., 2004a, 2007; Carlsen, Chua, Inglis, Sanderson & Franks, 2009). There was also a main effect for block ($F(3, 27) = 3.60, p = .026, \eta^2_p = .29$) which was due to a significant decrease in PMT from block 1 ($M = 132$ ms) to block 3 ($M = 116$ ms). This relatively small decrease in PMT with practice also suggests that participants fully prepared the required response in advance throughout the acquisition period (see Maslovat et al., 2008 for similar results), as a change in advance preparation is usually accompanied by a larger decrease in RT (e.g., Klapp, 1995).

Kinematics

Arm delay means for the four testing sessions for control and startle trials are shown in Figure 3.2. Arm delay showed a significant main effect for block ($F(3, 27) = 3.66, p = .036, \eta^2_p = .29$) and stimulus type, ($F(1, 9) = 24.64, p = .001, \eta^2_p = .73$). No significant interaction effects were found. These results confirmed that while participants improved performance of the arm delay with practice, performance was consistently different in control trials versus startle trials. Post hoc analyses of the block effect confirmed that performance on the first testing block was significantly different to performance on the remaining three blocks. For control trials, participants underestimated the required 100 ms between-arm delay in the first testing block ($M = 81$ ms) but
approached the criterion by the second block of testing \((M = 97 \text{ ms})\). Performance during startle trials also improved with practice; however the timing of the arm delay was significantly shortened throughout testing \((\text{early } M = 35\text{ms}, \text{ late } M = 59\text{ms})\).
Figure 3.2 Mean (SEM) between-arm delay for each of the four testing blocks. The criterion of 100ms is shown by a dotted line. Note the startling stimulus caused a significantly shorter delay.
Movement time results, separated by block, arm and stimulus type are shown in Figure 3.3. The analysis of MT confirmed a main effect for arm \(F(1, 9) = 48.16, p < .001, \eta^2_p = .84\) and stimulus type \(F(1, 9) = 13.10, p = .006, \eta^2_p = .59\). The main effect of arm was due to a slower MT for the left arm \((M = 320 \text{ ms})\) compared to the right \((M = 252 \text{ ms})\) and the main effect of stimulus type was due to a speeded MT during startle trials \((M = 263 \text{ ms})\) compared to control trials \((M = 308 \text{ ms})\). These two main effects combined for a significant arm by stimulus type interaction \(F(1, 9) = 5.54, p = .043, \eta^2_p = .38\), as the right arm MT was affected by the stimulus type (startle \(M = 217 \text{ ms}\) versus control \(M = 286 \text{ ms}\)) more than the left arm (startle \(M = 309 \text{ ms}\) versus control \(M = 331 \text{ ms}\)). There was also a significant stimulus type by block interaction \(F(3, 27) = 5.40, p = .008, \eta^2_p = .38\), whereby the control trials showed a greater effect of practice (block 1 \(M = 312 \text{ ms}\) versus block 4 \(M = 290 \text{ ms}\)) compared to startle trials (block 1 \(M = 273 \text{ ms}\) versus block 4 \(M = 264 \text{ ms}\)). The only significant effect found for endpoint CE was a main effect for stimulus type \(F(1, 9) = 7.33, p = .024, \eta^2_p = .45\). This effect was due to a higher positive error value (i.e., overshooting the target) in startle trials \((M = 6.2^\circ)\) compared to control trials \((M = 2.7^\circ)\).
Figure 3.3 Mean (SEM) movement time, separated by arm and block. Note the startling stimulus caused a greater decrease in movement time, especially for the right arm.
EMG boxplots, showing the triphasic burst for both limbs during control and startle trials (collapsed by time), are shown in Figure 3.4, along with SCM burst for startle trials. Analysis of AG1 onset confirmed a main effect for arm ($F(1, 9) = 133.95, p < .001, \eta^2_p = .94$), stimulus type ($F(1, 9) = 49.26, p < .001, \eta^2_p = .85$), and a significant arm by type interaction ($F(1, 9) = 23.49, p = .001, \eta^2_p = .72$). The main effect of arm was expected as participants were required to delay initiation of the left arm relative to the right. This resulted in a significantly longer AG1 onset for the left arm ($M = 181$ ms), compared to the right arm ($M = 123$ ms). The main effect of stimulus type was also expected as startle trials should result in a faster arm initiation ($M = 108$ ms) when compared to control trials ($M = 196$ ms). However we did not expect the arm by type interaction. This result was due to a larger decrease in AG1 onset during startle trials for the left arm (control $M = 236$ ms, startle $M = 125$ ms) compared to the right arm (control $M = 156$ ms, startle $M = 90$ ms). This result is consistent with the reduction in arm delay during startle trials (Figure 3.2) but suggests that the between-limb timing was altered when startled. This has not typically been reported in startle research as previous experiments with complex, multi-component movements have shown that the temporal structure of muscle activation patterns remains consistent during startle trials (Valls-Solé et al., 1999; MacKinnon et al., 2007; Maslovat et al., 2008; Queralt, Valls-Solé, & Castellote, 2008).
Figure 3.4 Plots of triphasic EMG configurations during startle and control trials, collapsed across testing blocks. Boxes represent EMG burst durations with mean (SEM) onsets and offsets with respect to stimulus onset. AG1 represents the initial agonist (triceps), ANT represents the antagonist (biceps), AG2 represents the second agonist burst, and SCM represents the startle indicator (sternocleidomastoid). Note the temporal compression of the within-limb EMG during startle trials, as well as a reduction in time between left and right AG1.
Although the relative (i.e., between-limb) onset of the initial agonist burst was decreased during startle trials we were also interested in any changes to the within limb EMG pattern were observed during startle trials. A main effect for stimulus type was found for the time period between AG1 and ANT ($F(1, 9) = 12.56, p = .006, \eta_p^2 = .58$), the time period between AG1 and AG2 ($F(1, 9) = 22.34, p = .001, \eta_p^2 = .71$) and the duration of AG2 burst ($F(1, 9) = 17.73, p = .002, \eta_p^2 = .66$). In all cases, the startling stimulus caused a decrease in time period between muscle activations. Thus, not only did the startling stimulus decrease the delay between arms, it also had the effect of temporally compressing the EMG pattern within each arm. The only other significant finding was a main effect for arm for the time period between AG1 to AG2 onset ($F(1, 9) = 7.26, p = .025, \eta_p^2 = .45$). The longer time period between agonist bursts for the left arm ($M = 217$ ms) versus the right arm ($M = 201$ ms) is consistent with the finding of increased movement time for the left arm. The analysis of the Q30 scores showed a significant effect for stimulus type ($F(1, 9) = 9.97, p = 0.012, \eta_p^2 = .43$). This was due to significantly greater EMG activity during startle trials ($M = 1.99$ mV*ms) compared to control trials ($M = 0.96$ mV*ms).

Discussion

The purpose of the current experiment was to determine if an asynchronous bimanual movement could be prepared in advance, and whether this preparation would change as a result of practice. We were unsure if this movement could be prepared in advance as it was thought that a sequencing component would be required to perform the movement correctly. Our results indicated that this movement could be prepared in advance, as the asynchronous bimanual movement was triggered by the startling stimulus
at a latency typically seen in startle experiments involving limb movements (Carlsen et al., 2004a, 2007, 2009; Maslovat et al., 2008), and faster than expected from stimulus intensity effects alone (Carlsen et al., 2007). However, the triggered movement observed during startle trials differed substantially from those in control trials, a result not typically seen in experiments that have used a startling stimulus to trigger a voluntary response. Although a between-arm timing delay was present in early acquisition startle trials, the delay was dramatically shorter than control trials (35 ms versus 80 ms). With practice, this delay became significantly closer to the target (100 ms) in both startle and control trials; however startle trials consistently produced a shortened between-limb delay (Figure 3.2). Examination of the muscle activation patterns revealed that the within-limb EMG timing was also altered in startle trials, consisting of a reduction in the timing between the initial agonist burst and both the antagonist and second agonist burst respectively (Figure 3.4) and resulting in faster movements to the targets (especially for the right arm, see Figure 3.3). Thus although an asynchronous bimanual movement was triggered by the startling stimulus, the movement appeared to be temporally compressed both in the between-arm delay and within-arm EMG pattern.

To explain this difference in movements during startle and control trials, we hypothesize that the addition of a precise timing requirement to the movement changed how the movement was prepared. Specifically, to accurately delay the left limb by 100 ms participants would have utilized some form of timing mechanism. While many timing models have been proposed, they often explain time duration estimation via a pulse accumulator (see Macar & Vidal, 2004; Taatgen, van Rijn, & Anderson, 2007; Block & Zakay, 2008 for recent reviews). For example, Block and Zakay (1996) proposed an
attention-gate model whereby a pacemaker produces pulses at a given rate. When attention is focused on timing (rather than an external stimuli), a gate is “opened” to monitor the pulses of the pacemaker. These pulses are accumulated until a threshold is reached, which is based on a reference memory store that would be affected by previous performance. Two important points come from the description of this model. First, the pulses of the pacemaker only become meaningful when attention is focused on the timing of an event, such as would be expected for an asynchronous movement with a specified delay. Second, the rate of pacemaker pulses is affected by the participant’s arousal level (Triesman, 1963; Block & Zakay, 1996). In fact, a number of studies have shown that when arousal level is increased, participants are prone to underestimating time intervals which has been attributed to an increase in pacemaker speed (Meck, 1996; Penton-Voak, Edwards, Percival, & Wearden, 1996; Gruber & Block, 2005). We suggest that the use of an intense startling stimulus may have increased participants’ arousal level, and thus affected the pacemaker rate. A faster pacemaker would result in a shorter between-arm delay and potentially a condensed within-arm EMG pattern.

While arousal was not specifically measured, there is indirect evidence from the current study suggesting that the startling stimulus increased neural activation. During startle trials, participants increased their endpoint error by overshooting the target and showed greater EMG activity (as measured by Q30). Both these results have been found in previous startle experiments and have been attributed to increased activation levels (Carlsen et al., 2004a; Maslovat et al., 2008). If the startling stimulus causes an increase in arousal level and thus the rate of the pacemaker, it may seem surprising that previous startle experiments have not shown a modification in timing of the movement. However,
the increase in pacemaker pulse-rate would only be evident for tasks that require
participants to specifically focus on timing, a manipulation which has not been explicitly
explored in previous startle experiments. There is considerable evidence that how a
movement is performed may affect the timing mechanism used. For example, it has been
suggested that timing in discrete movements is controlled by an explicit clock-like
mechanism while timing in continuous movements is an emergent property related to
movement control (Robertson et al., 1999; Zelaznik, Spencer, & Doffin, 2000; Zelaznik,
Spencer, & Ivry, 2002; Summers, Maeder, Hiraga, & Alexander, 2008). Similarly,
different neural systems have been implicated in tasks involving explicit timing (i.e.,
over estimate of duration) versus implicit timing (i.e., timing is a byproduct of a non-
temporal task goal, even if responses adhere to a strict temporal framework) (Coull &
Nobre, 2008). Thus, we believe the requirement of timing a specific delay duration
between the limbs required participants to implement a different timing mechanism than
would be used for a movement not requiring an explicit time estimation.

We have concluded that the current results suggest that the entire asynchronous
bimanual movement can be prepared in advance, and that differences between startle and
control trials can be explained by an increase in pacemaker pulse-rate due to the startling
stimulus. Before we discuss how this finding adds to our knowledge of advance
preparation, it is worthwhile investigating whether our results could be explained by a
different conclusion. One alternative is that participants only prepared the first movement
component in advance, with the second movement programmed on-line. However, if this
occurred we would predict the startling stimulus would have only triggered the right arm
movement while the left limb movement would have to be prepared after the “go” signal.
This should result in longer arm delays during startle trials rather than the shorter arm delays that we observed. Examination of individual startle trials confirmed that only six trials (out of 115) had a between-arm delay that was longer than the required 100 ms, making this alternative explanation unlikely. Another alternative explanation is that participants prepared both limb movements in advance, but not the sequencing/delay component. This preparation would have resulted in the startling stimulus triggering both arm movements such that the bimanual movement would be produced in a synchronous manner (i.e., no delay between the arms). Although a short between-arm delay (< 10 ms) occurred on some startle trials (9 out of 115 trials, all from three participants), this did not appear to be a consistent result. However, it is possible that the startle triggered both movements, and the reported arm delay simply represents an asymmetry in movement due to a right-hand dominance. Continuous bimanual movements, such as circle drawing have shown a delay in the non-dominant hand in the order of 15-40 ms when asked to move synchronously (Stucchi & Viviani, 1993; Swinnen, Jardin, & Meulenbroek, 1996). We do not think this explanation is applicable, as we have previously shown that a symmetrical bimanual movement can be performed with a minimal between-arm delay during both startle and control trials (approximately 1-2 ms; Maslovat et al., 2008). Additionally, the delay between arms increased during startle trials as a result of practice, a result which would not be predicted if the delay was solely due to differences in reaction time between the arms.

Although previous research involving unimanual movements has shown that multiple elements cannot be prepared in advance (e.g., Adam et al., 2000; Vindras & Viviani, 2005; Khan et al., 2006), our results suggest that preparation of a sequenced
bimanual movement may be qualitatively different. Specifically, the difficulty in preparing a multiple component unimanual movement may relate to uncertainty regarding the exact starting position of the second component, due to variability in the first movement. That is, if the performer does not know precisely where and when the second component is to be produced, it may be difficult to prepare the movement characteristics in advance. With practice, advance preparation of a sequenced unimanual movement may be possible (as shown by Klapp, 1995) because participants become more consistent with the initial component, thus allowing for the second movement to be prepared in advance and “chunked” with the first movement. These restrictions on preparation would not apply to a bimanual movement, as the effectors used are independent and thus the starting position of both movements is known in advance.

3 A number of methodologies have been used to examine the preparation processes associated with bimanual movements. These have included the examination of spatial assimilation effects for simultaneous and sequential discrete bimanual movements (e.g., Sherwood, 1994, 2006), as well as interference effects during dual-task performance conditions (see Pashler, 1994 for a review). Similarly, continuous bimanual tasks have also received extensive investigation to explore the control processes involved in limb coordination (see Swinnen & Wenderoth, 2004 for a recent review). A common finding in all paradigms is the difficulty in performing bimanual movements when different parameters are required for each limb, such as timing, amplitude, force or direction.
In conclusion, the current results suggest that an asynchronous bimanual movement can be prepared in advance and triggered by a startling stimulus. Furthermore, practice-related changes in preparation were evident in both control and startle trials, confirming that startle methodology is an effective tool to examine the preparation process during skill acquisition. We have also shown that a movement triggered by a startling stimulus can change in temporal structure if the participant is forced into an explicit timing requirement. When required to accurately time an interval, participants may use a timekeeper that is affected by the startling stimulus. Overall these results add to our knowledge of how advance preparation occurs for sequenced bimanual movements, and how practice improves the preparation process.
Bridging Summary to Following Chapters

The results of the current experiment provided evidence that an asynchronous bimanual movement could be prepared in advance and triggered by a startling stimulus. Similar to Experiment 1, improvements in performance (i.e., arm delay) with practice were found in both startle and control trials, although the delay was reduced in startle trials. The reduction in delay time for startle trials suggested that the preparation of timing may differ from that of movement amplitude. We hypothesized that participants relied on an internal timekeeper to perform the movement, and that the pulse rate of the timekeeper was affected by arousal level. To further investigate differences between spatially and temporally based movements our next experiment directly compared the preparation of movements defined with different goals. We expected movements that were defined with a temporal goal would be prepared in a different manner to those defined with a spatial goal, and these preparation differences would be reflected in the movements triggered by the startling stimulus.
4. Experiment 3

Motor Preparation of Spatially and Temporally Defined Movements: Evidence from Startle

Introduction

Researchers have employed many techniques to examine the processes associated with response preparation in an attempt to determine how we perform the many complex tasks in day to day life. One of the more recent methodologies used involves the use of a loud acoustic stimulus capable of eliciting a startle response (see Carlsen, Maslovat, Lam, Chua, & Franks, in press; Valls-Solé, Kumru, & Kofler, 2008 for recent reviews). During a simple reaction time (RT) task, where the required response is known in advance, replacing the “go” signal with a loud (>124dB) startling stimulus has been shown to elicit the prepared response at a much shorter latency. Given the dramatic reduction of premotor reaction times (<80ms), it has been hypothesized that the startling stimulus can act as a trigger for a pre-programmed response, bypassing the usual voluntary command processes (Valls-Solé, Rothwell, Goulart, Cossu, & Muñoz, 1999; Carlsen, Chua, Inglis, Sanderson, & Franks, 2004b). This hypothesis has been supported by a number of studies showing that startle effects are distinct from and larger than stimulus intensity effects (Carlsen, Dakin, Chua, & Franks, 2007), and only occur when the participant has prepared the response in advance (Valls-Solé et al., 1999; Carlsen, Chua, Inglis, Sanderson, & Franks, 2004a; Rothwell, 2006).

Studies employing a startling stimulus have consistently shown that the movement triggered during startle trials is similar in movement kinematics and EMG configurations to that of control trials. This has been shown for such diverse tasks as upper arm and wrist movements (e.g., Carlsen et al. 2004b, Maslovat, Carlsen, Ishimoto, Chua, & Franks, 2008; Valls-Solé, et al., 1999), stepping and gait initiation (MacKinnon et al., 2007; Reynolds & Day, 2007; Queralt, Valls-Solé, & Castellote, 2010), head
rotations (Oude Nijhuis et al., 2007; Siegmund, Inglis, & Sanderson, 2001), sit to stand (Queralt, Valls-Solé, & Castellote, 2008) and rise to tiptoes (Valls-Solé, et al., 1999). However, most of these experiments have used a spatially defined movement whereby participants move to a predetermined target as fast as possible. When a timing requirement is added to the movement, it appears that the startling stimulus triggers a movement with different characteristics than control trials. A startling stimulus was used during practice of a bimanual arm movement that required a 100 ms delay period between initiation of the limbs (Maslovat, Carlsen, Chua, & Franks, 2009). While participants were able to perform this delay accurately in control trials, the timing delay was dramatically shorter in startle trials. Examination of the muscle activation patterns revealed a difference in within-limb EMG timing for startle versus control trials whereby the triphasic muscle burst (i.e., between initial agonist onset and antagonist onset and between antagonist onset and second agonist onset) was compressed in startle trials.

To explain why the startle trials produced movements that were compressed in time, the authors hypothesized that the addition of a precise timing requirement changed how the movement was prepared. To accurately delay a limb by 100 ms participants would have relied on some sort of internal timer which was likely affected by the startling stimulus. The results and hypothesis were consistent with Block and Zakay’s (1996) attention-gate model of timing, whereby a pacemaker produces pulses at a given rate. When attention is focused on timing, a gate is “opened” to monitor the pulses of the pacemaker, which are accumulated until a threshold is reached. However, the rate of these pacemaker pulses is affected by the participant’s arousal level (Block & Zakay, 1996; Triesman, 1963). During startle trials, arousal is expected to increase, thus causing
an underestimation of time duration (Maslovat et al., 2009). It is worth noting that temporal control of a movement (Ivry, Keele, & Diener, 1988) and control of the triphasic EMG pattern (Flament & Hore, 1986; Hiraoka, Sugiyama, & Abe, 2009; Hore, Wild, & Diener, 1991) are both thought to be important functions of the cerebellum.

There is other evidence that the preparation and performance of a movement is dependent upon whether the goals of the task are expressed spatially or temporally. For example, the relationship between speed and accuracy of movement appears to be different depending on how movements are defined. In the original investigation of the speed-accuracy tradeoff, spatial characteristics of targets were manipulated and participants were required to tap back and forth as quickly as possible (Fitts, 1954). This manipulation produced a logarithmic relationship between the “index of difficulty” of the target and speed of movement. Alternatively, asking participants to perform a rapid single aiming movement to a given target in a required movement time produced a linear relationship between speed and accuracy, whereby faster movements produced more variability of endpoint and thus less accurate performance (Schmidt, Zelaznik, Hawkins, & Frank, 1978; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). One reason given for the difference in the speed-accuracy tradeoff was a difference in the movement goal, as in one scenario movement time is controlled while in the other spatial accuracy is maintained and controlled (Zelaznik, Mone, McCabe, & Theman, 1988). The use of a spatial target encouraged participants to use a time-minimization control strategy versus a temporal-precision strategy (Carlton, 1994).

While we have evidence that the process of preparation of a timed movement is different to that of a spatially defined movement, the underlying mechanisms of
movement preparation under temporally controlled conditions are still unclear. It has been suggested that the “strategy” underlying the control of single joint movements is dependent upon how the goals of the task are represented (Gottlieb, Corcos, & Agarwal, 1989b). When movements of varying distance are required to be performed as fast and accurately as possible (known as speed-insensitive movements), the organizing principle of the nervous system involves modulation of the duration of motor neuron excitation (Gottlieb, Corcos, & Agarwal, 1989a). This is reflected in the duration of the EMG burst of the agonist muscle. Conversely, when movements are required to be performed at different velocities (known as speed-sensitive movements), the organizing principle of the nervous system involves modulation of the amplitude or intensity of motor neuron excitation (Corcos, Gottlieb, & Agarwal, 1989). This is reflected in a change to the initial slope of the rise of the EMG burst in the agonist muscle. More recently, through the collection of fMRI and EEG data, it has been found that different neural activation patterns are involved in the timing of movement initiation as compared to planning of the specific sequence of motor output, further suggesting these processes may involve different mechanisms (Bortoletto & Cunnington, 2010).

The purpose of this study was to examine preparation differences in temporally defined versus spatially defined movements through the use of a startling stimulus and manipulation of the goals of the task. The use of a startling stimulus allowed us to determine if different control parameters were prepared and stored in advance for spatial versus temporally based movements. We also examined whether there was evidence of reliance on a timekeeper for the time-constrained movements, as this would be reflected by movements compressed in time. Participants performed movements of different
spatial amplitudes and temporal requirements, with startle trials interspersed with control trials. For the spatially defined movements, we expected participants to pre-program motor commands that would result in different agonist burst durations for the various movement amplitudes (Gottlieb et al., 1989a). As participants would not require the use of a timekeeper to complete these movements it would be expected that the startling stimulus would trigger a movement with similar kinematics and EMG pattern as compared to control trials but at much shorter onset latencies (Carlsen et al., 2004b). We predicted that the increased agonist burst duration with increasing movement amplitude would be present during control and startle trials as these commands would be prepared and stored in advance.

For the temporally defined movements, we expected participants to pre-program motor commands that would result in different rate of increase of agonist activation for the different movement velocities (Corcos et al., 1989). In addition, to perform the timed movement accurately, participants would be required to rely on an internal timekeeper whose pacemaker pulse would be accelerated on startle trials due to increased arousal level. Thus it was expected that the startling stimulus would trigger a movement at short onset latency with condensed kinematics and EMG pattern as compared to control trials (Maslovat et al., 2009). While we expected the modulation of agonist rise-rate with changing movement velocity, we were unsure if this effect would be observable on startle trials. Previous research has reported that a startling stimulus increases neural activation levels (Carlsen et al., 2004a), which has been shown to increase the rate of agonist rise (Maslovat et al., 2008, 2009). This increased activation may overshadow the differences in prepared intensity. In addition to independently examining the spatially and temporally
defined movements, we also directly compared movements that were defined by different goals. We predicted that the use of a timekeeper for the temporally constrained movements would result in movement compression on startle trials as compared to the spatially defined movements.

**Methods**

**Participants**
Fifteen right-handed volunteers with no obvious upper body abnormalities or sensory or motor dysfunctions participated in the study after giving informed consent. However, only data from twelve right-handed volunteers (4 male, 8 female; M = 20.9 yrs, SD = 1.5 yrs) were employed in the final analysis. Three participants did not show consistent activation in the sternocleidomastoid muscle during startle trials (which is thought to be the most reliable indicator of a startle response), and thus were excluded from the analysis (see Carlsen et al. in press, for more detail regarding the exclusion criteria for participants). All participants were naïve to the hypothesis under investigation and this study was conducted in accordance with ethical guidelines established by the University of British Columbia.

**Apparatus and Task**
Participants sat in a height-adjustable chair in front of a 22-inch color monitor (Acer X233W, 1152 x 864 pixels, 75 Hz refresh) resting on a table. Attached to the table on the right side of the monitor was a lightweight manipulanda that participants used to perform horizontal flexion-extension movements about the right elbow joint. Participants’ arms and hands were secured with Velcro straps to the manipulanda with the elbow joint aligned with the axis of rotation and the hands semi-supinated to grasp a
vertical metal rod. The home position for each arm was located such that a 30° extension movement resulted in the arms being straight ahead (i.e., perpendicular to the monitor on the table), and was defined as 0°. Targets were located on the table top at 20°, 40°, and 60° of extension from the home position.

In response to an auditory “go” signal, the participants were asked to perform either a spatially-defined movement to one of the three targets (day 1) or movement to the 20° target with a given timing requirement (day 2). Participants were instructed to look straight ahead at the monitor and respond by initiating a movement as fast as possible and performing the movement as accurately as possible. Accuracy was defined in terms of spatial error on day 1 and timing error on day 2. The timing requirement on day 2 for each participant was based on their performance on day 1. We took the mean time to peak displacement for each of the three targets as timing goals for the second day of testing. Thus the short movement on day 1 was comparable to the fastest movement on day 2, although the goal of the movement was represented in a different manner (spatially on day 1, temporally on day 2). The movement times to the medium and long target on day 1 resulted in a moderate and slow movement to the short target on day 2. For the timing requirement we used time to peak displacement rather than the full movement time as pilot testing revealed that most subjects took considerable time after peak displacement to stop their movement. This resulted in very long movement times which would have changed the kinematics of how the movements would be performed on day 2, thus not allowing a between day comparison of the short movement. Participants were informed that feedback would be provided based on peak displacement of the movement produced.
Participants performed two testing sessions (approximately 60 minutes) on consecutive days. Each testing session began with a maximal voluntary contraction (MVC) of the agonist (triceps) and antagonist (biceps) muscles of the right arm to allow for between-day comparisons of EMG activity. Next participants performed three blocks of trials, which included 10 practice trials and 46 testing trials. Each block contained movements to a single target (day 1) or time goal (day 2) and order of blocks was counterbalanced between participants. The order of movements was maintained between days for each participant. Thus, if a participant practiced the short (20°), medium (40°), and long (60°) movement in order on day 1, their presentation order on day 2 would have been fast, moderate and slow. During the testing phase of each movement, 6 of the 46 trials were startle trials, with no startles presented in the first 10 trials and no two consecutive startle trials. Augmented feedback was not provided during the trial, however terminal feedback was provided on the monitor for five seconds following the trial that included reaction time (RT, in ms) and an accuracy score, expressed as a constant error (CE) of either peak displacement (day 1, in degrees) or movement time to peak displacement (day 2, in ms). To encourage fast and accurate responses, a monetary bonus was offered for accurate movements and fast RTs respectively.

All trials began with a warning tone consisting of a short beep (80 +/-2 dB, 100 ms, 100 Hz) presented simultaneously with the word “Ready!” and a visual precue on the computer screen. The visual precue consisted on day 1 of either: short target (20°); medium target (40°); or long target (60°); and on day 2 as a specific time goal to reach the short target. The “go” signal followed the warning tone by a random foreperiod of 2500-3500 ms and could either consist of a control stimulus (80 +/-2 dB, 100 ms, 1000
Hz) or startling stimulus (124 +/-2 dB, 40 ms, 1000 Hz, <1 ms rise time). All auditory signals were generated by a customized computer program and were amplified and presented via a loudspeaker placed directly behind the head of the participant. The acoustic stimulus intensities were measured using a sound level meter (Cirrus Research model CR:252B) at a distance of 30 cm from the loudspeaker (approximately the distance to the ears of the participant).

Recording Equipment

Surface EMG data were collected from the muscle bellies of the following superficial muscles: right lateral head of the triceps brachii (agonist), right long head of the biceps brachii (antagonist), and right and left sternocleidomastoid (startle indicator) using preamplified surface electrodes connected via shielded cabling to an external amplifier system (Delsys Model DS-80). Recording sites were prepared and cleansed in order to decrease electrical impedance. The electrodes were oriented parallel to the muscle fibers, and then attached using double sided adhesive strips. A grounding electrode was placed on the participant’s right ulnar styloid process. Arm angular displacement was measured using potentiometers (Precision, MD157) attached to the central axis of the manipulanda, which had a precision of 0.07°/bit. A customized LabView® computer program controlled stimulus and feedback presentation, and initiated data collection at a rate of 1 kHz (National Instruments, PC-MIO-16E-1) 500 ms before the presentation of the “go” signal and terminated data collection 2000 ms following the “go” signal.
Data Reduction

Analysis was restricted to the testing trials only (practice trials were not analyzed). A total of 42 of the 3312 trials were discarded (1.3%). Reasons for discarding trials included displacement reaction time less than 80 ms (i.e., anticipation, 25 trials) or in excess of 500 ms (2 trials), movements to an incorrect target (13 trials), and startle trials in which no detectable startle response (SCM activity) was observed (2 trials).

Surface EMG burst onsets were defined as the point at which the EMG first began a sustained rise above baseline levels. The location of this point was determined by first displaying the EMG pattern with a superimposed line indicating the point at which activity increases to more than 2 standard deviations above baseline (mean of 100 ms of EMG activity preceding the go signal). Onset was then verified by visually locating and manually adjusting the onset mark to the point at which the activity first increased. This method allowed for correction of errors of the algorithm. EMG offsets were marked in a similar fashion, with the activity between EMG onset and EMG offset being defined as the duration of a muscle burst.

Initial movement onset was defined as the first point of change of more than 0.2° of angular displacement from the starting position following the “go” stimulus, while peak displacement was defined as the first point at which displacement decreased following movement initiation. Final position was defined as the point at which angular velocity fell below 8°/s and remained below this value for 50 ms. As previously mentioned we chose to use time to peak displacement as our criterion for movements on the second day as participants often require considerable time to slow their movements to
under 8°/s for 50 ms. We felt this marker would ensure the short movement on day 1 would be similar in kinematics to the fast movement on day 2.

**Dependent Measures and Statistical Analyses**

All dependent measures were analyzed separately for the spatially-based movements on day 1 and the temporally-based movements on day 2 via a 2 Stimulus Type (control, startle) x 3 Movement (short/fast, medium/moderate, long/slow) repeated measures analysis of variance (ANOVA). We also compared the short movement on day 1 to the fast movement on day 2 via a 2 Stimulus Type (control, startle) x 2 Day repeated measures ANOVA. These movements were compared because they were movements of the same amplitude but defined spatially on day 1 and temporally on day 2. We did not compare the other movements between days as they were movements of different amplitudes.

To compare EMG patterns, burst onsets and durations were calculated for the triphasic pattern for each movement including first agonist burst (AG1), antagonist burst (ANT), and second agonist burst (AG2). EMG dependent measures included time from stimulus onset to AG1 onset (i.e., premotor RT or PMT) to examine whether the startling stimulus initiated the movement at latency values that would suggest the movement was prepared in advance and triggered by the startling stimulus. We examined the relative timing between the onset of the first agonist burst and onset of the antagonist (AG1-ANT) and the first agonist burst and second agonist burst (AG1-AG2). We also separately analyzed the duration of each of the three burst durations. To quantify intensity of motor neuron excitation we integrated the rectified raw EMG trace for the first 30 ms of the first agonist burst, which represents the initial slope of the rise in EMG (Q30,
Corcos et al. 1989; Gottlieb et al. 1989; Khan et al. 1999; Maslovat et al. 2008, 2009). To compare kinematics of the movements, we examined time to peak velocity (TTPV), time to peak displacement (TTPD), and total movement time.

For the repeated measure ANOVAs, the Greenhouse-Geisser Epsilon factor was used to adjust the degrees of freedom for violations to sphericity. Uncorrected degrees of freedom are reported, with the corrected $p$ values. Partial eta squared ($\eta^2$) values are reported as a measure of effect size. The alpha level for the entire experiment was set at .05, and where appropriate significant results were examined via Tukey’s honestly significant difference (HSD) test and simple effects tests to determine the locus of the differences.

Results

A summary of the results for all dependent measures, including means and standard deviations are provided in Table 4.1. To represent overall performance, we created ensemble averages for each condition showing displacement and velocity curves in order to represent data from all trials from all participants (i.e., 480 trials for control, 72 trials for startle). This was achieved by normalizing each trial in time to displacement onset, which was considered time 0. These normalized averages are shown for control and startle trials for all three movements for spatially defined movements on day 1 (Figure 4.1, top panels), temporally constrained movements on day 2 (Figure 4.1, middle panels) and a comparison of the short movement on day 1 to the fast movement on day 2 (Figure 4.1, bottom panels). EMG boxplots are shown in Figure 4.2 with the relative timing of the triphasic burst for each condition (including SCM activation for startle trials) for day 1 (top panels) and day 2 (bottom panels). These represent grand means for
startle and control trials for each movement on each day, and are normalized with respect to the “go” signal (and thus show PMT differences as well). We have also provided ensemble group averages for rectified raw agonist and antagonist EMG activation for all conditions (Figure 4.3). These graphs represent trials normalized to displacement onset (time 0) and EMG activation normalized as a percentage of the MVC trials. Overall the results confirmed that the agonist duration was modulated during the spatially defined movements and agonist rise time was modulated during the temporally constrained movements. The startling stimulus had the effect of speeding up both spatially and temporally defined movements, however for the temporally based movements this compression was more pronounced for the slower movements.
Table 4.1 Experimental results for each day, stimulus type and movement, showing means and standard deviations (bracketed). AG1 = initial agonist burst (triceps), ANT = antagonist burst (biceps), AG2 = second agonist burst (triceps).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Startle</th>
<th>Day 1 – Spatially Defined Movements</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Short (20°)</td>
<td>Medium (40°)</td>
<td>Long (60°)</td>
</tr>
<tr>
<td>Premotor RT (ms)</td>
<td>127.6 (17.9)</td>
<td>130.7 (17.0)</td>
<td>137.0 (19.6)</td>
</tr>
<tr>
<td>AG1-ANT time (ms)</td>
<td>86.4 (25.5)</td>
<td>108.3 (27.7)</td>
<td>128.5 (29.4)</td>
</tr>
<tr>
<td>AG1-AG2 time (ms)</td>
<td>153.1 (22.4)</td>
<td>180.0 (25.7)</td>
<td>201.7 (28.8)</td>
</tr>
<tr>
<td>AG1 Duration (ms)</td>
<td>98.6 (16.2)</td>
<td>114.5 (15.7)</td>
<td>130.9 (16.9)</td>
</tr>
<tr>
<td>AN T Duration (ms)</td>
<td>92.4 (9.7)</td>
<td>106.1 (17.3)</td>
<td>111.0 (18.2)</td>
</tr>
<tr>
<td>AG2 Duration (ms)</td>
<td>78.2 (8.8)</td>
<td>84.9 (13.5)</td>
<td>92.0 (12.4)</td>
</tr>
<tr>
<td>AG1 Q30 (mV*ms)</td>
<td>1.52 (0.60)</td>
<td>1.64 (0.73)</td>
<td>1.67 (0.74)</td>
</tr>
<tr>
<td>Time to Peak Vel (ms)</td>
<td>74.5 (12.2)</td>
<td>96.3 (14.7)</td>
<td>106.5 (17.9)</td>
</tr>
<tr>
<td>Time to Peak Dx (ms)</td>
<td>161.1 (27.9)</td>
<td>206.8 (40.0)</td>
<td>256.7 (44.0)</td>
</tr>
<tr>
<td>Total Movement Time (ms)</td>
<td>242.4 (32.4)</td>
<td>285.0 (42.3)</td>
<td>344.4 (41.4)</td>
</tr>
</tbody>
</table>

| Variable                  | Fast             | Moderate          | Slow             | Fast             | Moderate          | Slow             | Day 2 – Temporally Defined Movements |
|---------------------------|------------------|-------------------|------------------|------------------|-------------------|------------------|
|                           | Control          | Startle           |                  |                  |                   |                  |
|                           | Short (20°)      | Medium (40°)      | Long (60°)       | Short (20°)      | Medium (40°)      | Long (60°)       |
| Premotor RT (ms)          | 124.6 (18.5)     | 128.5 (19.6)      | 126.7 (16.2)     | 85.4 (9.6)       | 85.9 (7.7)        | 87.6 (10.0)      |
| AG1-ANT time (ms)         | 81.5 (22.4)      | 91.4 (22.1)       | 101.1 (21.8)     | 65.5 (14.6)      | 71.1 (15.8)       | 72.3 (23.4)      |
| AG1-AG2 time (ms)         | 158.3 (17.1)     | 169.6 (18.8)      | 190.0 (22.9)     | 138.8 (10.3)     | 146.5 (12.9)      | 154.6 (20.7)     |
| AG1 Duration (ms)         | 100.6 (12.5)     | 107.2 (11.6)      | 113.0 (14.0)     | 92.2 (7.8)       | 96.3 (9.8)        | 95.8 (11.9)      |
| ANT Duration (ms)         | 102.8 (12.1)     | 106.7 (11.7)      | 117.9 (13.2)     | 91.5 (22.3)      | 96.8 (17.7)       | 100.05 (21.1)    |
| AG2 Duration (ms)         | 81.6 (6.3)       | 85.6 (6.6)        | 92.3 (11.5)      | 75.3 (7.3)       | 80.2 (8.7)        | 85.7 (12.0)      |
| AG1 Q30 (mV*ms)           | 1.56 (0.87)      | 1.29 (0.62)       | 1.08 (0.45)      | 2.33 (1.19)      | 2.12 (1.25)       | 2.32 (1.48)      |
| Time to Peak Vel (ms)     | 77.0 (10.3)      | 86.0 (12.7)       | 96.5 (16.7)      | 58.4 (5.6)       | 61.3 (7.5)        | 68.4 (11.7)      |
| Time to Peak Dx (ms)      | 171.2 (26.4)     | 195.6 (36.8)      | 239.0 (42.6)     | 126.5 (14.6)     | 137.9 (21.2)      | 165.9 (39.9)     |
| Total Movement Time (ms)  | 233.1 (25.3)     | 256.0 (31.3)      | 279.5 (34.1)     | 228.7 (37.3)     | 243.0 (46.7)      | 255.2 (53.2)     |
Figure 4.1 Ensemble averages for displacement (left panel) and velocity (right panel) for each movement on day 1 (top panel - 20°, 40°, and 60° movements) and day 2 (middle panel – fast, moderate, and slow movements) for non-startle (NS) and startle (ST) trials. All values were normalized to displacement onset which was considered relative time 0. Note the effect of startle on all movements on both days whereby movements are performed faster; however the startling stimulus had a differential rate of compression on the temporally-based movements on day 2 (middle panel). The lower panel compares the short movement on day 1 and the fast movement on day 2.
Figure 4.2 Plots of triphasic EMG configurations (first agonist burst, antagonist burst, second agonist burst) during startle and control trials for each movement on day 1 (top panel) and day 2 (bottom panel). Note the early latency of startle trials and the presence of sternocleidomastoid (SCM) activation as a startle indicator. Also note for spatially defined movements (top panel) agonist duration is affected by movement amplitude.
Figure 4.3 Group ensemble averages for EMG (primary y-axis) and displacement (secondary y-axis) for each movement. Trials are separated by control (left panels) and startle (right panels) values for spatially based (top panels) and temporally constrained (bottom panels) movements. Data was normalized to displacement onset (time 0) and rectified, raw agonist and antagonist values were normalized to a percentage of MVC. Note the difference in agonist duration for spatially based movements performed on day 1 (top panels) and the difference in agonist amplitude for temporally based movements performed on day 2 (bottom panels).
Mean PMT values for control and startle trials for all three movements on day 1 and 2 can be seen in the EMG boxplots (Figure 4.2). As expected, the startling stimulus caused participants to initiate the movements at significantly shorter PMT values on both day 1, $F(1, 11) = 88.05, p < .001, \eta^2_p = .89$, and day 2, $F(1, 11) = 44.20, p < .001, \eta^2_p = .80$. Startle trials were performed at latencies short enough ($M = 86$ ms for both days) to suggest that a pre-programmed response was triggered, bypassing the usual voluntary command and cortical processing pathways (Valls-Solé et al., 1999; Carlsen et al., 2004b). No differences between the various movements were found for startle or control trials on either day. The analysis of the short movement between days showed a main effect of stimulus type, $F(1, 11) = 55.34, p < .001, \eta^2_p = .83$, whereby startle trials were performed at a shorter latency ($M = 86$ ms) compared to control trials ($M = 126$ ms), but the PMTs did not differ for the two types of movement between days, $F<1$.

Spatially Based Movements

Examination of the relative phasing of the EMG pattern on day 1 revealed that the triphasic muscle pattern was compressed for shorter amplitude movements in comparison to the longer movements and by the startling stimulus for all movements. This was confirmed by a significant main effect for movement amplitude and stimulus for all EMG pattern dependent measures (AG1-ANT, AG1-AG2, and duration of all three bursts), with no significant interaction effects. We were most interested in the duration of the AG1 burst as this is thought to be the variable that is modulated for movements of different amplitudes (Gottlieb et al., 1989a). As predicted, the main effect for movement amplitude, $F(2, 22) = 80.01, p < .001, \eta^2_p = .88$, was due to a significant difference
between all three movements (short \( M = 95 \) ms, medium \( M = 111 \) ms, long \( M = 125 \) ms). The lack of Movement x Stimulus Type interaction and examination of means (Table 4.1) confirmed this effect was present for both control and startle trials. For the analysis of EMG rise time, Q30 showed a main effect for stimulus, \( F(1, 11) = 13.43, p = .004, \eta_p^2 = .55 \), due to higher activation for startle trials \( (M = 2.1 \text{ mV*ms}) \) as compared to control trials \( (M = 1.6 \text{ mV*ms}) \). No effect of movement amplitude was found for Q30 \( (p = .723) \), which is consistent with rise-time not being a control parameter for movements performed as fast as possible.

Consistent with the EMG pattern results, analysis of the kinematic variables confirmed that time to peak velocity and time to peak displacement were performed faster for startle trials as compared to control trials and for short amplitude movements compared to long amplitude movements. This was confirmed by both TTPV and TTPD showing a main effect for stimulus and movement. No interaction effects were found for TTPV but TTPD did have a significant Movement x Stimulus Type interaction, \( F(2, 22) = 4.58, p = .029, \eta_p^2 = .29 \). As all movements were significantly sped up by the startle, we examined the locus of the interaction effect by analyzing the decrease in TTPD between startle and control trials for each of the movements. This post-hoc analysis confirmed that the interaction was due to a greater decrease in TTPD for both the long \(-48 \text{ ms}\) and medium \(-48 \text{ ms}\) movements compared to the short movement \(-34 \text{ ms}\). Total movement time showed a main effect for type of movement, \( F(2, 22) = 82.48, p < .001, \eta_p^2 = .88 \), but was not affected by the startling stimulus \( (p = .852) \). Thus although the movements were sped up at the kinematic markers of TTPV and TTPD, they were completed in a similar time course in both startle and control trials.
**Temporally Based Movements**

Examination of the relative phasing of the EMG pattern on day 2 revealed that the triphasic muscle pattern was compressed for faster movements and by the startling stimulus for all movements, but also that the startling stimulus had a differential effect on the time between agonist bursts for the various movements. As with the spatially-defined movements, a significant main effect for movement speed and stimulus was found for all EMG pattern dependent measures. The time between AG1-AG2 also showed a Movement x Stimulus Type interaction effect, $F(2, 22) = 6.36, p = .016, \eta^2 = .37$, which we examined post-hoc by analyzing the decrease in time between agonist bursts for each of the movements as a result of the startling stimulus. The startling stimulus decreased the time between agonist bursts significantly more for the slow movement (-35 ms) as compared to the fast movement (-19 ms), with the moderate movement (-23 ms) not different than either of the other two movements. Although not predicted to be a control variable for temporally constrained movements (Corcos et al., 1989), the duration of AG1 showed a main effect for movement speed, $F(2, 22) = 7.47, p = .005, \eta^2 = .40$. Post-hoc tests confirmed this effect was due to a significant difference between the fast movement ($M = 96$ ms) and slow movement ($M = 104$ ms) with the moderate movement ($M = 102$ ms) not significantly different than the other movements.

As expected, the rise of EMG activity (Q30) was modulated to produce the various movement velocities, as shown by a significant effect of movement speed, $F(2, 22) = 4.92, p = .017, \eta^2 = .31$. Post-hoc tests confirmed this effect was due to a higher Q30 for the fast movement ($M = 1.9$ mV*ms) as compared to both the moderate ($M = 1.7$ mV*ms) and slow ($M = 1.7$ mV*ms) movements. Although the Movement x Stimulus
Type interaction was not significant \( (p = .122) \), examination of means (Table 4.1) suggested that the main effect for movement speed was more prevalent on control trials. For control trials the Q30 was highest for the fastest movement \( (M = 1.6 \text{ mV*ms}) \), followed by the moderate movement \( (M = 1.3 \text{ mV*ms}) \), followed by the slow movement \( (M = 1.1 \text{ mV*ms}) \), whereas for startle trials both the fast \( (M = 2.3 \text{ mV*ms}) \) and slow \( (M = 2.3 \text{ mV*ms}) \) movements were performed at slightly higher values than the moderate movement \( (M = 2.1 \text{ mV*ms}) \). Q30 also showed a main effect for stimulus, \( F(1, 11) = 21.56, p = .001, \eta_p^2 = .66 \), due to higher activation for startle trials \( (M = 2.3 \text{ mV*ms}) \) as compared to control trials \( (M = 1.3 \text{ mV*ms}) \).

In addition to confirming EMG rise-time as a control parameter for timing-based movements, we were also interested in the effect of stimulus type and movement speed on the movement kinematics. While the time between AG1-AG2 was differentially affected by the startling stimulus, so too were the kinematic variables, such that the slower movements were sped up more by the startling stimulus as compared to the faster movements. Both TTPV and TTPD showed a main effect for stimulus and movement as well as a significant Movement x Stimulus Type interaction. For TTPV, \( F(2, 22) = 6.65, p = .006, \eta_p^2 = .37 \), this interaction was due to a greater decrease for the startle trials for the slow movement (-28 ms) as compared to the fast movement (-19 ms), with the moderate movement (-25 ms) not different than either of the other two movements. Similarly the interaction for TTPD, \( F(2, 22) = 6.76, p = .007, \eta_p^2 = .38 \), was due to a greater decrease for startle trials of the slow movement (-73 ms) compared to the fast movement (-45 ms), with the moderate movement (-58 ms) not different than the either of the other two movements. While the startling stimulus sped up the slow movements
more than the fast movements, it did not result in participants performing all movements at the same velocity values (see Figure 4.1, middle panel). To confirm this we separately analyzed the startle trials of the three types of movements on day 2 and determined that all three movements were significantly different to each other with respect to TTPV and TTPD (both p values <.001). Total movement time showed a main effect for type of movement, $F(2, 22) = 9.53, p = .004, \eta_p^2 = .46$, but was not affected by the startling stimulus ($p = .101$). Similar to the spatially based movements the temporally constrained movements were completed in a similar time course in both startle and control trials, although they were sped up at the kinematic markers of TTPV and TTPD during startle trials.

Comparison of Different Movement Goals

The comparison between EMG patterns of the short movement on day 1 and 2 revealed that while the startle trials resulted in a compressed movement, the relative timing between the first agonist burst and antagonist burst was more affected by the startling stimulus on day 2 (temporally constrained) compared to day 1 (spatially constrained). A main effect for stimulus was found for all dependent measures but for this analysis we were more concerned with any differences between the testing days and hence the movement goals. The AG1-ANT time interval showed a main effect for day, $F(1, 11) = 5.71, p = .036, \eta_p^2 = .34$, which was due to a significantly shorter time between AG1-ANT for temporally constrained movements ($M = 74$ ms) compared to spatially based movements ($M = 82$ ms). Most importantly, the time between AG1-ANT showed a Day x Stimulus Type interaction effect, $F(1, 11) = 6.36, p = .028, \eta_p^2 = .37$, which was due to a significant difference between startle trials for spatially based movements ($M = \ldots$
78 ms) compared to temporally constrained movements ($M = 65$ ms), but no difference between control trials (spatial $M = 86$ ms; temporal $M = 82$ ms). As this difference in time between muscle burst onsets for startle trials was relatively small (13 ms), we performed a further post-hoc analysis of the time between AG1 and ANT expressed as a percentage of the total movement time to confirm the presence of this effect. Again, a significant Day x Stimulus Type interaction was seen, $F(1, 11) = 8.38$, $p = .015$, $\eta_p^2 = .42$, whereby the startling trials caused a significant reduction in time between AG1-ANT for temporally defined movements (from 35% of the total movement time for control trials to 29% for startle trials) whereas no difference was found for spatially defined movements (from 35% of the total movement time for control trials to 33% for startle trials). Thus, although the time differences were small in magnitude they were consistently observed between the different trial types. The time difference between the first agonist burst and antagonist is a critical component of performing the movement correctly as it determines when the braking force is applied to stop at the proper position and time.

For the kinematic variables, a comparison between the short movement on day 1 and the fast movement on day 2 showed a main effect for stimulus type only ($p < .001$) for both TTPV and TTPD. No significant effects were found for total movement time.

Discussion

We compared the preparation of temporally and spatially defined movements through the use of a startling stimulus and manipulation of the goals of the task. We predicted that spatially defined movements would be modulated by agonist burst duration, whereas temporally constrained movements would be modulated by agonist burst rise time (Gottlieb et al., 1989b). Overall the results supported the use of different
control parameters depending on how the movement was defined. For spatially defined movements, the duration of the agonist burst was varied for the different movement amplitudes and this effect was maintained in both startle and control trials. Rise time of the agonist burst did not appear to be a controlling variable for spatially-based movements as no differences were found between movement amplitudes. Conversely for temporally based movements, the rise time of the agonist burst was modulated as differences were found for the different movement velocities. Although this effect was not statistically dependent on the type of stimulus, there did appear to be a more consistent relationship between movement velocity and Q30 values for control trials as compared to startle trials. This is not surprising as EMG rise time was increased during startle trials, likely due to the increased activation associated with being startled (Carlsen et al., 2004a; Maslovat et al., 2008, 2009).

Temporally based movements also showed differences in agonist duration, which was not predicted; however the magnitude of duration differences between movements was much smaller in the timing-based movements (8 ms) as compared to the spatially-based movements (30 ms). The startling stimulus triggered all movements, irrespective of how they were defined, at very short latencies (~85 ms) that were consistent with other studies involving upper arm movements (e.g., Carlsen et al., 2004a, 2004b; Maslovat et al., 2008, 2009). This confirms that the preparation of motor commands that result in different control parameters occurred prior to the “go” signal such that they were stored in advance and triggered by the startling stimulus.

We also tested for evidence in favour of a model of movement control for temporally-based movements that utilizes an internal timekeeper. We expected startle
trials for the spatially defined movements to trigger a movement with similar kinematic and EMG characteristics as control trials (Carlsen et al., 2004b), as no timekeeper would be required. For temporally constrained trials we expected startle trials to trigger movements with condensed kinematics and EMG characteristics due to the use of an internal timekeeper whose pulse rate is accelerated by a startling stimulus (Maslovat et al., 2009). We found that the startling stimulus sped up both spatially and temporally defined movements (Figures 4.1 & 4.2), thus only partially supporting our hypothesis. For the spatially defined movements the startling stimulus affected all movements in a similar manner; however for the temporally defined movements the startling stimulus had a differential effect on the various movements, with slower movements compressed to a greater extent than faster movements. This was shown in the timing between agonist bursts, as well as TTPV and TTPD.

While we have attributed the proportional compression of timed movements (Figure 4.1, middle panel) to the reliance on a timekeeper whose pulse-rate is accelerated by the startling stimulus, it is possible that the differential effect of the startling stimulus was instead due to the nature of the slower movements. Increased activation caused by the startling stimulus could have had a greater effect on the lower velocity movements as compared to the higher velocity movements due to a ceiling effect (i.e., the faster movements would already be performed closer to maximal velocity). To further examine whether reliance on a timekeeper was responsible for the observed effects, we directly compared the performance of the short movement on day 1 and 2 as these movements differed only in terms of how the movement goal was presented to the participants. On day 1, participants were asked to move as fast as possible to a spatial target of 20° while
on day 2 they were asked to move to a 20° target with a time goal similar to how they performed the movement on day 1. Consistent with the utilization of a timekeeper whose pacemaker pulse-rate is dependent on arousal level, the startling stimulus had a differential effect when the movement was performed with spatial versus temporal goals. The time between the first agonist burst and the antagonist burst was shorter for startle trials when movements were defined in a temporal manner, even though the movements did not differ on control trials.

An unexpected result was that the startling stimulus sped up the spatially defined movements. Based on previous research (Carlsen et al., 2004b) we expected similar movement kinematics and EMG patterns for startle and control trials for spatially defined movements. In the current experiment the TTPD for control trials was almost identical for the spatially defined movements as compared to the results from Carlsen et al. (2004b, see Table 1), yet movement compression was not shown for startle trials in this earlier experiment. Carlsen et al. (2004b) did find higher variability for peak displacement on startle trials which may have masked any effects of the startling stimulus. Similar to the work by Carlsen et al. (2004b), the startling stimulus did not have an effect on total movement time for spatially defined targets, nor did it affect total movement time for temporally constrained movements. This means that participants exhibited a longer time between peak displacement and movement completion which may have been due to participants attempting to slow their movements after the transient effects of the startling stimulus which is thought to affect cortical processing for a brief period of time (Carlsen et al., 2004a).
In conclusion, we have provided evidence that temporally defined movements are prepared differently than spatially defined movements. Consistent with the theory presented by Gottlieb et al. (1989b), spatial movements were modulated by agonist duration while timed movements were modulated by agonist rise time. The introduction of a startling stimulus sped up both spatially and timing-based movements; however a greater effect was found for movements defined by a temporal goal, and for slow movements as compared to fast movements. These results are consistent with the hypothesis that timing-based movements rely on an internal timekeeper in which the pacemaker pulses are affected by the participant’s arousal level and provide further understanding of the preparation of timed movements.
Bridging Summary to Following Chapters

The results of the current experiment provided evidence that temporally constrained movements are prepared in a different manner to spatially targeted movements. Our next experiment returned to our examination of motor preparation of a sequenced movement, and how this preparation may change with practice. The results of Experiment 2 confirmed that between-limb sequencing could be prepared in advance, as shown by an asynchronous bimanual movement being triggered by a startling stimulus. However, sequenced bimanual movements may be prepared in a different manner to sequenced unimanual movements as bimanual movement elements are relatively independent because they do not require the same limb. Our next study examined motor preparation during extended practice (four days) of a sequenced unimanual movement. We were interested in the examination of movement “chunking” whereby multiple element movements could potentially be re-coded and controlled by a single motor representation. We examined preparation of unimanual movements in both a simple RT and choice RT paradigm to study motor preparation when the movement was and was not known in advance.
5. Experiment 4

Motor Preparation and the Effects of Practice: Evidence from Startle

Introduction

The examination of preparation for sequenced movements has a long history in behavioural science (e.g., Woodworth, 1899; Lashley, 1951; Keele, 1968; see Rhodes, Bullock, Verwey, Averbeck, & Page, 2004; Khan, Helsen, & Franks, 2010 for reviews). Although there is ample evidence that preparation time may increase with a more complex response, there is still debate as to what aspect of complexity affects programming and why. Furthermore, comparatively less work has examined how practice affects response programming of movements of different complexities. The purpose of the present experiments was to investigate motor preparation for upper limb movements, and examine any changes to the preparation process that occurred as a result of extensive practice.

A number of different methodologies have been employed to examine motor preparation. One avenue has been to examine performance in a simple reaction time (RT) paradigm, whereby the response to the “go” stimulus is known in advance. In a seminal study, Henry and Rogers (1960) found an increase in simple RT with increasing complexity of the required movement. The authors explained this finding via a “memory drum theory”, which suggested that more complex movements required retrieval of more elements from memory, thus increasing reaction time. Similar results were shown by Sternberg, Monsell, Knoll, and Wright (1978) for speech and typewriting, in which the number of letters typed or words spoken impacted the reaction time of the participants. As with Henry and Rogers, Sternberg et al. attributed the increase in RT to additional time required to retrieve the response units from a memory buffer. However, a potential confound in these experiments was that it was assumed that motor preparation did not
occur until after the “go” signal. As the tasks were performed in a simple reaction time paradigm it may have been possible to prepare the required response in advance (see Klapp, 1977, 1996; Henry, 1980; Rosenbaum, 1985 for reviews).

To examine response preparation both when advance preparation could and could not occur, Klapp (1995, 2003) performed a series of experiments manipulating response complexity in the form of response duration (i.e., longer response element) and number of components in both a simple and choice RT paradigm. In the simple RT situation (when pre-programming could occur), RT did not change for a single component movement of different durations but did increase when extra components of the movement were added. However, in a choice RT situation (when pre-programming could not occur), RT changed for a single component movement of different durations but did not change when extra components of the movement were added. To explain these differential effects on RT, two different components of response programming were proposed: one process involving the preparation of the internal features of a movement element (INT) and the other process involving preparation of the sequencing of the movement elements (SEQ). Klapp hypothesized that for a known response, INT could be completed in advance of the “go” signal, whereas SEQ could only occur following the “go” signal. When the response is unknown, both INT and SEQ are performed following the “go” signal with INT being the rate-determining step. In a simple RT task, increasing movement duration only affects the INT processing, which could be performed in advance, whereas increasing the number of components affects SEQ processing, which is performed after the “go” signal. Thus simple RT is sensitive to the number of response elements but not the complexity of the element itself. Conversely, in a choice RT task,
increasing response element complexity affects RT due to longer INT programming (which must occur following the “go” signal), while increasing response elements does not affect RT because SEQ is prepared faster than INT.

Changes in preparation as a result of practice were also examined by Klapp (1995). Although simple reaction times were initially higher for multiple component responses compared to single component responses (a difference of 62 ms) this effect was minimized after 8 days of practice (reduced to 2 ms). This result was interpreted as evidence for “chunking”, whereby the multiple component movement was eventually recoded into a single element, and could thus be fully prepared in advance. Similarly, the maintenance or increase in choice reaction time differences between single and multiple element responses with practice were also taken as evidence for chunking. If multiple element movements are recoded into a single chunk, it would be expected that internal features would become more complex, resulting in longer choice reaction times.

The notion of movement chunking has been described via a “gear-shift analogy” (MacKay, cited in Schmidt & Lee, 2005, pp. 422). Early in practice the process of shifting gears in a manually-operated car may involve numerous separate movement elements that are all individually prepared and executed. However, with practice the learner blends the separate components into a single movement that may be prepared as a single action. The concept of motor chunking suggests that multiple elements are recoded as a single unit of action, such that advance preparation of the entire movement can occur if the response is known. However, there is also evidence from the practice of key press sequences that extensive practice also enables improved concurrent processing, whereby retrieval of the next key press occurs during the performance of the current movement
(Verwey, 1994, 1995, 1996, 2001, 2003; Verwey & Eikelboom, 2003). This would suggest that practice can also result in improvements to online programming in addition to improved advance preparation.

In the present experiments we implemented a startling acoustic stimulus as this methodology has been used to examine the preparation processes associated with various voluntary movements. During a simple reaction time task, replacing the auditory “go” signal with a loud (>124dB) startling stimulus has been shown to elicit the prepared action at a much shorter latency, with similar kinematics and EMG configurations (see Carlsen, Maslovat, Lam, Chua, & Franks, in press; Valls-Solé, Kumru, & Kofler, 2008 for reviews). Due to dramatic shortening of premotor reaction times (<70 ms), it has been hypothesized that the startle can act as a trigger for a pre-programmed response, bypassing the usual voluntary command processes (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004b; Valls-Solé, Rothwell, Goulart, Cossu, & Muñoz, 1999). This hypothesis has been supported by a number of studies showing that startle effects are distinct from and larger than stimulus intensity effects (Carlsen, Dakin, Chua, & Franks, 2007), and only occur when the participant has prepared the response in advance (Valls-Solé et al., 1999; Carlsen, Chua, Inglis, Sanderson, & Franks, 2004a; Rothwell, 2006). When uncertainty exists regarding what movement is required (such as a discrimination or choice reaction time task), advance preparation is unlikely to occur and thus the startle does not trigger the movement (Carlsen et al., 2004a, Carlsen, Chua, Dakin, Inglis, Sanderson, & Franks, 2008). Thus the use of a startling stimulus can act as a probe for what is pre-programmed, as prepared movements would be expected to be triggered (with similar movement characteristics) at a shorter latency when compared to control trials.
The startling stimulus has been used as a tool to examine how pre-programming changes during the learning process (Maslovat, Carlsen, Chua, & Franks, 2009; Maslovat, Carlsen, Ishimoto, Chua, & Franks, 2008). By examining the response to startle trials provided at various points in the acquisition process it is possible to determine what is prepared as learning progresses. That is, whatever advance movement preparation changes occur during practice should be reflected in the triggered movement when a startle stimulus is provided. Thus not only can the limits of advance preparation be examined by startle methodology, we can also gain information as to whether these limits change as a task is practiced. In this way both RT and response to the startling stimulus provide a window into motor preparation and its changes with practice.

Information pertaining to motor preparation has also been provided by studying how the reflexive response to a startling stimulus changes with repeated exposure. Previous research has shown for humans that the reflexive EMG activity in muscles other than orbicularis oculi habituates within two to six repetitions of the auditory stimulus (Brown, Rothwell, Thompson, Britton, Day, & Marsden, 1991). However, this habituation does not appear to occur when participants are preparing for an upcoming voluntary action and thus the startle response can be elicited repeatedly (Carlsen, Chua, Inglis, Sanderson, & Franks, 2003, Valls-Solé, Valldeoriola, Tolosa, & Nobbe, 1997). Therefore, no habituation of the startle response (i.e., SCM activation) would be expected in a simple RT paradigm when advance preparation is possible, but the lack of preparation in a choice RT paradigm may cause an attenuation of the startle response with repeated exposure to the startling stimulus. This would be reflected by a decreased
activation in startle indicators in the choice RT situation only and would provide an additional indication that participants were unable to engage in advance preparation.

In the following experiments we examined the role of practice for motor preparation in both a simple (Experiment 1) and choice (Experiment 2) RT paradigm for unimanual movements of varying complexities. Specifically these movements were: a) single component movement to a short target, b) single component movement to a long target, and c) two-component movement to targets in the same direction (i.e., two-step). Thus we have manipulated both the complexity of the movement elements (long versus short movements, i.e., INT features) and number of movement elements (one target versus two target movements, i.e., SEQ features). In the simple RT paradigm, response selection need not occur during the RT interval as participants are aware of the required response in advance. Therefore any RT differences can be attributed to differences in response programming, which may occur before or following the “go” stimulus. For the choice RT paradigm, both response selection and programming must be performed in the RT interval, thus RT changes may be attributed to either of these processes. Because we were most interested in how motor preparation changes with response complexity and practice, we focussed our analysis within each experiment rather than comparisons between simple and choice RT.

Experiment 1: Simple RT

When the required movement is known in advance, motor preparation can occur before the “go” stimulus. According to Klapp’s (1995, 2003) theoretical framework, during simple RT the internal structure of each movement element (i.e., muscle activation timing and force) can be prepared in advance, but not the sequencing of the elements.
Based on this framework, we predicted both single target movements (short and long) should be performed at a similar RT in control trials, as they only differ in terms of internal features. For the two-step movement, initial RTs were predicted to be higher than the single element movements due to a sequencing requirement. However, if this multiple element movement is recoded into a single chunk with practice, this RT difference should be minimal or absent by the end of practice.

The effects of the startling stimulus provided information pertaining to the preparation processes associated with the various movements. We expected that participants would continuously show SCM activation to the startling stimulus as motor preparation is thought to prevent habituation of the startle response (Carlsen et al., 2003; Valls-Solé et al., 1997). We also predicted that advance preparation of the entire single element movements should result in the short and long movement being triggered by the startling stimulus, with similar kinematics and EMG activation patterns as compared to their respective non-startle control trials (e.g., Carlsen et al., 2004b; Maslovat et al., 2008). Conversely, for the two-step movement, if participants were unable to prepare the sequencing component of these movements (at least early in practice), two possible scenarios during startle trials could occur. If movement components are prepared and stored in a short term memory buffer which is continuously cycled to find the correct element (Klapp, 2003; Sternberg et al., 1978), we would expect little or no reduction in reaction time for startle trials. This is because the first movement element is not immediately accessible and thus cannot be triggered by the startling stimulus. Another possibility is that the first element of the movement would be triggered by the startle with the second component programmed online.
Methods

Participants

Fourteen right-handed volunteers with no obvious upper body abnormalities or sensory or motor dysfunctions participated in the study after giving informed consent. However, only data from ten right-handed volunteers (3 male, 7 female; M = 21.2 yrs, SD = 1.9 yrs) were employed in the final analysis. Four participants did not show consistent activation in the sternocleidomastoid muscle during startle trials (which is thought to be the most reliable indicator of a startle response), and thus were excluded from the analysis (see Carlsen et al. in press for more detail regarding the exclusion criteria for participants). All participants were naïve to the hypothesis under investigation and this study was conducted in accordance with ethical guidelines established by the University of British Columbia.

Apparatus and Task

Participants sat in a height-adjustable chair in front of a 22-inch color monitor (Acer X233W, 1152 x 864 pixels, 75 Hz refresh) resting on a table. Attached to the table on the right side of the monitor was a lightweight manipulanda that participants used to perform horizontal flexion-extension movements about the right elbow joint. Participants’ arms and hands were secured with Velcro straps to the manipulanda with the elbow joint aligned with the axis of rotation and the hands semi-supinated to grasp a vertical metal rod. The home position for each arm was located such that a 30° extension movement resulted in the arms being straight ahead (i.e., perpendicular to the monitor on the table), and was defined as 0°. Targets were located on the table top at 20° and 40° of extension from the home position. The two targets and home position had weak magnets
attached such that participants could feel the position of the target but were not
constrained to a physical end position.

In response to an auditory “go” signal, the participants were asked to perform one
of three unimanual targeted movements. Participants were instructed to look straight
ahead at the monitor and respond by making a movement “as fast and as accurately as
possible” from the starting position and to stop at the final targets. All trials began with a
warning tone consisting of a short beep (80 +/-2 dB, 100 ms, 100 Hz) presented
simultaneously with the word “Ready!” and the visual precue on the computer screen.
The visual precue consisted of either: a short arrow (-->), representing a 20° movement to
the short target; a long arrow (---->), representing a 40° movement to the long target; or a
double short arrow (-->-->), representing a two-step movement whereby participants
stopped at the first 20° target before continuing to the 40° target. The “go” signal
followed the warning tone by a random foreperiod of 2500-3500 ms and could either
consist of a control stimulus (80 +/-2 dB, 100 ms, 1000 Hz) or startling stimulus (124 +/-2 dB, 40 ms, 1000 Hz, <1 ms rise time). All auditory signals were generated by a
customized computer program and were amplified and presented via a loudspeaker
placed directly behind the head of the participant. The acoustic stimulus intensities were
measured using a sound level meter (Cirrus Research model CR:252B) at a distance of 30
cm from the loudspeaker (approximately the distance to the ears of the participant).

Participants performed four testing sessions (approximately 60 minutes each) over
consecutive days. Each testing session began with a maximal voluntary contraction
(MVC) of the agonist (triceps) and antagonist (biceps) muscles of the right arm to allow
for between-day comparisons of EMG activity. Next participants performed three blocks
of 45 trials, with each block consisting of 15 trials of each movement pseudorandomly presented (no more than two trials of the same movement in a row), for a total of 45 trials per movement per day. Although participants were aware of the required movement before the “go” stimulus, we chose to present the movements in random order as this has been shown to be more effective than a blocked schedule for encouraging movement chunking (Wright, Black, Immink, Brueckner, & Magnuson, 2004). To minimize participants’ exposure to the startling stimulus, startle trials were only presented on the first and last day of testing. On these days an additional six startle trials (two for each type of movement) were pseudo-randomly presented (not on the first trial or on two consecutive trials) in each of the three acquisition blocks for a total of 18 startle trials (six per movement). Augmented feedback was not provided during the trial, however terminal feedback was provided on the monitor for three seconds following the trial that included reaction time (RT, in ms). To encourage fast and accurate responses, a monetary bonus was offered for fast RTs.

**Recording Equipment and Data Reduction**

Surface EMG data were collected from the muscle bellies of the following superficial muscles: right lateral head of the triceps brachii (TRI - agonist), right long head of the biceps brachii (BIC - antagonist), and right and left sternocleidomastoid (SCM - startle indicator) using preamplified surface electrodes connected via shielded cabling to an external amplifier system (Delsys Model DS-80). Recording sites were prepared and cleansed in order to decrease electrical impedance. The electrodes were oriented parallel to the muscle fibers, and then attached using double sided adhesive strips. A grounding electrode was placed on the participant’s right ulnar styloid process.
Arm angular displacement was measured using potentiometers (Precision, MD157) attached to the central axis of the manipulanda, which had a precision of 0.07°/bit. A customized LabView® computer program controlled stimulus and feedback presentation, and initiated data collection at a rate of 1 kHz (National Instruments, PC-MIO-16E-1) 500 ms before the presentation of the “go” signal and terminated data collection 2000 ms following the “go” signal.

A total of 122 of the 5760 trials were discarded (2.1%). Reasons for discarding trials included premotor reaction time less than 50 ms (i.e., anticipation, 55 trials) or in excess of 500 ms (7 trials), incorrect movements (45 trials), and startle trials in which no detectable startle response (SCM activity) was observed (15 trials). Surface EMG burst onsets were defined as the point at which the EMG first began a sustained rise above baseline levels. The location of this point was determined by first displaying the EMG pattern with a superimposed line indicating the point at which activity increased to more than 2 standard deviations above baseline (mean of 100 ms of EMG activity preceding the go signal). Onset was then verified by visually locating and manually adjusting the onset mark to the point at which the activity first increased. This method allowed for correction of errors of the algorithm. EMG offsets were marked in a similar fashion, with the activity between EMG onset and EMG offset being defined as the duration of a muscle burst. Initial movement onset was defined as the first point of change of more than 0.2° of angular displacement from the starting position following the “go” stimulus, while final position was defined as the point at which angular velocity fell below 8°/s and remained below this value for 50 ms.
Dependent Measures and Statistical Analyses

**EMG**

Although previous researchers have used displacement RT as a primary dependent measure (e.g., Klapp, 1995), we chose instead to examine premotor RT (time from the stimulus onset to agonist EMG onset) as this time interval is thought to best represent processing that occurs after the “go” signal. The latency of premotor RT in startle trials has been used as support for triggering of a pre-programmed response (Carlsen et al., 2004b, Valls-Solé et al., 1999). Premotor RT was analyzed via a 2 Day (day 1, day 4) x 3 Movement (1 short, long, two-step) x 2 Stimulus Type (control, startle) repeated measures analysis of variance (ANOVA).

To examine any habituation effects in the startle indicator muscles, we integrated the rectified raw EMG trace for the left and right SCM muscles for the time period of 50-150 ms following the “go” signal (SCM iEMG). We chose this time period as it reliably captures the onset and offset of SCM activation when startled (Brown et al., 1991; Carlsen et al., 2007, Maslovat et al., 2008, 2009; Valls-Solé, Solé, Valldeoriola, Muñoz, Gonzalez, & Tolosa, 1995). Because EMG amplitudes differed between subjects, SCM iEMG was normalized to the first block of testing each day and then analyzed via a 2 Side (left, right) x 2 Day (day 1, day 4) x 3 Block repeated measures ANOVA.

**Kinematics**

In the examination of motor preparation it is often challenging to distinguish between changes in online preparation as opposed to advance preparation, although many different techniques have been used (see Khan, et al., 2006 for a review). It has been suggested that changes in trial-to-trial movement variability best capture differences in
modes of preparation (Elliott & Hansen, in press) and thus we have included an analysis of within-subject variability of the produced movement in startle trials as compared to control trials. We expected that advance preparation would be reflected by similar movement variability for both startle and control trials, as a similar movement should be released/triggered following the “go” signal. Alternately, online programming should result in greater variability in startle as compared to control trials, due to the startling stimulus interfering with cortical processing (Carlsen et al., 2004a) or the inability to smoothly integrate the components of the multiple element movement. If the first movement element is triggered by the startling stimulus without the usual voluntary command, performers should have more difficulty preparing the second movement element online which would be reflected in increased movement variability of the second component. Although it is possible that the startling stimulus results in a greater amplitude movement due to increased neural excitation (Carlsen et al., 2004a, Maslovat et al., 2008), this should not change the within-subject variability as all startle trials should be similarly affected. Furthermore, while practice may reduce movement variability it should result in a similar decrease in both startle and control trials. Thus it is not the variability of the movement itself we were most concerned with, but rather a comparison between startle and control trials of the consistency of the produced movement.

We analyzed movement consistency for the initial, pre-programmed phase of all three types of movements, as well as the second component of the two-step movement. For the first movement component we examined variability of the first 100ms from movement onset as this portion of the movement should not be affected by feedback or
online corrections. For the second movement component we examined variability from
initiation of the second movement to completion to determine if this movement was
prepared prior to the “go” signal or during execution of the first component. As the
duration of the second movement component varied from trial to trial, we normalized all
trials such that the movement time of the second component was scaled from 0 to 100%
and thus separated into 100 data points (i.e., for a 200 ms movement we examined the
movement position every 2 ms). Thus all variability calculations were performed on 100
data points per trial. To calculate a variability score, we calculated within-subject
standard deviations across trials for each data point for each condition. From these values
we calculated an overall average that represented how consistent the produced movement
was from trial to trial for each condition for a single subject. The variability for the first
100ms (VAR₁) was analyzed via a 2 Day (day 1, day 4) x 3 Movement (short, long, two-
step) x 2 Stimulus Type (control, startle) repeated measures ANOVA. The variability for
the second movement component (VAR₂) was analyzed for the two-step movement via a
2 Day (day 1, day 4) x 2 Stimulus Type (control, startle) repeated measures ANOVA.

For the repeated measure ANOVAs, the Greenhouse-Geisser Epsilon factor was
used to adjust the degrees of freedom for violations to sphericity. Uncorrected degrees of
freedom are reported, with the corrected $p$ values and epsilon value. Partial eta squared
($\eta^2$) values reported as a measure of effect size. The alpha level for the entire
experiment was set at .05, and significant results were examined via Tukey’s honestly
significant difference (HSD) test and simple effects tests to determine the locus of the
differences.
Results

To represent overall performance of the movements for startle and control trials, we created ensemble averages for day 4 showing rectified raw EMG activation (including SCM for startle trials) and displacement. This was achieved by normalizing each trial in time to displacement onset (which was considered time 0) and normalizing EMG activation to a percentage of the maximal value within a trial. These averages represent data from all trials from all participants (i.e., 450 trials for control, 60 trials for startle) and are shown for control and startle trials for all three movements from day 4 in Figure 5.1. A summary of the results for the main dependent measures, including mean and standard deviations, are provided in Table 5.1.
Table 5.1 Simple RT experimental results for each stimulus type, day and movement, showing means and standard deviations (bracketed). Note that VAR₂ only has values for the two-step movement.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Day 1</th>
<th></th>
<th>Day 4</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Startle</td>
<td>Control</td>
<td>Startle</td>
</tr>
<tr>
<td></td>
<td>Short Long Two-Step</td>
<td>Short Long Two-Step</td>
<td>Short Long Two-Step</td>
<td>Short Long Two-Step</td>
</tr>
<tr>
<td>Premotor RT (ms)</td>
<td>122.9 (16.0) 127.0 (17.1) 138.2 (23.6)</td>
<td>85.0 (8.8) 83.2 (9.0) 86.1 (8.9)</td>
<td>105.2 (11.8) 107.1 (13.0) 107.7 (16.4)</td>
<td>81.5 (6.6) 78.3 (8.5) 78.8 (7.1)</td>
</tr>
<tr>
<td>VAR₁ (deg)</td>
<td>1.64 (0.56) 1.89 (0.65) 1.62 (0.61)</td>
<td>1.66 (0.77) 2.20 (0.96) 2.19 (0.74)</td>
<td>1.54 (0.26) 1.86 (0.35) 1.70 (0.38)</td>
<td>1.40 (0.76) 1.27 (0.52) 1.44 (0.65)</td>
</tr>
<tr>
<td>VAR₂ (deg)</td>
<td>--- --- 4.22 (1.23)</td>
<td>--- --- 5.28 (1.58)</td>
<td>--- --- 3.42 (0.96)</td>
<td>--- --- 3.71 (0.88)</td>
</tr>
</tbody>
</table>
Figure 5.1 Simple RT group ensemble averages for each movement on day 4, separated by control (left panels) and startle (right panels) values. Agonist and antagonist values (grey lines) are rectified raw EMG, normalized to a percentage of the maximal value within each trial, with left and right SCM (black lines) shown on startle trials. All values are normalized to displacement onset (dark black line) which was considered relative time 0. Note the consistent bilateral increase in SCM activation prior to displacement onset for startle trials.
EMG

Mean RT values are shown for control and startle trials for day 1 and 4 in Figure 5.2. As predicted, RTs for control trials were longer for the two component movements on day 1; however this difference was minimized with practice. For startle trials, RT values were lower than control trials, and no changes occurred with practice nor were there differences observed for the various movements. These results were confirmed by a number of main effects and interaction effects. The main effect for day, $F(1, 9) = 18.59$, $p = .002$, $\varepsilon = 1$, $\eta_p^2 = .67$, confirmed an overall decrease in RT from day 1 ($M = 107$ ms) to day 4 ($M = 93$ ms), however this effect interacted with both stimulus type and movement. The Day x Movement effect, $F(2, 18) = 6.79$, $p = .025$, $\varepsilon = .54$, $\eta_p^2 = .43$, was due to a higher RT for the two-step movement ($M = 112$ ms) as compared to the short ($M = 105$ ms) and long ($M = 104$ ms) movements on day 1 but not on day 4 (two-step $M = 93$ ms, short $M = 93$ ms, long $M = 93$ ms). The Day x Stimulus effect, $F(1, 9) = 26.19$, $p = .001$, $\varepsilon = 1$, $\eta_p^2 = .74$, was due to a significant decrease in RT for control trials (23 ms), while RT did not significantly change for startle trials with practice (5 ms). The main effect for stimulus type, $F(1, 9) = 81.44$, $p < .001$, $\varepsilon = 1$, $\eta_p^2 = .90$, was due to a significant decrease in RT for startle ($M = 82$ ms) as compared to control trials ($M = 118$ ms); however the Stimulus x Movement effect, $F(2, 18) = 8.51$, $p = .007$, $\eta_p^2 = .49$, confirmed the two-step movement had a higher RT ($M = 123$ ms) than the short ($M = 117$ ms) and long ($M = 114$ ms) movement for control trials but no movement differences for startle trials (two-step $M = 82$ ms, short $M = 83$ ms, long $M = 81$ ms). Lastly the main effect for movement, $F(2, 18) = 4.37$, $p = .033$, $\varepsilon = .92$, $\eta_p^2 = .33$, was due to a higher overall RT for the two-step
movement ($M = 103$ ms) as compared to both the short ($M = 99$ ms) and long ($M = 99$ ms) movements.
Figure 5.2 Mean premotor RT values (SEM) for simple RT paradigm, separated by day and condition. An asterisk (*) denotes a significant difference for day 1 control trials between the two-step and other two movements. Note the short latency and consistency of startle RT values for both type of movement and day of testing.
The analysis of normalized SCM iEMG did not yield differences across practice
days but did show a main effect for block within each practice day, $F(2, 18) = 7.02, p =
.013, \epsilon = .718, \eta^2_p = .44$, due to a significant decrease in activation of the startle indicator
from the first block of trials ($M = 1.0$) to the third block of trials ($M = .75$), while the
second block ($M = .86$) was not significantly different to any other blocks.

Kinematics

Our hypothesis was that within-subject movement variability would be similar in
control and startle trials for movements prepared in advance but higher for startle trials if
the movement was programmed online. As expected, analysis of mean variability of the
first 100ms of the movement ($\text{VAR}_1$) was not different between startle and control trials,
confirming that the consistency of the initial component was similar when triggered by
the startle as compared to control trials. Although there was a significant Day x Stimulus
interaction effect, $F(1, 9) = 8.29, p = .018, \epsilon = 1, \eta^2_p = .48$, post hoc analyses revealed
that this effect was due to a significant decrease in variability for startle trials from day 1
($M = 2.02^\circ$) to day 4 ($M = 1.37^\circ$) whereas control trials stayed relatively constant from
day 1 ($M = 1.72^\circ$) to day 4 ($M = 1.70^\circ$). This result indicates participants improved at
their ability to consistently prepare the initial movement component in advance, as the
movement triggered by the startling stimulus was less variable following practice. No
differences were found between startle and control trial variability on either day. The
analysis of variability for the second movement component of the two-step movement
($\text{VAR}_2$) decreased with practice from day 1 ($M = 4.75^\circ$) as compared to day 4 ($M =
3.57^\circ$), $F(1, 9) = 19.76, p = .002, \epsilon = 1, \eta^2_p = .69$, but was unaffected by the type of
stimulus ($p = .167$).
Discussion

The purpose of this first experiment was to examine the effects of practice on advance and online motor preparation of different types of unimanual movements when the required response was known in advance (i.e., simple RT). We manipulated movement complexity by including movements of different durations and number of elements. Participants were able to perform all movements in both the startle and control conditions, with only a small percentage of trials discarded (2.1%), mostly due to anticipation.

Changes to RT with practice for control trials (Figure 5.2) were similar to those previously observed with a keypress and speech tasks (Klapp, 1995, 2003). A comparison between movement types revealed no RT differences between the long and short single component movements, which are thought to only differ in internal features that can be prepared in advance. Furthermore, the two-step movement did have a longer RT early in practice (i.e. sequence length effect), which has previously been attributed to sequencing that can only be performed following the “go” stimulus. However, with extensive practice this difference was minimized such that by day 4 the two-step movement had a comparable RT to the single component movements.

Although RT measures decreased for the different movements during control trials, RT for startle trials was similar for all movements both before and after practice (Figure 5.2). The latency of RT during startle trials was consistent with previous experiments involving arm movements where it has been suggested that such short reaction times are due to triggering of a pre-programmed response (i.e., Carlsen et al. 2004a, 2007; Carlsen, Chua, Summers, Inglis, Sanderson, & Franks, 2009; Maslovat et
al., 2008, 2009). The lack of a practice effect for startle trials is what would be expected if the startling stimulus triggered the response, bypassing the usual voluntary command and cortical processing pathways (Valls-Solé et al., 1999; Carlsen et al., 2004b).

Although we expected the single component movements to be triggered at this short latency, we did not know if the two-step movement would show a similar effect as we were unsure if the entire movement could be prepared in advance and stored in a similar manner to the less complex movements. The triggering of the two-step movement at similar latencies to the single element movements suggests that participants either prepared the entire movement in advance, or that the first element of the movement was triggered by the startling stimulus, with the second component prepared online.

To determine whether only the first movement element or the entire movement was prepared in advance, we examined within-subject movement variability between startle and control trials to determine if the triggered movement was performed with similar consistency in both types of trials. For the first 100ms movement segment within-subject variability decreased for startle trials with practice; however no difference was found between startle and control trials. This result indicated that the initial movement was prepared in advance and this preparation became more consistent with practice, such that the startling stimulus triggered a very consistent response by the end of practice.

Although variability of the second component of the two-step movement decreased with practice it was not affected by the startling stimulus before or after practice. Given that the two-step movement was triggered by the startling stimulus at similar latencies to the single element movements and with similar consistency as control trials, we believe that the entire two-step movement was prepared in advance throughout the practice phase. We
will return to the explanation as to why control RT values for the two component movement were higher early in practice when we consider theoretical contributions of motor preparation in the general discussion.

The examination of EMG activation of the SCM provided information pertaining to whether participants habituated to the startling stimulus and hence indirect evidence for advance preparation. Although we expected that SCM activation would not habituate in the simple RT paradigm due to advance preparation, we did see a significant decrease in activation from the first block of trials to the last block of trials, implying some habituation occurred. However, SCM activation still occurred on over 95% of the total startle trials (345 of 360) and those discarded due to a lack of activation were equally distributed throughout the three blocks of trials (6 in block 1, 3 in block 2, 6 in block 3). In addition, the decrease in integrated EMG activity in the SCM was still at 75% of that of the initial block, similar to non-habituated levels previously reported in the literature (Carlsen et al., 2003; Valls-Solé et al., 1997).

Experiment 2: Choice RT

In Experiment 1 we examined unimanual motor preparation in a simple RT paradigm when the required movement is known in advance. In Experiment 2 a choice RT paradigm was used, whereby participants were not aware of the required movement until the “go” stimulus. According to Klapp’s (1995, 2003) theoretical framework, during choice RT both sequencing (SEQ) and the internal structure (INT) of each movement element must be performed following the “go” signal with INT being the rate-determining step. Thus choice RT is determined by the relative complexity of the first movement element rather than the number of elements. Based on this framework, we
predicted that the long movement should have a longer RT as compared to the short movement due to more complex internal features (i.e., longer muscle activation duration). As sequencing is not the rate-determining step, we also predicted that initially the short and two-step movements should be performed at a similar RT as the internal features of the first component are the same; however if the two-step movement becomes chunked with practice, this should result in an increase in internal features which should create a longer RT as compared to the short movement by the final day.

The startling stimulus should produce very different results for the choice RT paradigm. The lack of advance preparation should not allow for movement triggering at latencies such as those observed in the simple RT paradigm. In fact, we would expect similar RT values in control and startle trials (e.g., Carlsen et al., 2004a); although a stimulus intensity effect may be seen due to the louder “go” stimulus (Woodworth, 1938, p. 318; Carlsen et al., 2007). Furthermore, as the startling stimulus is not bypassing voluntary commands to trigger the movement, we would expect to see a practice effect in startle trials (a result not observed in the simple RT paradigm). Lastly we predicted that the lack of advance preparation in the choice RT paradigm would result in a habituation to the startling stimulus. This would be evidenced by either a reduction in the number of startle trials showing SCM activation and/or a significant decrease in SCM activation as the testing session progressed.

Methods

Except where noted below, methods were identical to those described in Experiment 1.
Participants

Thirteen right-handed volunteers (who did not take part in Experiment 1) with no obvious upper body abnormalities or sensory or motor dysfunctions participated in the study after giving informed consent. We did not reject participants who did not show a reliable startle indicator during choice RT trials, as we expected habituation to the startle to occur. However, participants were also subjected to simple RT trials at the end of each testing day (see Apparatus and Task below), which included three startle trials when advance preparation was possible. Three subjects did not show consistent activation in the SCM muscle during these simple RT startle trials, and thus were excluded from the analysis. Therefore only data from ten right-handed volunteers (3 male, 7 female; M = 20.0 yrs, SD = 1.5 yrs) were employed in the final analysis. All participants were naïve to the hypothesis under investigation and this study was conducted in accordance with ethical guidelines established by the University of British Columbia.

Apparatus and Task

Participants performed the same number of trials of the three movements outlined in Experiment 1. However, in Experiment 2 the visual precue that was displayed on the screen was presented coincident with the “go” stimulus such that participants could not prepare the movement in advance. As the three movements used in Experiment 1 all involved extension to begin the movement, we wanted to avoid any partial preparation of a non-specific extension movement that could be triggered by the startling stimulus (Carlsen et al., 2009). Thus we included a fourth movement, whereby participants were required to make a flexion movement of a similar magnitude to the short movement (no target was provided for this movement). This movement was represented by a visual
precue of a short arrow pointed left (←). Twenty of these “flexion catch” trials were pseudo-randomly presented during each block, such that no more than two in a row were presented and were not analyzed with the other movements of interest.

We hypothesized that the lack of advance preparation would cause habituation to the startling stimulus. To test if participants were habituating to the startling stimulus or were simply “non-startlers”, we concluded the first and last testing day with 10 additional flexion movements that were precued in advance (i.e., simple RT paradigm). During these 10 trials, three startle trials were pseudo-randomly presented such that a startle did not occur on the first trials, nor were there two consecutive startle trials. If participants did not show a startle response on these trials, they were excluded from the analysis as we deemed those participants to be non-startlers. The addition of the flexion catch trials and simple RT flexion trials increased the number of trials performed in Experiment 2. On day two and three participants performed a total of 195 trials (45 of each of the three movements as outlined in Experiment 1 plus 60 flexion catch trials), while on day 1 and 4 participants performed a total of 223 trials (195 as above, plus 18 startle trials as outlined in Experiment 1, plus 10 simple RT trials).

Data Reduction

A total of 204 of the 8,360 trials were discarded (2.4%). By far the most common reason for discarding trials was for incorrect movements (193 trials), as would be expected when advance preparation could not occur. Other reasons included displacement reaction time shorter than 90 ms (i.e., anticipation, 1 trial) or longer than 900 ms (2 trials). As outlined above, we did not discard startle trials during the choice RT paradigm when SCM activity was lacking (total of 72 trials) as we expected participants
to habituate to the startle. However we did discard 8 startle trials (out of 60) in the simple RT flexion paradigm as the premotor RT values were above 120 ms. These were discarded as these values were more than four standard deviations above the values we observed for Experiment 1 and thus were not considered representative startle trials.

**Dependent Measures and Statistical Analyses**

In addition to the analyses described in Experiment 1, premotor RT of the simple RT trials for the flexion movement was analyzed via a 2 Day (day 1, day 4) x 2 Stimulus Type (control, startle) repeated measures ANOVA to examine the effects of startle when the movement type was known in advance. In addition to the examination of habituation effects in the startle indicator muscles, we also compared the SCM iEMG data from the last block of choice trials to the simple flexion movements via a 2 Side (left, right) x 2 Day (day 1, day 4) x 2 Condition (choice block 3, simple RT) repeated measures ANOVA.

**Results**

As with Experiment 1, we have represented “typical” performance of the three movements for startle and control trials via ensemble averages for day 4 (Figure 5.3) and have summarized the results for the main dependent measures, including mean and standard deviations (Table 5.2).
Table 5.2 Choice RT experimental results for each stimulus type, day and movement, showing means and standard deviations (bracketed). Note that VAR₂ only has values for the two-step movement.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Control</th>
<th>Startle</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Short</td>
<td>Long</td>
</tr>
<tr>
<td>Day 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Premotor RT (ms)</td>
<td>378.2 (75.7)</td>
<td>389.0 (78.9)</td>
</tr>
<tr>
<td>VAR₁ (deg)</td>
<td>1.71 (0.60)</td>
<td>2.17 (0.78)</td>
</tr>
<tr>
<td>VAR₂ (deg)</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>Day 4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Premotor RT (ms)</td>
<td>282.2 (66.4)</td>
<td>282.4 (61.3)</td>
</tr>
<tr>
<td>VAR₁ (deg)</td>
<td>1.07 (0.18)</td>
<td>1.30 (0.45)</td>
</tr>
<tr>
<td>VAR₂ (deg)</td>
<td>---</td>
<td>---</td>
</tr>
</tbody>
</table>
Figure 5.3 Choice RT group ensemble averages for each movement on day 4, separated by control (left panels) and startle (right panels) values. Agonist and antagonist values (grey lines) are rectified raw EMG, normalized to a percentage of the maximal value within each trial, with left and right SCM (black lines) shown on startle trials. All values are normalized to displacement onset (dark black line) which was considered relative time 0. Note the lack of significant bilateral SCM activation for startle trials.
EMG

Mean RT values are shown for control and startle trials on day 1 and day 4 in Figure 5.4. Participants reduced their RT with practice from day 1 ($M = 378$ ms) to day 4 ($M = 281$ ms), as confirmed by a main effect for day, $F(1, 9) = 43.93$, $p < .001$, $\varepsilon = 1$, $\eta^2_p = .83$. Although there was a main effect for movement, $F(2, 18) = 8.56$, $p = .004$, $\varepsilon = .90$, $\eta^2_p = .49$, this effect was dependent on the stimulus type as shown by a Stimulus x Movement interaction, $F(2, 18) = 13.47$, $p = .001$, $\varepsilon = .799$, $\eta^2_p = .60$. Post-hoc analyses confirmed that for control trials, the two-step movement had a longer RT ($M = 345$ ms) as compared to the short movement ($M = 330$ ms), with the long movement ($M = 336$ ms) not significantly different from either movement. For startle trials, both the two-step ($M = 327$ ms) and short ($M = 333$ ms) movements had significantly longer RTs than the long movement ($M = 309$ ms). This result occurred because the startling stimulus had different effects on the three movements. While the short movement was largely unaffected by the startling stimulus (RT increased 3 ms for startle compared to control), both the long and two-step movement showed large decreases in RT on startle trials (decrease of 26 ms and 18 ms respectively). Although the Stimulus x Movement x Day interaction failed to reach statistical significance, $F(2, 18) = 4.06$, $p = .063$, $\varepsilon = .617$, $\eta^2_p = .31$, practice did appear to affect performance of the various movements differentially as by day 4 all movements were performed at similar latencies in both startle and control trials.
**Figure 5.4** Mean premotor RT values (SEM) for choice RT paradigm, separated by day and condition. An asterisk (*) denotes a significant differences between the short and two-step for control trials and between the long movement and both the two-step and short movements on startle trials. Note the long latency of startle RT values and the decrease in startle RT values with practice.
For the simple flexion movements, RT decreased more with practice for control trials (32 ms) as compared to startle trials (13 ms), as confirmed by a Day x Stimulus interaction, $F(1, 9) = 8.32, p = .018$, $\varepsilon = 1$, $\eta^2_p = .48$. RT also decreased across days (day 1 $M = 131$ ms, day 4 $M = 108$ ms), $F(1, 9) = 45.01, p < .001$, $\varepsilon = 1$, $\eta^2_p = .83$, and was faster for startle trials ($M = 94$ ms) as compared to control trials ($M = 145$ ms), $F(1, 9) = 75.33, p < .001$, $\eta^2_p = .89$.

The analysis of normalized SCM iEMG showed a main effect for block, $F(2, 18) = 43.74, p < .001$, $\varepsilon = .787$, $\eta^2_p = .83$, due to a significant decrease in activation for each block of trials (block 1 $M = 1.00$, block 2 $M = .50$, block 3 $M = .17$). There was also a significant increase in SCM iEMG from the last block of testing in the choice situation to the simple RT block of trials ($M = 1.87$), $F(1, 9) = 5.74, p = .040$, $\varepsilon = 1$, $\eta^2_p = .39$. Thus, by block 3 SCM activation had reduced to approximately 17% of the original values; however when participants were put into a simple RT task whereby they could prepare the movement in advance, activation levels returned to almost double baseline values.

**Kinematics**

We hypothesized that the lack of advance preparation would result in increased variability for the startle trials as compared to the control trials. Analysis of variability for the first 100 ms confirmed this prediction as startle trials were overall more variable ($M = 2.1^{\circ}$) than control trials ($M = 1.5^{\circ}$), $F(1, 9) = 8.10, p = .019$, $\varepsilon = 1$, $\eta^2_p = .47$. Participants also improved their consistency from day 1 ($M = 2.2^{\circ}$) to day 4 ($M = 1.4^{\circ}$), $F(1, 9) = 16.09, p = .003$, $\varepsilon = 1$, $\eta^2_p = .64$. The only other significant effect was a main effect for movement, $F(2, 18) = 5.89, p = .013$, $\varepsilon = .931$, $\eta^2_p = .40$, which was due to the long movement having greater variability than the short or two-step movement. For the second
component of the two-step movement, participants decreased variability with practice (day 1, $M = 4.6^\circ$, day 4, $M = 3.4^\circ$), $F(1, 9) = 7.22, p = .025, \varepsilon = 1, \eta^2_p = .44$, however the startling stimulus did not have an effect on movement consistency ($p = .835$).

**Discussion**

The purpose of this experiment was to examine the effects of practice on motor preparation of different types of unimanual movements when advance preparation could not occur (i.e., choice RT). As with the simple RT paradigm, participants were able to perform all movements in both the startle and control condition, with only a small percentage of trials discarded (2.4%), due mostly to incorrect movements. However, the lack of advance preparation resulted in a very different set of results. One difference that can be seen in the ensemble averages (Figure 5.3, right panels) is the lack of consistent EMG SCM activation during startle trials due to habituation, which was not seen in Experiment 1 (Figure 5.1, right panels).

RT decreased with practice, but we were most concerned with a comparison of RT values between movements. In contrast to the predictions we made based on Klapp’s (1995, 2003) theoretical model, we found no difference between the long and short movements, but an increased RT in control trials for the two-step movement as compared to the short movement (see Figure 5.4). The lack of difference between the single element movements may be due to the entire movement not being prepared in advance but rather as an initial movement to be modified on-line (as has been shown for large amplitude movements, see Klapp, 1975). The increased RT for the two-step movement may mean that sequencing is an important determinant of preparation time during choice RT paradigms (as originally suggested by Henry, 1980; see also Rosenbaum, Saltzman, &
Kingman, 1984). An alternate explanation is that the two-step movement was fully prepared before movement was initiated (as suggested in Experiment 1) and thus had more complex internal features as compared to the single element movements. It is also possible that the addition of a second movement element changed the internal features of the first movement. Requiring participants to integrate a second movement component may have resulted in more intricate motor commands to produce the initial movement, which would be reflected in an increased RT.

As predicted, the startling stimulus did not trigger any of the movements at latencies observed when the movement was known in advance (Figure 5.4, cf. Figure 5.2). Although the startling stimulus did reduce RT on day 1 for all but the short movement, values were still in the 300-400 ms range which is well beyond what would be expected if the movement was triggered by the startle. This reduction in RT for startle trials is likely a stimulus intensity effect whereby more intense stimuli produce faster responses (Woodworth, 1938, p. 318). Furthermore, startle trials showed a practice effect which would not be expected if movements were being triggered by the startle. These results were clearly not because participants were “non-startlers” as results of the simple flexion movement confirmed that participants were capable of being startled. Once put back into a simple RT paradigm, SCM activation returned to above baseline values and startle RT values were comparable to those with Experiment 1 and showed little change with practice.

The examination of between-trial variability produced different results to those in Experiment 1. Startle trials produced greater variability of the first 100 ms of the movement on both days of testing for all movements, which we attribute to the lack of
advance preparation. This result is consistent with the startling stimulus interfering with cortical processing. Similar to the work by Carlsen et al. (2004a), we found over double the percentage of movement errors for startle trials (5.0%, 18 of 360 trials) compared to control trials (2.2%, 175 of 7800), which may be due to this interference effect. The startling stimulus did not, however, affect variability of the second component of the two-step movement. This would suggest that by the time the participants initiated the second movement element they had overcome any interference by the startling stimulus resulting in a similar movement consistency.

The examination of EMG activation of the SCM provided strong evidence that a lack of advance preparation resulted in habituation to the startling stimulus as activation in block 3 was reduced to approximately 17% of the normalized activation in block one (compared to 75% in Experiment 1). However, when participants were put back into a simple RT task where they could prepare the movement in advance, SCM activation increased to 187% of the initial activation. Furthermore, SCM activation was absent on 20% of the startle trials in the choice RT paradigm (72 of 360; as compared to 4% in Experiment 1), with the greatest number in testing block 3 (8 in block 1, 21 in block 2, 43 in block 3). These results imply that habituation of the startle response still occurs during general motor preparation, whereby participants know a movement is required but not the specific details of the movement.

General Discussion

Motor Preparation and Practice

The purpose of the current research was to examine how extended practice of different unimanual movements affected motor preparation in both a simple and choice
reaction time experiment. We chose two single element movements that differed in movement amplitude (short versus long) and a two-element movement (two-step). Practice resulted in less time required to initiate the movement following the “go” signal and the production of more consistent movements; however we were most concerned with how RT changed with practice for the various movements.

In the simple RT experiment we found that the multiple subcomponent movement had a longer RT compared to single element movements; however, with extended practice the sequence length effect was reduced such that all movements were performed with a similar RT. Conversely, changing the complexity of the single element movement (by increasing movement amplitude), did not affect RT. These results replicate previous research involving keypress tasks (Klapp, 1995) and confirm that the internal features of a movement element can be prepared in advance of the “go” stimulus. In the choice reaction time experiment, participants were forced to prepare the movement following the “go” stimulus. However, in contrast to the predictions of Klapp’s model, increasing the complexity of the single element did not result in a higher RT, but increasing the number of movement elements did. These results suggest that internal features of the first movement element are not the only determinant of choice RT.

Motor Preparation and Startle

In the current experiments we also used a startling stimulus to probe the prepared response both early and late in learning. As a startling stimulus is thought to trigger a prepared response at very short latency, examination of the movement in response to a startle allowed for a more detailed determination of what was prepared in advance as opposed to after the “go” stimulus. For the simple RT paradigm, the startling stimulus
triggered both the single and multiple element movements at RT values consistent with other startle experiments (~80 ms). While this would be expected for the single element movements, the short latencies associated with the two-step movement confirmed that multiple component movements can be triggered by the startling stimulus and that at least a component of these more complex movements can be stored in advance. Another important finding is that RT values for startle trials did not change with extended practice, which is consistent with the theory that movements triggered by a startling stimulus do not involve cortical processing and are released without voluntary commands. For the choice RT paradigm, the startling stimulus produced shorter RT values for most movements on the first day of testing in comparison to control trials. However, considering the latencies were in the 300-400 ms range and reduced with practice, we deemed this effect to be one of stimulus intensity rather than triggering by the startling stimulus. Furthermore, participants showed a strong habituation to the startle in the choice paradigm, a result we attributed to the lack of advance preparation (Brown et al., 1991; Valls-Solé et al., 1997).

Movement consistency allowed us to infer changes in preparation as a result of practice. We did this by comparing between-trial variability on startle and control trials for the initial, preprogrammed portion of the movement and the second component of the two-step movement. We hypothesized that if advance preparation occurred, movement variability should be similar between startle and control trials as startle is thought to trigger a response prepared in advance. Conversely, if preparation occurred after the “go” stimulus, the startle trials would produce a more variable movement due to a reduction in the ability to smoothly integrate the movement components and a cortical interference
effect of the startling stimulus. During simple RT, the startling stimulus triggered a movement of similar consistency to control trials for both the initial portion of the movement (i.e., first 100 ms) and the second component of the two-step movement. This implies that all three movements were fully prepared in advance and triggered by the startling stimulus. Variability of the first 100 ms decreased with practice for startle trials and variability of the second component of the two-step movement decreased with practice trials for both control and startle trials, confirming an improvement in the advance preparation of the movement with practice. During choice RT, we expected participants to rely to a greater extent on preparation following the “go” stimulus, as they were unable to prepare the response in advance. As predicted, this mode of preparation was reflected in an increased variability of the initial movement in startle trials on both days of practice. However, variability of the second movement component was not affected by the startling stimulus, suggesting that by the time participants initiated the second element they were able to overcome any interference caused by the startle.

Theoretical Contribution to Motor Preparation

The examination of how movement complexity affects motor preparation has resulted in a wide array of theoretical models. One of the more prevalent theories offered by Klapp (1995, 2003) separates the preparation of the internal features of individual movement element (INT) from the sequencing of elements (SEQ). Similar to the work by Sternberg et al. (1978), this theory assumes that when a multi-element response is known in advance, all movement elements are prepared and stored in a large capacity memory buffer prior to the “go” stimulus. This buffer is continuously cycled which does not allow the performer immediate access to the initial element. Thus the extra reaction time
associated with sequenced movements in a simple RT paradigm is thought to be due to
the scanning of the buffer and organizing of the various elements into the correct serial
order for output. This sequence length effect does not affect choice RT because each
response element is individually loaded during the RT interval in the correct order and
thus no scanning time is required.

The results of the simple RT experiment replicate much of the previous research
examining response preparation, but are not compatible with the explanation of the
preparation processes, namely that the first movement element must be located by
scanning a memory buffer. Our results suggest that when the movement is known in
advance, at least the initial element of a sequenced movement can be stored and
immediately accessible when the “go” signal occurs. This was shown by the startling
stimulus triggering the initial movement element of the two-step movement at latencies
associated with subcortical storage and release (~80 ms). If scanning time was required to
locate the first element we would have expected startle latencies for a multiple element
movement to be similar to control trials or at the very least longer than the single element
movements. Although our results do not preclude the advance loading of individual
movement elements into a memory buffer, they do not support the scanning of such a
buffer to determine the proper order of the elements.

Triggering of the first movement element in the simple RT paradigm could have
occurred under two possible scenarios. One option is that participants only prepared the
first movement element and were able to implement the second element online. Given the
transient interference of the startling stimulus and the time required to execute the first
element, it is conceivable that participants were able perform the entire movement
accurately while only preparing the first element in advance. However, this explanation is unlikely as this method of preparation should not result in an increased RT for control trials for the two-step movement. Further, results of the variability analysis would suggest that the second movement component was not prepared online. Instead we believe that participants were able to prepare the entire two-step movement in advance as a single movement element and thus the entire movement was triggered by the startling stimulus. This explanation is consistent with both the startle RT and movement variability data.

If participants prepared the entire two-step movement in advance, sequencing would not need to occur following the “go” signal, and thus is not the reason why control trial RT values were elevated relative to single element movements. An alternate explanation is that rather than a sequencing requirement, more complex movement patterns may require activation of more “neuromotor coordination structures” (Henry & Rogers, 1960) or “cortical subassemblies of neurons” (Wickens, Hyland, & Anson, 1994). In these frameworks, the increased reaction time to a sequenced movement is attributed to a more extensive neural network that must be activated for longer sequences to be produced (Verwey, 1999). Thus, rather than assuming RT differences are due to search/retrieval processes, we suggest that these differences are instead due to initiation/implementation processes. While the “complexity effect” (Henry & Rogers, 1960) has typically been found by increasing the number of elements, there is research that suggests simple reaction time is also related to the complexity of a single element movement. For example, it has been shown that increasing the accuracy demands of a single component aiming movement can result in increased RT (Lajoie & Franks, 1997; Sidaway, 1991), a result which cannot be due to a sequencing requirement. Assuming
more accurate movements require greater neural coordination, these results are in line with our hypothesis that complexity relates to activation of a more detailed neural network. The fact that RT differences are minimized with practice would imply that participants became more efficient at organizing the movement at a neural level, such that a more complex movement no longer required additional time to initiate following the “go” signal.

The explanation that more complex movement patterns require activation of more complex cortical structures is also consistent with other findings from the current experiments. As it is thought that the stored motor commands are triggered by the startling stimulus without cortical involvement, we would not expect a change in RT based on movement complexity for startle trials on either day of testing. Furthermore, if greater neural activation is required to initiate more complex movements we would expect a RT effect of movement complexity in control trials regardless of whether or not the movement is known in advance. This was indeed the case in the current experiments as a sequenced movement resulted in longer control RT values for both choice and simple RT paradigms.

The hypothesis that complexity relates to neural activation rather than sequencing, although consistent with the current results, is not in line with research involving key pressing and speech articulation (e.g., Klapp, 1995, 2003). These studies failed to find an effect of sequencing in choice RT paradigms, which would be expected if initiation time increases with more complex movements. There are a few possible reasons for this discrepancy. One possibility is that the effects of organizing a more complex neural structure may be more apparent in tasks involving larger muscle groups, such as in the
current experiments. A second possibility is that the effects of more complex movements in choice RT paradigms may be masked by the increased time required to perform response selection during the reaction time interval. A third possibility is that when participants are not able to perform advance preparation, they may adopt a strategy whereby they only prepare the initial element prior to movement initiation, thus negating the complexity effect for sequenced movements yet maintaining the increased RT for longer duration single element movements. Further research is required to determine if these disparate results can be attributed to the types of tasks/effectors used by the various experimenters or processing differences between simple and choice RT.

**Conclusion**

Motor preparation of sequenced movements has been a topic of research for over a century, yet we are still trying to determine how movement complexity affects motor programming. In the current experiments we combined extended practice with a startling stimulus for unimanual responses in both a simple and choice RT paradigm. The use of the startling stimulus allowed for determination of preparation prior to the “go” stimulus and thus was a useful complement to the reaction time analysis. Examination of movement consistency allowed us to infer how preparation changed as a result of practice, resulting in a comprehensive analysis of the preparatory processes involved in different types of unimanual movements and an evaluation of motor preparation theories.

Our key findings were that for simple RT, we found a sequence length effect for RT in control trials, which was absent after four days of practice. During startle trials, all movements were triggered at a short latency and with similar consistency to control trials. Collectively these results suggested that participants prepared the entire sequenced
movement in advance. For choice RT, movement sequencing also affected RT values; however due to lack of advance preparation the startling stimulus did not trigger any of the movements, movements were more variable than control trials, and participants showed habituation to the startling stimulus.

Additional Information

In addition to the three movements we have reported in the current experiment, participant also performed a two component unimanual reversal movement that involved movement out to a $20^\circ$ target followed by a change of direction back to the starting position. Results of this movement are summarized in Appendix A.
The first four experiments of this dissertation described how motor preparation of various movements changed with physical practice. The examination of asymmetrical (Experiment 1) and asynchronous (Experiment 2) bimanual movements showed that pre-programming changes can occur even within a single session of physical practice. Evidence was also provided that the goals of the movement can alter the preparatory processes, as spatially defined movements appeared to be prepared in a different manner to those that are temporally-based (Experiment 3). We also examined how extended practice can affect motor preparation for tasks of various complexities in both a simple and choice RT paradigm (Experiment 4). This study showed that long-term practice can benefit not only advance preparation but also movement preparation processes that occur after the “go” stimulus. Collectively, these results confirmed that performance benefits that occur with practice are at least partially attributable to more consistent and accurate motor preparation of the required movement, as well as providing specific information as to how various unimanual and bimanual movements are prepared.

The last two studies focus on the preparatory processes associated with other forms of practice. Recent evidence suggests that when observing or performing motor imagery of an action, the motor system is engaged in a similar manner as if the response was being physically performed. It is hypothesized that imagined or observed actions are simulated such that preparation and organization of the movement occurs, only to be inhibited at some point prior to execution (Jeannerod, 2001). To test this hypothesis, we used startle methodology during imagery and observation to determine if participants prepared and stored motor commands, which could then be triggered by a startling
stimulus even though it was not intended to be overtly performed (Experiment 5). In Experiment 6, we used observational practice of a novel bimanual coordination skill to determine what is acquired while watching a learning model perform a complex motor task. In addition to traditional behavioural measures, we also examined perceptual measures (i.e., pattern recognition) and changes in cortical activation patterns as a result of both physical and observational practice. The results of this study contribute to cognitive mediation models of motor learning and allowed for insight into the potential processes associated with skill observation. These final two experiments provide information pertaining to less traditional forms of practice which are extremely important for those learners who are unable to perform physical practice due to injury or debilitation.
6. Experiment 5

Using Startle as a Probe of Motor Preparation During Imagery and Skill Observation

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Introduction

Physical practice is the most common means to improve performance; however motor skill research has also focused on how motor imagery and observation impact learning. Although many positive effects of imagery and observation have been reported, the explanations for why these benefits occur are varied (for recent reviews, see Ashford, Bennett, & Davids, 2006; Feltz & Landers, 2007; Guillot & Collet, 2005; Maslovat, Hayes, Horn, & Hodges, 2010; Munzert, Lorey, & Zentgraf, 2009). While imagery and observation may be important for determining strategic information regarding how to perform a task, learning benefits have also been shown in measures that are attributed to involvement of the motor system. This has included such performance outcome measures as force enhancement (Porro, Facchin, Fusi, Dri, & Fadiga, 2007; Ranganathan, Siemionow, Liu, Sahgal, & Yue, 2004), movement speed (Gentili, Papaxanthis & Pozzo, 2006), and flexibility (Guillot, Tolleron, & Collet, 2010). There is also evidence for changes in neurophysiological measures following imagery and observation such as altered movement representations in the primary motor cortex (Stefan et al., 2005; Stefan, Classen, Celnik, & Cohen, 2008), and functional reorganization of cerebral and cerebellar structures (Jackson, Lafleur, Malouin, Richards, & Doyon, 2003). The recent discovery of a common neural network involved in both covert and overt movements, known as the mirror neuron system (MNS), has led to the suggestion that observation and imagery involve neurophysiological activation of the motor system, even though no physical movement occurs (Decety, 1996; Fadiga & Craighero, 2003, 2004; Iacoboni, 2005; Jeannerod, 2001; Rizzolatti & Craighero, 2004; Rizzolatti & Fabbri-Destro, 2010; Rizzolatti, Fogassi, & Gallese, 2001). There is a wealth of research providing evidence
for motor involvement at the cortical, subcortical, and spinal levels during imagery and observation, although it is not clear what this involvement represents and if it is reflective of motor preparation. The purpose of this experiment is to determine whether activation of the motor system during imagery and observation is a result of movement preparation similar to that seen during overt actions.

Cortical involvement during observation and imagery has primarily been examined through the use of such techniques as functional magnetic resonance imaging (fMRI), transcranial magnetic stimulation (TMS), and electroencephalography (EEG) (see Fadiga, Craighero, & Oliver, 2005; Jeannerod & Frak, 1999; for reviews). For example, brain imaging has shown similar patterns of activation in MNS areas during observation and imagery of gymnastic movements that are highly related to the actual execution of the actions being viewed or imagined, suggesting a common neural system for these processes (Munzert, Zentgraf, Stark, & Vaitl, 2008). TMS-induced motor evoked potentials, which are thought to infer movement preparation, are comparable during observation, imagery and actual hand movements (Clark, Tremblay, & Ste-Marie, 2003; see also Kumru, Soto, Casanova, & Valls-Solé, 2008). The observation and imagery of hand movements has also been shown to generate a lateralized readiness potentials (LRP; a measure of the preparation of a specific unilateral response) consistent with the laterality of the hand being imagined or observed (Kranczioch, Mathews, Dean, & Sterr, 2009; Touzalin-Chretien & Dufour, 2008). There is also evidence for a desynchronization of EEG mu rhythms during observation of precision grip movements, a process that occurs during active movement and is thought to be involved in motor preparation (Muthukumaraswamy & Johnson, 2004; Muthukumaraswamy, Johnson, &
McNair, 2004). In addition to cortical involvement, Frey and Gerry (2006) found increased neural activation in subcortical regions (basal ganglia and cerebellum) during observation of a sequenced assembly task and spinal activation changes (as measured by H-reflex) have also been shown during observation (Baldissera, Cavallari, Craighero, & Fadiga, 2001) and imagery (Bonnet, Decety, Jeannerod, & Requin, 1997). More direct evidence for a MNS has been recently shown in humans via single neuron recordings that respond to both action execution and observation (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010).

The similarity in activation patterns between action, observation, and imagery has led to the hypothesis that the motor system is part of a simulation (Jeannerod, 2001) or emulation (Grush, 2004) network that can be activated during overt, observed, and imagined movements. During imagery and observation, preparation and organization of the movement still occurs such that it is regarded by the motor system as a real action, only to be inhibited somewhere “downstream” in the nervous system (Bonnet et al., 1997; Jeannerod, 1994). These claims are supported by research indicating activation in the inferior frontal cortex, an area associated with inhibitory processes, increases during imagery but is suppressed during execution (Dieber, Ibanez, Honda, Sadato, Raman, & Hallet, 1998; see also Jackson, Jackson, & Roberts, 1999; Rubia et al., 2001). Further evidence in support of this inhibition hypothesis is shown by imagined movements being executed unknowingly by a patient with bilateral parietal lesions, which is an important neural substrate for differentiation between real and imagined movements (Schwoebel, Boronat, & Coslett, 2002; see also Wilson, 2003).
Although similar neurological activation is typically seen during motor execution and motor imagery or observation, this does not necessarily mean that the processes governing these actions are equivalent (see Holmes & Calmels, 2008 for a review).

Differences have been noted between imagined, observed, and executed movements in cortical activation (Carrillo-de-la-Pena, Galdo-Alvarez, & Lastra-Barreira, 2008; Munzert et al., 2008; Solodkin, Hlustik, Chen, & Small, 2004; Wilson 2003), spinal activation (Baldissera et al., 2001), autonomic nervous system levels (Demouget, Normand, Denise, & Papaxanthis, 2009), as well as time to complete a movement (Rodriguez, Llanos, Gonzalez, & Sabate, 2008) and quality of decision making (Walsh & Rosenbaum, 2009).

While it is clear that there is activation of various levels of the motor system during imagery and observation, it is not clear if this activation relates to motor preparation and if these processes are similar in covert and overt actions. One methodology used to examine response preparation involves the use of a startling acoustic stimulus. During a simple reaction time task, replacing the auditory “go” signal with a loud startle tone (>124dB) has been shown to elicit a prepared action at a much shorter latency, with kinematics and EMG configurations largely unchanged (see Carlsen, Maslovat, Lam, Chua, & Franks, in press; Valls-Solé, Kumru, & Kofler, 2008 for recent reviews). Due to dramatic shortening of premotor reaction times (i.e. premotor RT <70 ms), it has been hypothesized that when the response is known in advance, it can be prepared and stored in subcortical areas and triggered at short latency by a startling stimulus (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004b; Valls-Solé, Rothwell, Goulart, Cossu, & Muñoz, 1999). Thus a startling stimulus can act as a probe for whether or not a movement has been prepared and stored in anticipation of a movement. We
hypothesized that if participants simulate the movement during imagery and observation in a similar manner to executed movements (as suggested by Jeannerod, 2001), a motor plan would be prepared and stored subcortically. If so, the startling stimulus should directly trigger all or part of this motor plan even though no movement was intended. This result would provide evidence that movement preparation does occur during observation and imagery and that the processes involved approximate those of executed actions.

Methods

Participants

Sixteen right-handed volunteers with no obvious upper body abnormalities or sensory or motor dysfunctions participated in the study after giving informed consent. However, only data from ten right-handed volunteers (4 male, 6 female; M = 21.2 yrs, SD = 2.1 yrs) were employed in the final analysis. Six participants did not show consistent activation in the sternocleidomastoid (SCM) muscle during startle trials (which is thought to be the most reliable indicator of a startle response), and thus were excluded from the analysis (see Carlsen et al., in press, for more detail regarding the exclusion criteria for participants). Although the percentage of rejected participants was higher than typically observed in startle experiments, the current study did not involve many startle trials with an intended movement. Conservatively, we chose to reject any participant that did not show SCM activation in any of the three trials to ensure the remaining participants consistently showed a startle response. All participants were naïve to the hypothesis under investigation and this study was conducted in accordance with ethical guidelines established by the University of British Columbia.
Apparatus and Task

Testing sessions occurred with two participants seated in height-adjustable chairs across a table from each other. One participant was a confederate to the researchers (unknown to the other participant) and was used for the entire study. A 22-inch computer monitor (Acer X233W, 1152 x 864 pixels, 75 Hz refresh) was on a table beside each participant. In front of each participant were two telegraph keys requiring 2 N to close (i.e., simply resting the hand on the switch was sufficient to close it), on which participants placed their hands to depress the switch (see Figure 6.1). Participants were asked to keep their fingers straight such that opening of the switch was achieved through wrist (rather than finger) extension. All auditory signals were generated by a customized computer program and were amplified and presented via a loudspeaker placed directly behind the head of the participant. The acoustic stimulus intensities were measured using a sound level meter (Cirrus Research model CR:252B) at a distance of 30 cm from the loudspeaker (approximately the distance to the ears of the participant).
Figure 6.1 Experimental set-up including location of monitor, telegraph keys and participants.
Experimental Design

All trials began with a warning tone consisting of a short beep (80 +/-2 dB, 100 ms, 100 Hz), followed by a “go” signal presented 3000 ms later which could either be a control stimulus (80 +/-2 dB, 100 ms, 1000 Hz) or startling stimulus (124 +/-2 dB, 40 ms, 1000 Hz, <1 ms rise time). To begin the experiment we wanted to assess the participant’s baseline of activity during control and startle trials when no movement was required. To this end, we presented three trials whereby the participant was asked to sit quietly with both right and left telegraph key depressed. For the first trial the “go” signal was a startling stimulus and provided an indication of the participant’s reflexive startle response when there were no instructions to prepare a movement. For the next two trials participants were instructed to close their eyes for one trial and observe the confederate’s left hand for one trial (order counterbalanced). Both trials were in response to a control stimulus in order to provide a baseline of activity for the imagery and observation trials respectively.

Next, participants were told they would be performing a key-lift reaction time task in competition with each other to examine the effects of different types of practice. The confederate always performed a left hand key-lift, while the participant always performed a right hand key-lift. We chose this arrangement so that participants would be observing a mirror-image of themselves performing the movement, which has been suggested to share the same representation for simulated movements (Anquetil & Jeannerod, 2007). Participants performed five testing blocks of 10 trials which alternated between physical practice and imagery or observation. For all physical practice trials, a reward bonus (CDN $0.25 per trial) was offered for the participant that had the fastest
reaction time (RT). This monetary incentive was introduced to encourage the participant to be maximally engaged in the task for all trials. RT was displayed on the computer screen for five seconds following each physical practice trial with no feedback provided to either the participant or confederate for the imagery and observation trials.

The first block of trials consisted of control trials (i.e., no startle) of physical practice for both participants (for trial details and order of testing see Table 6.1). For the second block of trials, only the confederate performed physical practice while the participant either performed imagery or observation (order counterbalanced with block four; all participants performed both imagery and observation). For imagery trials participants were asked to close their eyes and imagine feeling themselves lifting off the key in response to the “go” signal, without actually performing the movement. Before the block of imagery trials, participants were asked to perform a single imagery trial and rate their ability to imagine the movement on a visual and kinesthetic imagery scale of the Movement Imagery Questionnaire – Revised (MIQ-R; Hall & Martin, 1997). For the observation trials, participants were asked to watch the confederate’s left hand, in an attempt to improve their own performance. No instructions were given as to how to do this, or what characteristics to observe. During this block of imagery or observation trials, three startle trials were presented; one on the second trial and the other two pseudo-randomly presented in the last eight trials (never two consecutive startle trials). The third block of trials consisted of control trials of physical practice for both participants. The fourth block consisted of either imagery or observation trials as detailed above, with three startle trials interspersed (order counterbalanced with block two; all participants performed both imagery and observation). Participants then performed a final block of
physical practice with three startle trials interspersed as described above. Thus, all participants performed 30 trials of physical practice, 10 trials of observation, and 10 trials of imagery. There were 10 startle trials in total, one as a control (no movement), three during each of imagery and observation conditions, and three during the last block of physical practice.
Table 6.1 Summary of testing conditions including number of trials (Control = C, Startle = ST) and instructions given to participant. Note all trials began with both left and right keys depressed. Trials marked with an asterisk (* or **) were counterbalanced between participants.

<table>
<thead>
<tr>
<th>Condition</th>
<th># of Trials</th>
<th>Instructions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Startle Baseline</td>
<td>1ST</td>
<td>Sit quietly</td>
</tr>
<tr>
<td>Imagery Baseline*</td>
<td>1C</td>
<td>Close your eyes</td>
</tr>
<tr>
<td>Observation Baseline*</td>
<td>1C</td>
<td>Watch the confederate’s left hand</td>
</tr>
<tr>
<td>Physical Practice</td>
<td>10C</td>
<td>Lift your right hand off the key as soon as possible following the “go” stimulus</td>
</tr>
<tr>
<td>Imagery Practice**</td>
<td>7C: 3ST</td>
<td>Close your eyes and imagine lifting your right hand off the key as soon as possible following the “go” stimulus</td>
</tr>
<tr>
<td>Physical Practice</td>
<td>10C</td>
<td>Lift your right hand off the key as soon as possible following the “go” stimulus</td>
</tr>
<tr>
<td>Observational Practice**</td>
<td>7C: 3ST</td>
<td>Watch the confederate’s left hand and try to pick up any information to improve your performance</td>
</tr>
<tr>
<td>Physical Practice</td>
<td>7C: 3ST</td>
<td>Lift your right hand off the key as soon as possible following the “go” stimulus</td>
</tr>
</tbody>
</table>
**Recording Equipment**

Surface EMG data were collected from both participant and confederate for the muscle bellies of the following superficial muscles: right and left extensor carpi radialis longus (ECR - agonist), and right and left sternocleidomastoid (SCM - startle indicator) using preamplified surface electrodes connected via shielded cabling to an external amplifier system (Delsys Model DS-80). Recording sites were prepared and cleansed in order to decrease electrical impedance. The electrodes were oriented parallel to the muscle fibers, and then attached using double sided adhesive strips. A grounding electrode was placed on the ulnar styloid process (left for participant, right for confederate). Displacement RT of key lift off was monitored using the contact switch of the telegraph key. Attached to the participant’s two telegraph keys (Western Union Design, #808k1) were strain gauges (JP Technologies, PA06-250BA-120) wired to an instrumentation amplifier (Northwood Instruments, Model IA-02) that provided a voltage proportional to force (precision of 0.011N; range of 0-10N). A customized LabView® computer program controlled stimulus and feedback presentation, and initiated data collection at a rate of 1 kHz (National Instruments, PC-MIO-16E-1) 500 ms before the presentation of the “go” signal and terminated data collection 2000 ms following the “go” signal.

**Data Reduction**

A total of 10 of the 540 trials were discarded (1.9%). Reasons for discarding trials included the switch not being fully depressed to start the trial (6 trials), displacement reaction time shorter than 50 ms (which was assumed to be due to anticipation, 3 trials) or longer than 300 ms (1 trial).
Surface EMG burst onsets were defined as the point at which the EMG first began a sustained rise above baseline levels. The location of this point was determined by first displaying the EMG pattern with a superimposed line indicating the point at which activity increased to more than 2 standard deviations above baseline (mean of 100 ms of EMG activity preceding the go signal). Onset was then verified by visually locating and manually adjusting the onset mark to the point at which activity first increased. This method allowed for correction of errors due to the strictness of the algorithm. Force onset was determined in a similar manner by determining the time at which force increased 2 standard deviations above baseline. Initial movement onset was defined as the first point at which contact with the switch was broken.

We examined EMG, force and switch activity for the left and right hand of the participant between 50-300 ms following the “go” signal for all trials. This resulted in a classification for each trial as either a full, partial or no response. A full response required contact to be broken with the switch, along with a significant increase in force and EMG activation in the ECR. A partial response occurred if contact with the switch was not broken, yet there was a significant increase in force and EMG activation. Trials were classified as no response if there was no switch release or force increase, even if EMG activity occurred. We did not consider EMG activation alone as indication of a response because for startle trials this could be due to the startle response rather than any release of a prepared movement.

**Dependent Measures and Analyses**

To determine if the startle response triggered the movement during overt preparation (i.e., physical practice), we compared premotor RT (PMT; time from the
stimulus onset to agonist EMG onset) for startle and control trials in the final physical testing block via a paired-samples t-test, with an alpha level was set at .05. We also examined the incidence of full and partial responses for each participant in both left and right hands during the first three trials when no movement was prepared, and for both control and startle trials for the imagery and observation block as well as the final block of physical practice.

Results and Discussion

During the last block of physical practice PMT was significantly shorter on startle trials ($M = 78$ ms) as compared to control trials ($M = 119$ ms), $t(9) = 6.628$, $p < .001$. The short latency of PMT during startle trials was consistent with previous experiments involving arm movements where it has been suggested that such short reaction times are due to triggering of a pre-programmed response (i.e., Carlsen et al., 2004b; Carlsen, Chua, Inglis, Sanderson, & Franks, 2004a; Maslovat, Carlsen, Ishimoto, Chua, & Franks, 2008; Maslovat, Carlsen, Chua, & Franks, 2009).

We next examined participants’ responses to the first three baseline trials when they were not instructed to prepare a movement. As expected, the second and third trials which involved a control “go” stimulus during either passive observation or with eyes closed did not produce any type of response (full or partial). However, for the first trial when a startling stimulus was delivered without any instruction to move, four participants showed a bilateral response whereby both arms showed either a full or partial key lift. No unilateral responses were seen. Thus the reflexive startle response can cause a key lift to occur, although when it appeared this response was seen in both arms simultaneously.

Based on the results of the baseline startle trials, where there was either a bilateral
response or no response, we rationalized that the presence of a unilateral response in the right arm for the imagery and observation trials would suggest that a specific prepared movement had been triggered by the startling stimulus. For the physical practice trials, we observed a 100% full response rate in the right hand for both control and startle trials, confirming that participants always lifted the key on physical practice trials. For the left hand during physical practice trials, we observed one control trial with a full response (1%) and a total of two startle trials with a partial response (7%). The low error rates indicate that participants were able to perform the unimanual task correctly in both startle and control conditions.

For the imagery trials, we observed a full response in the right arm for a total of two control stimulus trials (3%) and a partial response in a total of twelve control stimulus trials (17%) and seven startle stimulus trials (23%). For the observation trials, no full responses were seen in either arm. However, partial responses were observed in the right arm for a total of three control stimulus trials (4%) and six startle stimulus trials (20%). No full or partial responses were observed in the left arm during either imagery or observation trials. The incidence of a left and right response by participant and condition is shown for control and startle trials in Figure 6.2. Three out of ten participants failed to show any response during either imagery or observation trials, whereas a further three only showed a response during imagery trials. One participant responded only in the observation condition.
Figure 6.2 Incidence of partial unilateral responses, by participant, for imagery (top panel) and observation (bottom panel). Subject numbers with an asterisk (*) denote those that performed imagery trials first. Note these subjects showed a higher response rate during observation trials (bottom panel).
The presence of partial unilateral responses for startle trials (20%) in both imagery and observation conditions provides support for the idea that a specific motor plan was prepared and stored during these conditions, for at least two-thirds of the participants. However, it is unclear why a unilateral response did not occur on every startle trial or for every person. One possibility is that participants did not prepare a movement on all trials. As no physical movement was required, it is conceivable that participants were more focused on the possibility of a startling stimulus being delivered, rather than engaging in the conditions encouraged through the imagery or observation instructions. There is some support for this suggestion as a post-hoc examination of the first startle trial in the imagery condition showed that half the participants showed a response (50% response rate compared to 23% overall); however the incidence of response for the first startle trial in the observation condition was not different for the first trial as compared to the overall mean (20% in both instances).

An alternate explanation is that movement preparation occurred on every trial but the prepared motor commands were not always triggered by the startling stimulus. Movement initiation is often explained via an accumulator model, whereby a response is triggered when activation levels grow over time to reach a threshold level (Hanes & Schall, 2006). Differences in initiation time can be attributed to differences in rate of activation accumulation (Carpenter & Williams, 1995) or differences in threshold levels (Nazir & Jacobs, 1991). It is possible that imagery and observation involve inhibitory processes that either decrease the rate of activation accumulation or increase the threshold level required to initiate the movement. While it would be expected that a startling stimulus would increase the overall excitability of the nervous system (Carlsen et al.,
2004b; Maslovat et al., 2008, 2009), this may not be sufficient to initiate the movement on every trial. Given that the exact mechanisms of movement inhibition are unclear, this explanation would require further investigation, likely with more detailed electrophysiological recording of various levels of the nervous system (cortical, subcortical, spinal).

When movement initiation did occur, it is not surprising that the vast majority of responses were only partial movements as the activation levels observed in imagery and observation are often much reduced compared to the overt movement (Holmes & Calmels, 2008). We examined the EMG activity for the partial responses during imagery and observation to determine if the unilateral responses occurred at latencies consistent with physical movement trials. EMG onset (i.e., PMT) was similar for control trials during imagery/observation \((M = 134 \text{ ms}, n = 15 \text{ trials})\) and physical movement \((M = 119 \text{ ms}, n = 70 \text{ trials})\); however startle trials were performed at a longer PMT during imagery/observation \((M = 139 \text{ ms}, n = 13 \text{ trials})\) as compared to physical movement \((M = 78 \text{ ms}, n = 30 \text{ trials})\). Examination of the individual trials revealed that five of the thirteen startle trials that showed a response had a PMT of below 100 ms, as would be expected with a movement triggered by the startling stimulus. Thus, although some startle trials occurred at latencies associated with subcortical triggering, this did not occur on a consistent basis.

To further compare EMG activation during imagery, observation and physical movement, we created ensemble averages showing rectified raw EMG for both limbs, normalized to the “go” signal. These averages are shown in Figure 6.3 for control and startle trials and represent mean data from all trials involving partial responses for
imagery (12 control, 7 startle) and observation (3 control, 6 startle), as compared to physical movement (70 control trials, 30 startle trials). For control trials (top panel), there was a burst of right agonist activation during imagery trials (light black line) that occurred at a similar latency to physical practice (dark black line), although the amplitude of activation was much smaller. This effect was not observed for observation trials (grey line) nor was any significant EMG activation found in the left agonist for any control trial conditions (shown as negative values in Figure 6.3). For startle trials there was not a consistent unilateral activation pattern during either imagery or observation (bottom panel). While there did appear to be activation during observation around 50-150 ms after the “go” signal, this activation was bilateral and thus is likely attributable to the reflexive startle response rather than indicative of preparatory processes. The lack of effects may be attributed to the reflexive muscle activity caused by the startling stimulus, which masked any unilateral effects due to preparation of a specific arm movement.
Figure 6.3 Ensemble averages showing rectified raw EMG for right agonist (positive values) and left agonist (negative values), normalized to the “go” signal. Values are shown for control (top panel) and startle (bottom panel) conditions separated by physical movement trials (dark black line) and imagery (light black line) and observation (grey line) trials that showed a partial response. Note the presence of a right agonist response during imagery trials in the control condition that is similar in time but reduced in amplitude as compared to physical movement trials.
The presence of EMG activation during control trials provides a potential confound to the present experiment. It has been suggested that motor imagery can only be considered imagery if no EMG activity is observed (Stinear, Byblow, Steyvers, Levin & Swinnen, 2006). These authors argue that motor imagery, by definition, is a cognitive process that does not result in any outflow from the spinal motor neuron pool. However, early explanations for the benefits of imagery involved the suggestion that a similar muscular activation pattern, although reduced in amplitude, should be observed during imagined movements (Jacobson, 1930; Suinn, 1976; Wehner, Vogt, & Stadler, 1984; and more recently Bonnet et al., 1997). It was hypothesized that this residual EMG activity was due to an incomplete inhibition of the motor commands. Others have suggested that this is not a viable explanation as the time course of EMG rarely parallels that of overt movement and could be due to generalized activation that may occur in other, non-involved muscles (see Feltz & Landers, 2007 for a review; see also Personnier, Ballay, & Papaxanthis, 2010 for recent results). In the current experiment the EMG activation during imagery control trials occurred in a similar time-course to executed movements and was only present in the imagined limb (Figure 6.3, top panel). Thus, while it could be argued that the presence of EMG activation means that, by definition, participants were not merely engaging in imagery, the results do provide evidence in support for the hypothesis that imagery results in low-gain neuromuscular activation.

At the conclusion of the experiment all participants reported being able to imagine themselves perform the movement, as also indicated by their self-reported ratings on the MIQ-R for both kinesthetic ($M = 5.5, SD = 1.1$) and visual ($M = 5.6, SD = 1.3$) imagery (max = 7). We also asked participants what they were doing during observation trials.
Recall that participants were counterbalanced such that they either first performed observation trials (N = 5; 3 females, 2 males) or imagery trials (N = 5; 3 females, 2 males). None of the participants that performed observation trials first reported using any sort of imagery during these trials, but rather talked about looking for strategic information such as how the confederate lifted off the key. For the five participants that performed imagery trials first, three participants reported also performing imagery during the observation trials while the other two reported looking for strategic cues from the confederate. To examine if order of trials affected the processes undertaken by the participants we analyzed post-hoc the incidence of responses separately for participants that began with imagery versus observation. For the imagery trials, there was little difference in response incidence. The imagery-first group showed a 27% response rate in startle trials (26% in control trials) compared to the observation-first group that showed a 20% response rate in startle trials (14% in control trials). However the group differences were much larger for the observation trials. The imagery-first group showed a 33% response rate in startle trials (9% in control trials), the observation-first group only showed a 7% response rate in control trials (0% in control trials). Thus it appears that performance of imagery trials primed the participants to employ imagery during observation, which did not occur when observation was performed before imagery (see Figure 6.2).

A final discussion point involves the bilateral response shown by four participants to the startle stimulus during the first control trial when no movement was required. Although this is not an unexpected reflexive startle response, a bilateral response was not seen for startle trials during physical practice, imagery or observation. This suggests that
the reflexive bilateral startle response was altered when participants were asked to
perform a movement, engage in imagery or watch movements being performed, such that
the reflexive movement in the non-involved limb was inhibited. This has been repeatedly
shown with experiments involving physical movements whereby the reflexive flexion
startle response (Brown, Rothwell, Thompson, Britton, Day, & Marsden, 1991) is
modified by motor preparation of an extension movement (e.g., Carlsen et al., 2004a,
2004b; Maslovat et al., 2008, 2009). What we have shown here is that modification of the
reflexive startle response also occurs during the process of observation or imagery.

In summary, the presence of unilateral partial responses on approximately 20% of
the imagery and observation startle trials provides support for the idea that movements
can be prepared and triggered to some degree by a startling stimulus, even though no
overt movement is required. For these trials, it is currently unknown if the startling
stimulus only partially triggered the response or if the movement was only partially
prepared. We have also shown that previous exposure to imagery increases the likelihood
of a partial response for startle trials during observation. The fact that observation alone
rarely produced a response during startle or control trials (see Figures 6.2 & 6.3) raises
the question of whether similar processes are engaged during observation as during
physical practice (Holmes & Calmels, 2008). These data provide some evidence that
when movement simulation is explicitly encouraged via imagery instructions, participants
engage in response preparation that at least in part resembles what is seen during physical
movement with the exception of the final motor response. A startling stimulus is able to
at least partially trigger this response on select trials, which might suggest an increasing
of neural activation to a threshold whereby motor commands are released and muscle activity is observed.
Bridging Summary to Following Chapters

The current experiment provided evidence that during imagery and observation a startling stimulus can trigger a partial response, at least on some trials. This result supports previous work suggesting these processes may involve response preparation in a similar manner to movements intended to be performed (Jeannerod, 2001). However, the lack of partial responses when observation was not preceded by imagery and the inconsistency of EMG activation during observation trials suggest that imagery and observation may involve different processes depending on the conditions under which observation occurs. One of these conditions may relate to whether or not the observed movement is within the observer’s repertoire. To further examine the processes involved in observation, our next experiment examined observational practice of a model learning a novel skill. We chose a bimanual coordination task that has been shown to be difficult to extract strategic knowledge so that any improvements in performance due to observation could be attributed to involvement of the motor system. To gain a better understanding of what is being acquired during observation we used behavioural, perceptual, and neurophysiological measures of both the models’ and observers’ performance.
7. Experiment 6

Observational Practice Benefits are Limited to Perceptual Improvements in the Acquisition of a Novel Coordination Skill

\(^7\)

\(^7\) A version of chapter 7 has been published. Maslovat, D., Hodges, N. J., Krigolson, O. E., & Handy, R. C. (2010). Observational Practice Benefits are Limited to Perceptual Improvements in the Acquisition of a Novel Coordination Skill. *Experimental Brain Research, 204*, 119-130.
Introduction

Motor skill acquisition often involves the transfer of information between an instructor and learner in an attempt to accelerate the learning process. One of the most common and efficient methods of transfer involves the use of demonstrations (Bandura, 1986; McCullagh & Weiss, 2001). The process by which an observer adapts his or her movements as a result of watching a model is known as observational learning (see Maslovat, Hayes, Horn, & Hodges, 2010; Horn & Williams, 2004; Hodges, Williams, Hayes, & Breslin, 2007; Vogt & Thomaschke, 2007 for recent reviews). A meta-analysis of the observational learning literature has shown that this process is more effective than practice alone (Ashford, Bennett, & Davids, 2006). However, the process and the conditions by which observation of an action produces learning benefits are still unclear.

In an attempt to isolate the effects of observation, researchers have made a distinction between observational learning and observational practice (Vogt & Thomaschke, 2007). While observational learning typically involves the alternation between demonstrations and physical practice, during observational practice the observer only watches a model as they acquire a skill. Observational practice thus affords the opportunity to test how observation alone affects the acquisition of motor skills. In the current study we aimed to determine what is acquired during observational practice of a novel bimanual coordination skill through perceptual and behavioural measures of performance.

Different reasons have been proposed for the positive effects of observation. Recently, researchers have suggested that the observer’s motor system is covertly activated during observation, so termed ‘early mediation’ (Vogt, 2002; Vogt & Thomaschke, 2007). Accordingly, any improvements in performing the motor skill after
watching are attributed to the priming of the motor system during the observation stage. Alternatively, improvements due to observation have more traditionally thought to be strategic in nature, involving motor system activation only once physical practice has begun, so termed ‘late mediation’. Trying to separate these two explanations has provided a significant challenge to researchers.

There is considerable evidence showing that observers are able to deduce cognitive strategies for performing through watching a model. Observational practice has shown to be as effective as physical practice during error recognition of a serial key press task (Black & Wright, 2000; Black, Wright, Magnuson, & Brueckner, 2005) and in adapting a learned strategy during a tracking task (Shea, Wright, Wulf, & Whitacre, 2000). Further, it appears that the strategy used by the model is adopted by the observer, regardless of whether it is most beneficial for task performance. In one study, observers watched a model demonstrate either a conservative or risky strategy during a ball-flicking task (Martens, Burwitz, & Zuckerman, 1976). The observers imitated the strategy of the model they observed, even though the more risky approach yielded poorer performance. Similarly, more recent results from Al-Abood, Davids, Bennett, Ashfor, & Martinez-Marin (2001) showed that observers mimicked the underarm throwing strategy employed by a model in a dart-throwing task. This was in comparison to the overarm strategy used by control participants, even though the type of strategy had no bearing on overall target success. Therefore, although demonstrations may function to constrain the strategy employed by the observer, this is not always an effective method, particularly if the strategy adopted by the observer is not directly related to task success.
Despite the acquisition of more cognitive strategic knowledge as a result of watching a model, there is also evidence that observation activates the motor system and that this process is responsible for positive learning effects (i.e., early mediation). Mattar and Gribble (2005, see also Brown, Wilson, & Gribble, 2009) showed benefits of observational practice when participants watched a model learn to move a robotic arm in a perturbed, dynamic environment. Benefits were seen in terms of time savings for observers in comparison to actors when they first received physical practice performing in the new environment. While the authors could not conclusively rule out that observers developed a cognitive strategy during observation, the observers improved even when they were required to perform a cognitively demanding task during observation. The authors argued therefore, that learning occurred via implicit activation of the motor system. Similar conclusions were reached by Heyes and Foster (2002), who found that the degree of positive transfer following observational practice of a key-board sequence task was effector-dependent. Because of the specificity of learning to the observed limb, learning was believed to be a result of motoric encoding of the observed action rather than a more general strategic benefit.

Convincing evidence supporting motor involvement during observation has been provided through study of an area of the brain shown to be active during observation for imitation, known as the mirror neuron system (MNS). Researchers have shown similar cortical activation patterns during both observation and physical production of a movement, which has been attributed to the automatic elicitation of a motor representation of the action during observation (for reviews see Fadiga & Craighero, 2004; Rizzolatti & Craighero, 2004; Iacoboni, 2005). There has, however, been some
debate as to the presence or extent of motoric activation during observation for skills that are not within a person’s motor repertoire and hence what might be considered true motor skill acquisition. For example, Calvo-Merino et al. (2005, 2006) showed that brain activation in areas associated with the MNS were significantly reduced or did not occur during observation of skills which were not typically performed by the observer (such as female moves for male dancers, see also Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004).

To try and understand the processes engaged during observational practice, a number of researchers have examined the effectiveness of demonstrations in the acquisition of novel, two-joint coordination movements (Buchanan & Dean, 2010; Hodges & Franks, 2000, 2001, 2002; Buchanan, Ryu, Zihlman, & Wright, 2008). Benefits from using a coordination task are that participants are typically unable to perform the movements without considerable practice and due to their novelty, they do not have any prior knowledge of an effective strategy which can be used to perform these movements. The acquisition of these types of coordination patterns can be studied in relation to existing performance capabilities, as well as in terms of transfer to non-practiced movement patterns (Zanone & Kelso, 1997; Kelso & Zanone, 2002), thus permitting insight into how learning is achieved and generalized.

In the examination of bimanual coordination, two inherently stable (i.e., intrinsic) movement patterns have been identified. These stable patterns include a strong symmetrical in-phase pattern (i.e., 0° relative phasing of the hands), and a somewhat weaker anti-phase pattern (i.e., 180° relative phasing of the hands). Because of the stability of these two patterns and the instability of relative phase patterns intermediate to
these two attractors, researchers interested in motor learning have often required participants to learn a pattern half-way between in-phase and anti-phase, that is 90° relative phasing of the hands (e.g., Zanone & Kelso, 1992a, 1997; Lee, Swinnen, & Verschueren, 1995; Swinnen, Lee, Verschueren, Serrien, & Bogaerds, 1997; Kovacs, Buchanan, & Shea, 2009a). There is evidence that development of a 90° bimanual coordination pattern also results in positive transfer to the symmetrical pattern of coordination (i.e., 270° relative phasing where the opposite hand leads; Zanone & Kelso, 1992b, 1997; cf. Maslovat, Bredin, Chua, & Franks, 2005) as well as positive transfer to other effector systems (Amazeen, 2002; Kelso & Zanone, 2002; Buchanan, 2004; Buchanan, Zihlman, Ryu, & Wright, 2007). It is unclear whether this transfer is mediated by explicit, strategic processes, although the absence of effector specificity may suggest so (e.g., Heyes & Foster, 2002).

Researchers who have studied the effectiveness of demonstrations during the acquisition of a 90° pattern have not found the observational process to be an effective medium (see Hodges & Franks, 2000, 2001, 2002). There are two potential reasons for these results. First, is a lack of salient strategic information conveyed in a “correct” demonstration, especially when provided sparingly in an observational learning context. This would hinder any more cognitive mediated benefits from observing. Second, the novelty of the skill is expected to hinder or prevent motor system activation during observation (see Milton, Small, & Solodkin, 2008 for a review of this evidence). To address these strategic limitations, Buchanan et al. (2008) required observers to watch a learning model acquire a novel, unimanual coordination movement whereby the wrist and elbow joints were moving at a 90° offset. During these single limb movements, the lead-
lag relationship between the limb segments may be more perceptually distinct as compared to a bimanual movement, providing more strategic information to the observer. For example, Breslin et al. (2005, 2006, 2009) showed that observers were better able to fixate, detect and replicate within-limb coordination of the arm after watching a cricket bowling action, than between-arm coordination (see also Collier & Wright, 1995; Buchanan et al., 2008 for similar discussions about the differences between these types of coordination tasks). Further, Buchanan et al. allowed the models to adopt one of two possible strategies to produce the 90° movement (wrist leading or wrist lagging). Because the observers adopted the strategy of the model they observed, the authors concluded that the wrist lead-lag strategy was beneficially recognized and employed by the observers.

This cognitively mediated benefit as a result of observing was further underscored by a subsequent study involving observational practice of a 90° bimanual pattern, whereby the models were either allowed to explore various strategies or were constrained to a single strategy (Buchanan & Dean, 2010). Actors who were constrained to a single strategy improved faster and performed better on retention tests than actors who practiced without these constraints. However, observers who watched the actors perform without strategy constraints were more accurate than those who watched a single strategy actor. The authors concluded that watching the exploration of various strategies was an effective learning technique, although they were not able to conclude whether these benefits were a result of cognitive-strategic (late mediation) or motoric (early mediation) processes.

Strategic explanations associated with benefits from observing a model were originally proposed by Bandura (1971). According to his cognitive mediation model,
behaviour is stored in representational form which then mediates an action response. During observation, this cognitive representation is continually updated through comparisons between the observed act and the observer’s internal representation of the act. Observation of multiple strategies would be expected to offer more distinguishing information than observation of a single strategy, acting to improve the effectiveness of this internal representation through distinctiveness and elaboration. However, observation of a single strategy would still provide information to the observer pertaining to what to do, as well as what not to do. This is especially true for observation of a learning model that would, presumably, show variability in demonstrations at least early in the acquisition period.

Evidence in support of the development of some sort of perceptual-cognitive representation preceding motor learning was shown by Caroll and Bandura (1982, 1990). Observers were able to distinguish between correct and incorrect versions of a desired motor skill before they were able to correctly perform the skill. This suggests that strategic or perceptual advantages were one of the immediate benefits of watching and that this cognitive-perceptual process mediated later performance of the motor skill. This ability to discriminate between correct and incorrect movement patterns as a result of observation was also shown in a bimanual coordination task by Hodges et al. (2003). However, this perceptual discrimination ability was only realized by participants who received both correct demonstrations and movement-based feedback about their own performance. As with the results of Buchanan and colleagues (2008, 2010), and in line with the cognitive mediation account of observational learning, it appears that the observer needs to see differences across performance attempts to improve and that the
more varied these experiences are, the more effective is the perceptual-cognitive representation of the skill.

The development of visual discrimination in a bimanual coordination task is especially important because it has been implied that perception is coupled to, and essential for, accurate physical performance. In a series of studies, Bingham and colleagues (Bingham, Schmidt, & Zaal, 1999; Bingham, Zaal, Shull, & Collins, 2001; Zaal, Bingham, & Schmidt, 2000; Wilson, Collins, & Bingham, 2005) provided evidence that visual perception of relative phasing between two stimuli followed a similar pattern to that observed for pattern production. Perception of in-phase movements were most accurate followed by anti-phase movements, with any other pattern judged unreliably (with poorest performance at 90°). The authors suggested that at least part of the problem with producing a novel relative phase pattern is the difficulty in correctly perceiving the movement. Therefore, it would be important to look at how observation affects both the perception and production of the movement pattern in order to make conclusions as to the processes encouraged by observational practice. Although we would not expect improvements on a motor task without corresponding perceptual improvements, we might expect perceptual improvements without corresponding changes in behavioural measures. Any perceptual discrimination improvements in the absence of behavioural improvements would support a late mediation or strategic account of observational practice, with physical practice necessary for behavioural benefits to be observed.

To test these ideas, we examined the changes in both physical performance and perceptual discrimination following physical and observational practice of a novel bi-manual coordination skill. To ensure observers watched a novice model progress through
the learning process observers were yoked to, and observed a participant in the physical practice group. We expected the physical practice group to improve at both physical performance and perceptual discrimination of the practiced task due to extensive physical (visuo-motor) practice and because of the close coupling seen between action capabilities and perceptual capabilities (Bingham et al., 1999, 2001; Zaal et al., 2000; Wilson et al., 2005). Although we expected variability in performance by the model over the course of practice, only one lead-lag strategy was conveyed by the visual metronome. Therefore, because observers watched a model that was not given the opportunity to explore different strategies, we did not expect the observational practice group to improve on the behavioural performance measures (Hodges & Franks, 2000, 2001, 2002; cf., Buchanan & Dean, 2010). However, based on Bandura’s (1971) cognitive mediation model, we predicted that observers would improve on the perceptual discrimination measures. Repeated observation of a learning model should allow the observers the opportunity to determine correct and incorrect movement patterns in the absence of physical practice. This result would speak more to strategic or cognitively mediated processes of learning (late mediation), rather than more recent beliefs that observational practice activates the motor system during the observation process (early mediation) and that benefits are a result of this more direct route. We also examined physical and perceptual performance on the symmetry partner of the practiced task, whereby the opposite hand leads the pattern. Although physical practice can result in positive transfer to the symmetrical partner (Zanone & Kelso, 1992b, 1997), it is unclear if observational practice would produce similar benefits. We did not expect the observational practice group to show transfer benefits in physical performance measures, although improvements in the
perception of the symmetry partner might be expected if the benefits of observation are strategic in nature.

Methods

Participants and Group Assignment

A total of 36 university-aged \( M = 23.1 \) yrs, \( SD = 3.6 \) yrs self-declared right-handed participants (14 male, 22 female) were randomly assigned to one of three groups (12 per group): physical practice, observational practice, and control group. Participants performed either four sessions (physical and observation group) or two sessions (control group) on separate days spread over one week. All participants’ first and last sessions were approximately half an hour and involved testing of physical performance and visual discrimination of various coordination patterns (including the to-be-learned pattern), providing a measure of performance before and following practice. In between these testing sessions, the physical and observation groups performed two acquisition sessions on consecutive days that were approximately one hour in duration and consisted of repeated practice of a 90° phase offset bimanual coordination pattern. During acquisition, each participant in the observation group watched a participant in the physical practice group. In this way the observers were able to see repeated demonstrations of an actual participant learning the skill. All participants received remuneration ($35 CDN for physical and observation groups; $10 CDN for control group) and were naïve to the purpose of the experiment. The study was conducted in accordance with the ethical guidelines of the University of British Columbia.
Task and Apparatus

The required coordination pattern was specified to the participant by two green vertical lines (10 inches in length) on a computer screen which moved in a 40° peak to peak movement range in the manner of an inverted pendulum (i.e., rotation around the bottom of the line). The task was to move two lightweight manipulanda, via horizontal elbow flexion and extension to follow the movements of these lines or pendula on the screen. Movement of the right line was to be mirrored by the right manipulandum while movement of the left line was to be mirrored by the left manipulandum. Presentation of different relative phase patterns of the pendula was controlled by altering the relative timing of the movements of the green lines.

A schematic of the apparatus and participant position is illustrated in Figure 7.1. When physically performing coordination patterns, participants were seated approximately 30 inches in front of a 17-inch color monitor (VGA 640 x 480 pixels, 60 Hz refresh). Attached to the table on each side of the monitor were the manipulanda. Participants’ arms and hands were secured with Velcro straps to the manipulanda with the elbow joint aligned with the axis of rotation and the hands pronated. The required movement amplitude was 20° (resulting in a 40° peak to peak movement range), specified by “in” and “out” markers on the table for each arm, which translated to a 15 cm movement on the computer screen. Angular position was recorded using two optical encoders (Dynapar, E20-2500-130), one attached to the shaft of each manipulandum. Three-axis Quadrature Encoder interface cards (Advantech, PCL-833) enabled high-speed sampling of angular position at a rate of 1000 Hz and a spatial resolution of 0.036°/bit. A computer motherboard was used to generate the audio metronome tones.
The metronome signal was amplified by a speaker on each side of the monitor (Multi-Media, Model #EP-691). During observation trials, the observer was seated in a chair approximately 1 m in height so that they could view both the performer’s hands and computer screen. The observer’s hands were loosely strapped to their thighs to ensure no physical movement of the limbs occurred during observation trials. During all trials both observers and performers had full vision of their hands.
Figure 7.1 Schematic display of apparatus set-up and design including location of monitor, speakers, and manipulanda (midpoint table markers not shown). The “X” indicates the location of the observer during acquisition trials.
Testing Protocols

Details of group procedures including number of trials and specific feedback are described below and displayed in Table 7.1. Participants in all three groups began with a single testing session on day one that involved a “scanning run” to measure performance on a variety of relative phase patterns (i.e., pre-test). These procedures were also adopted on day four after all practice trials had been completed (i.e., post-test). Participants performed 24 trials each lasting 20 seconds, consisting of three trials of eight different relative phase patterns comprising the entire range of possible patterns, separated by 45° (i.e., 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°). These trials were presented at a rate of 1 Hz in a pseudo-random order, such that a single pattern was never repeated three times in a row. Following each trial, participants were asked to determine which pattern they had just performed by a rating system that designated whether the limbs were moving in a symmetrical (i.e., in-phase, 0°) or alternating fashion (i.e., anti-phase, 180°), or if the right or left hand was leading the movement by one-quarter, one-half or three-quarters of a cycle (see Figure 7.2 with the corresponding relative phases shown in brackets). Following the pre-test scanning run a single 20 second trial was presented whereby participants attempted to perform a 90° relative phase movement at 1 Hz. In this trial the pendula on the computer screen disappeared after five seconds and the participant was required to continue to perform the movement without any visual information (i.e., faded feedback). This trial allowed for assessment of performance without the guide of the pacing pendula. This trial was also completed post-practice on day four, at the end of the post-test scanning run. No augmented feedback about performance was provided during the pre-test or post-test trials.
Table 7.1 Summary of testing conditions including number of trials, display shown, feedback, and pattern performed.

<table>
<thead>
<tr>
<th>Condition</th>
<th>Trials</th>
<th>Display</th>
<th>Feedback</th>
<th>Pattern</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Day 1 (all groups)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-Test</td>
<td>24</td>
<td>1 Hz Pendula</td>
<td>None</td>
<td>Random presentation of 3 trials each of: 0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°</td>
</tr>
<tr>
<td>Faded Feedback</td>
<td>1</td>
<td>5s of 1 Hz Pendula</td>
<td>None</td>
<td>90°</td>
</tr>
<tr>
<td><strong>Day 2 (physical and observational groups only)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acquisition</td>
<td>20</td>
<td>0.75 Hz Pendula</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.75 Hz Lissajous</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>0.85 Hz Pendula</td>
<td>Terminal</td>
<td>90°</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.85 Lissajous</td>
<td>RMSE</td>
<td></td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>1 Hz Pendula</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Day 3 (physical and observational groups only)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acquisition</td>
<td>20</td>
<td>0.85 Hz Pendula</td>
<td>Terminal</td>
<td>90°</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.85 Hz Lissajous</td>
<td>RMSE</td>
<td></td>
</tr>
<tr>
<td></td>
<td>55</td>
<td>1 Hz Pendula</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Day 4 (all groups)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Post-Test</td>
<td>24</td>
<td>1 Hz Pendula</td>
<td>None</td>
<td>Random presentation of 3 trials each of: 0°, 45°, 90°, 135°, 180°, 225°, 270°, 315°</td>
</tr>
<tr>
<td>Faded Feedback</td>
<td>1</td>
<td>5s of 1 Hz Pendula</td>
<td>None</td>
<td>90°</td>
</tr>
</tbody>
</table>
Figure 7.2 Display for relative phase perceptual discrimination. Note relative phases shown in brackets for information only (not shown to participants).
Following the pre-test scanning were two acquisition sessions on day two and three. During practice, a physical practice participant was paired with an observational practice participant. Participants in the physical practice group performed 80 trials per day (16 blocks of five trials, 20 seconds per trial) of a $90^\circ$ relative phase pattern with the right hand leading (with the yoked observational practice participant watching). To facilitate improvement in the physical practice participants, feedback and speed of movement were manipulated. For the first day of acquisition, participants performed four blocks of trials with pendula presented at 0.75 Hz, followed by a single block of trials with Lissajous feedback and a metronome of 0.75 Hz. The next four blocks involved pendula presented at 0.85 Hz, followed by another single block of Lissajous feedback at 0.85 Hz. The last six blocks were performed with pendula presented at 1 Hz (the speed of the pre and post-test scanning runs). No metronome was used for the pendula trials as movement frequency was manipulated by the speed of the moving lines.

Lissajous feedback involved a real-time displacement-displacement plot of the two limbs, with movements of the right manipulandum producing horizontal movements of the cursor on the screen and movements of the left manipulandum producing vertical movements of the cursor on the screen. Participants saw a circular Lissajous template projected on the computer screen and the actors’ movement was superimposed over the template (60 Hz refresh rate), showing the current position of the actor and the previous 500 ms of movement. Actors were asked to complete an entire cycle of movement for each metronome pulse. This feedback method has repeatedly been shown to be effective in encouraging acquisition of this difficult coordination movement (e.g., Swinnen et al., 1997; Hodges & Franks, 2001; Kovacs, Buchanan, & Shea, 2009a; Maslovat, Brunke,
Chua, & Franks, 2009). Therefore, we interspersed these trials with the pendula trials in order to ensure that the actors were correctly performing the coordination movement and that the observers were watching correct trials by the end of the 2 days of practice.

The second day of acquisition consisted of four blocks of pendula presented at 0.85 Hz, one block of Lissajous feedback at 0.85 Hz, followed by 11 blocks of pendula presented at 1 Hz. At the end of all acquisition trials, numerical terminal feedback was provided on the computer screen for seven seconds showing the RMSE (root mean squared error) of relative phase for the entire trial (i.e., error information based both on mean and SD in relative phase). This information was available to both the physical and observational practice participant.

Data Analysis

Physical Performance Measures

Continuous measures of relative phase were calculated at a rate of 1000 Hz for all complete cycles of movement within the final 15 seconds of each trial. Relative phase of the left arm in relation to the right was calculated for each point after the speed and position of the limbs was re-scaled to the interval [-1, 1]. The phase angles were calculated using the methods described by Scholz and Kelso (1989), and then quantified using circular statistics (Mardia, 1972) from which two measures of performance were determined. Absolute error (AE) of relative phase provided an index of accuracy and was determined by calculating the AE of each relative phase value and then taking a grand mean for each trial. Within-trial standard deviation (SD) of mean relative phase was used as a measure of consistency.
To determine if improvement occurred for the physical practice group, we analyzed relative phase AE during acquisition for the blocks of trials with pendula presentation only. Although 32 total blocks were performed during acquisition, the three blocks involving Lissajous feedback were removed, resulting in a 29 block univariate, repeated measures analysis of variance (ANOVA). To compare physical performance on the to-be-learned (90°) pattern as a function of practice, we used each participant’s three-trial mean from the pre and post scanning runs. We also analyzed each participant’s three-trial mean AE and SD for the 270° pattern. Relative phase AE and SD were independently analyzed via a 3 Group (physical, observation, control) by 2 Block (pre-test, post-test) ANOVA with repeated measures on the last factor. We analyzed the single trial of faded feedback in a similar manner.

Alpha level for the entire experiment was set at .05, with partial eta squared ($\eta_p^2$) values reported as measures of effect size. Significant results for the repeated measures ANOVAs were examined post-hoc via Tukey’s honestly significant difference (HSD) test to determine the locus of the differences. The Greenhouse-Geisser Epsilon factor was

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8 Additional analyses were performed comparing all 8 relative phase patterns across the pre and post test for AE and SD of relative phase. For AE a Group x Pattern x Test (pre versus post) effect was observed, $F(14, 231) = 4.46, p < .001, \eta_p^2 = .21$. Post hoc analysis of this interaction showed that only the physical practice group improved on the 45° and 90° pattern from pre to post test. No improvements across practice were noted for the observational practice and control groups for any patterns. For SD no groups showed decreased variability for any patterns as a function of practice, despite a significant three-way interaction, $F(14, 231) = 2.31, p = .005, \eta_p^2 = .12$. 
used to adjust the degrees of freedom for violations to sphericity (Greenhouse & Geisser, 1959).

**Perceptual Performance Measures**

We separately analyzed the proportion of trials where participants either correctly identified the pattern (regardless of whether they determined which hand was leading), or the leading hand (regardless of whether they determined the correct pattern). As with the physical performance measures, we calculated each participants’ mean based on the three 90° and 270° trials during pre-test and post-test sessions. Data from these trials were subjected to an arcsine square root transform before analysis to correct for violations to normality and analyzed in a 3 Group (physical, observation, control) by 2 Block (pre-test, post-test) ANOVA, with repeated measures on the last factor.

**Results**

**Physical Performance Measures**

The physical practice group improved at the 90° pattern during acquisition, as shown by a significant block effect for relative phase AE, $F(28, 308) = 14.76, p < .001$, $\eta_p^2 = .57$. Relative phase error for the group decreased from a maximum of 73.0° during the first block to a minimum of 19.9° on the twentieth block.

Figure 7.3 illustrates the relative phase AE for the 90° pattern, for all three groups during the pre-test and post-test sessions. AE was generally higher overall for the control group ($M = 76.6°$), but only in comparison to the physical practice group ($M = 50.6°$), which was confirmed by a main effect for group, $F(2, 33) = 7.10, p = .003$, $\eta_p^2 = .30$ and follow up post hoc tests. Although there was a general decrease between the pre-test ($M = 77.5°$) and post-test ($M = 51.6°$) as shown by a main effect for block, $F(1, 33) = 33.54, p$
< .001, \eta_p^2 = .50, importantly there was also a Group x Block interaction, \( F(2, 33) = 11.56, p < .001, \eta_p^2 = .41 \). Post hoc analyses yielded no significant group differences in the pre-test, but a significant group effect in the post test due to the physical practice group having less error than both the observational practice and control groups. Post hoc comparison across pre-test and post-tests confirmed only the physical practice group showed a significant decrease in error \( (p < .001) \). The only significant finding in the analysis of within trial SD of relative phase was a block effect \( F(1, 33) = 5.39, p = .027, \eta_p^2 = .14 \), which was due to a general decrease in variability from the pre-test \( (M = 29.1^\circ) \) to the post-test \( (M = 24.1^\circ) \).
Figure 7.3 Relative phase AE (SD) for pre and post-test 90° trials, separated by group. An asterisk denotes a significant difference between the physical practice group and both the observational practice and control groups in the post-test.
The faded feedback trial comparisons yielded similar results to those above. For relative phase AE, a significant group effect, \( F(2, 33) = 5.03, p = .012, \eta^2_p = .23 \) was due to a significantly higher error for the observational practice group \((M = 77.6^\circ)\) in comparison to the physical practice group \((M = 51.1^\circ)\) only. A block effect was also found due to less error in the post-test \((M = 49.9^\circ)\) compared to the pre-test \((M = 83.1^\circ)\), \( F(1, 33) = 22.59, p < .001, \eta^2_p = .41 \). The Group x Block interaction was not significant, \( F(2, 33) = 3.07, p = .060, \eta^2_p = .16 \), although a similar trend as detailed above was shown, such that the physical practice group showed the greatest decrease in error between the pre-test \((M = 79.9^\circ)\) and post-test \((M = 22.3^\circ)\). No significant effects were found for relative phase SD. There was no evidence of positive transfer to the 270° pattern as seen by a lack of change in AE from pre-test \((M = 82.6^\circ)\) to post-test \((M = 87.3^\circ)\), \( F<1 \). Further, none of the effects involving group were significant. Similarly, SD failed to show any effects related to consistency improvements on the 270° pattern.

To more specifically determine what had changed or been acquired as a function of practice, we looked at the pre and post-test trials of the 90° pattern in terms of relative phase bins. The percentage of time spent within relative phase regions of 30° (i.e., -15°-15°, 15°-45°, 45°-75°, 75°-105°, etc.) were calculated for each trial. Pre and post-test means for each relative phase bin are shown in Figure 7.4 in order to give a description of change for each group. The physical practice group showed a change from a pre-test bimodal distribution of intrinsic in-phase (0°) and anti-phase (180°), to a post-test unimodal distribution around the target pattern (90°). Although the observational practice group showed a change in distribution following practice such that in-phase movements were no longer performed, this did not result in greater time spent around the to-be-
learned pattern. The control group continued to show a bimodal distribution around 0° and 180°, although the peak around 0° had shifted closer to the 180° pattern. To more generally examine if participants utilized any strategic knowledge regarding the correct lead-lag relationship, we also analyzed the pre and post-test trials of the 90° pattern in terms of time spent with a right-hand lead (i.e., relative phase between 15°-165°). Only the physical practice group showed a significant increase \( (p > .001) \) from pre-test \( (M = 31.3\%) \) to post-test \( (M = 92.5\%) \). Neither the observational practice group (pre-test, \( M = 42.7\%; \) post-test, \( M = 60.2\%) \) nor the control group (pre-test, \( M = 32.5\%; \) post-test, \( M = 46.8\%) \) showed a significant change across practice.
Figure 7.4 Relative phase distribution for pre and post-test 90° trials, separated by group.

Note the shift in the physical practice group away from in-phase (0°) and anti-phase (180°) movement towards the to-be-learned pattern (90°). Also note the shift of the observational practice group away from in-phase (0°).
Perceptual Performance Measures

Figure 7.5 illustrates the proportion of patterns correctly recognized by the three groups for the 90° pattern during the pre-test and post-test sessions. Pattern discrimination accuracy improved from the pre-test ($M = 31\%$) to the post-test ($M = 69\%$) as evidenced by a main effect for block $F(2, 33) = 33.26, p < .001, \eta^2_p = .50$. Importantly, a main effect for group $F(2, 33) = 5.14, p = .011, \eta^2_p = .24$, and a Group x Block interaction $F(2, 33) = 6.72, p = .004, \eta^2_p = .29$ showed that pattern discrimination accuracy depended on the group assignment. The control group ($M = 35\%$) showed lower accuracy overall in comparison to the physical practice ($M = 56\%$) and observational practice ($M = 61\%$) groups. As evidenced by the two-way interaction, these differences were a result of significant group effects in the post-test only, with the physical and observational practice groups being more accurate than the control group but not significantly different from each other. However, only the physical practice group showed an increase in accuracy across the testing sessions ($p < .001$) in comparison to the observational practice ($p = .067$) and control groups ($p = .196$). In terms of participants’ ability to discriminate the correct leading hand, there were no significant differences across the three groups. The only significant effect was a main effect for block, $F(2, 33) = 4.20, p = .049, \eta^2_p = .11$, which was due to a general improvement in accuracy across the pre-test (44%) and post-test (61%).
Figure 7.5 Proportion of correct pattern discrimination (SD) for pre and post-test 90° trials, separated by group. An asterisk denotes a significant difference between the control group and both the physical practice and observational practice groups in the post-test.
Participants also improved from pre-test ($M = 31\%$) to post-test ($M = 64\%$) at pattern recognition for the $270^\circ$ pattern as evidence by a main effect for block $F(1, 33) = 23.72, p < .001, \eta_p^2 = .42$, but there were no significant effects involving group (physical practice pre-test $M = 25\%$, post-test $M = 78\%$; observational practice pre-test $M = 44\%$, post-test $M = 69\%$, control group pre-test $M = 25\%$, post-test $M = 44\%$). The only significant effect for hand determination for the $270^\circ$ pattern was a Group x Block interaction $F(2, 33) = 4.21, p = .023, \eta_p^2 = .20$. Although post hoc analyses yielded no significant group differences in the pre-test or post-test, comparisons across the pre and post-tests showed that only the physical practice group improved in their ability to discriminate ($p = .010$).

Discussion

In order to test what is acquired through observational and physical practice and whether behavioural improvements are mediated by improvements in cognitive discrimination, we analyzed physical and perceptual measures of performance following practice of a novel bimanual coordination skill. By yoking an observational practice group with a physical practice group, participants were able to observe a learning model throughout acquisition. Despite significant opportunities to watch a paired participant improve at the $90^\circ$ movement pattern, we did not find any physical performance benefits for the observational practice group as a result of this type of practice. While the physical practice group showed relatively large decreases in performance error, the observational practice group performed in a similar manner to the control group who did not watch or practice the movement pattern. Therefore, we did not find evidence supporting an early mediation account of observational practice, whereby performance benefits would be
expected immediately as a result of motoric activation during the observation stage. This finding is in line with conclusions from research where participants have been trained on a similar skill in an observational learning protocol. In these studies, demonstrations interspersed with practice failed to improve performance relative to discovery learning conditions (Hodges & Franks, 2000, 2001, 2002).

Despite the lack of physical performance benefits, the observers did show benefits in terms of cognitive-perceptual measures of performance and their ability to discriminate the learned pattern. At the end of acquisition the observational practice group was able to distinguish the practiced pattern as well as the physical practice group, and more accurately than the control group. This is consistent with Bandura’s (1971) cognitive mediation model of observational learning, whereby repeated observations are believed to promote a better internal representation of the action, even in the absence of physical practice. Difficulties in perception of relative phase have been linked to difficulties in the production of relative phase. Specifically, it has been hypothesized that a lack of perceptual detection of deviations from the intended movement does not allow participants to correct their movements, and thus hampers their ability to acquire a new coordination pattern (Bingham et al., 1999, 2001; Zaal et al., 2000; Wilson et al., 2005). Thus, the ability of the observers to distinguish between different relative phase patterns may still represent a positive learning effect even though physical performance of the pattern did not improve. Improved perceptual discrimination without physical practice has recently been demonstrated by Calvo-Merino and colleagues (in press). Expert ballet dancers were compared to novices in the discrimination of point light displays of ballet movements. Expertise differences were found for movements that were common to both
genders, as well as those that were only practiced by one gender. For the single gender movements, expertise differences were found for the gender that did not physically practice the skill but had extensive visual expertise. This result suggests that visual experience alone is sufficient to show an improvement in perceptual discrimination.

When we take a closer look at the data from our study we can see that the perceptual benefits for the observational practice group were indeed reflected in the relative phase distribution data and hence suggestive of strategically-mediated improvements. Observational practice resulted in a decrease in the amount of time around in-phase movements (0° relative phase), suggesting that participants were aware that this was not the desired movement (see Figure 7.4). Elsewhere it has been shown that learning of this novel coordination movement proceeds by a break away from more stable, yet undesired movement behaviours or “attractors” (e.g., Zanone & Kelso, 1992b; Lee et al., 1995). Despite the potential benefits of this strategic knowledge, it did not result in more time around the desired 90° relative phase pattern, perhaps as a result of knowing what was not required.

Although we never tested participants in a physical practice reacquisition session to determine whether there would be time savings in later acquisition of this observed movement, we have reason to suspect this would be the case. First, observers were better able to discern the desired movement pattern in the post test as compared to control participants showing some benefits of observation had occurred, although limited to the perceptual-cognitive level. Second, others have shown time savings from watching a model during later physical practice (e.g., Mattar & Gribble, 2005). Although these latter authors argue that learning was due to the extracting of information at the level of motor
execution (i.e., how to make movements rather than what movements to make), it is possible at least some of the benefit was due to cognitive or strategic mechanisms.

Overall, our results provide little evidence for positive transfer to performance of the symmetrical partner (270°). In the examination of physical performance measures, no improvement was found for any group in terms of reduced error or variability. This result is contrary to findings by Zanone and Kelso (1992b, 1997) and is likely due to differences in the type of feedback available during practice and the absence of more descriptive or qualitative feedback regarding relative phase in our experiment (see also Maslovat et al., 2005). All three groups did however show an improvement in pattern discrimination for the 270° pattern, but the lack of group differences suggests that this improvement was not due to physical or observational practice as neither group outperformed the control group. While there was a group difference observed for recognition of which hand was leading, only the physical practice group significantly improved on this measure. Thus the observational practice group did not outperform the control group on either pattern or hand recognition for the symmetry partner of the observed pattern. Although we have argued for strategic benefits as a result of observational practice, it does not appear that these benefits were general enough to apply to other coordination patterns. It is possible that this lack of transfer of perceptual benefits may at least partially relate to the position of the observer. During observation, participants were always positioned to the left of the model, thus only able to see the movement from one perspective (Figure 7.1). This may have resulted in a limitation in the generalization of any strategic benefits.
Based on our data we argue that observation is limited in its effectiveness as a motor learning medium for these types of dual-limb coordination tasks and that benefits as a result of watching are primarily cognitive-perceptual in nature. However, it is possible that observation conditions, in comparison to physical practice, created difficulties in attention allocation (see Kovacs et al. 2009a; Kovacs, Buchanan, & Shea, 2009b, 2010). Observers were able to watch both the moving pendula on the computer screen (correct model) and the person performing the task (learning model). This may have led to attention being split between two information sources, which would not have occurred for the physical practice participants. However, either (or both) source(s) of information would be potentially beneficial for the observer, conveying information about the desired relative phase, as shown on the computer or demonstrated by the participant, as well as online errors in performance, which could be ascertained through comparisons of the two sources of information. Furthermore, observers were encouraged to be actively engaged in watching the model and trying to (privately) estimate the error score presented at the end of each trial. Observers also received a high number of demonstrations (160 trials) and showed a similar level of accuracy as the physical practice group when tested on perceptual discrimination of the practiced task. Thus we believe that the lack of improvement for the observers was unlikely a result of divided attention.

In conclusion, we have provided evidence that while observation of a novel coordination movement can improve cognitive-perceptual performance in comparison to control conditions, physical practice is necessary for improved behavioural performance. It has been suggested that for covert motor simulation to take place during observation,
the performer must be trying to improve on an already learned skill, rather than acquiring a motor skill de novo (Milton et al., 2008). The data from the current study support this view, showing limits as a result of observation without physical practice and providing support for a late mediation account (in terms of perception to action transfer) of the observational learning process (Vogt & Thomaschke, 2007). Although physical performance did not improve with observation, the additional measurement of perceptual discrimination allowed us insight into other possible benefits of observational practice and the mediating processes. Improved perceptual recognition may still represent significant advances in the understanding of a coordinated novel visuo-motor task, even though overt performance does not improve. These results may also help explain some of the disparate results found in studies examining the benefits of observation in the acquisition of a novel skill. When strategic knowledge can only be applied with limited effectiveness to the solving of a motor task, observational practice will not show the same performance improvements as would be apparent from tasks where a particular strategy leads to the solving of the motor problem.

Additional Information

In addition to the behavioural and perceptual measures, we also measured neurological changes associated with physical and observational practice for a subset of five participants (three from the physical practice group, two from the observational practice group). These results are summarized in Appendix B.
8. Conclusion
The goal of this dissertation was to examine change in the preparation of movements as a result of practice, in order to gain a better understanding of the learning process. To examine preparatory processes we utilized startle methodology within a learning paradigm for movements of varying complexities. The presentation of a startling stimulus is thought to cause the release of a prepared response that is stored in subcortical structures, and thus has been used as a probe for motor preparation (Carlsen, Maslovat, Lam, Chua, & Franks, in press; Valls-Solé, Kumru, & Kofler, 2008). This methodology has not been previously used to determine how motor preparation may change as a learner acquires a skill or task. The first four studies involved examination of motor preparation changes as a result of physical practice while the last two studies examined the processes associated with mental imagery and observation.

**Motor Preparation and Physical Practice**

We examined motor preparation changes during physical practice for a variety of bimanual and unimanual movements. The first two studies involved bimanual movements in which the two limbs either differed in movement amplitude (Experiment 1) or in the timing of movement onset (Experiment 2). Both studies validated the use of startle methodology in a learning context; not only did participants improve their performance with practice on non-startle trials, the startling stimulus also triggered a more accurate movement as learning progressed. These results confirmed that improvements in performance with practice are at least partially attributable to a change in advance preparation of the motor commands, such that movements are performed more accurately. These studies also provided specific information as to how participants prepare bimanual movements that are asymmetrical or asynchronous in nature.
When participants perform a synchronous bimanual movement, typically the start
and endpoint of the movement are synchronized in time, even if different amplitudes are
required (Kelso, Southard, & Goodman, 1979). Although it has been suggested that
amplitudes can be independently pre-programmed for each limb during bimanual
movements (Heuer, 1986, 1993; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979),
there is also evidence that asymmetry between the limbs can cause interference such that
both arm move in a similar pattern (Walter & Swinnen, 1990). This coupling of limbs can
be overcome with practice (Walter & Swinnen, 1992; see Walter, Swinnen, & Franz,
1993 for a review) which may indicate a change in the preparation of the movement. In
Experiment 1 participants practiced an asymmetrical bimanual movement whereby one
limb moved double the amplitude of the other. Participants performed the movement with
the timing of the triphasic EMG pattern (i.e., first agonist burst, antagonist burst, second
agonist burst) constant between the limbs but a different force amplitude, a result
indicative of a common preparation process for both limbs. With practice, improvements
in performance were achieved by pre-programming a more accurate ratio of force
activation between the left and right limb, rather than any changes to EMG timing. This
method of preparation appeared to be linked to the bimanual nature of the task as
unimanual movements of different amplitudes are performed with different relative
timing (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004b; Wadman, van der Denier
Gon, Geuze, & Mol, 1979) and the pattern of EMG for unimanual movements also
changes with practice (Gabriel & Boucher, 1998, 2000; Liang et al., 2000).

Experiment 1 provided evidence that synchronous bimanual movements were
prepared in advance even when the movement amplitudes were asymmetrical. To further
test the limits of advance preparation, we wanted to examine whether asynchronous bimanual movements could also be pre-programmed (Experiment 2). Sequential movements have a long history of research (e.g., Woodworth, 1899; Lashley, 1951; Keele, 1968) as they allow insight into the processes associated with preparation and execution of multiple component movements. An asynchronous bimanual movement was used whereby initiation of the left limb was delayed by 100 ms as compared to the right limb. With practice, participants improved at the timing requirement in both control and startle trials; however, we found that preparation of timing was modified by the startling stimulus. Startle trials resulted in a reduced delay between left and right arm initiation and a temporally-compressed within-arm EMG pattern. To explain this result we hypothesized that participants relied on an internal timekeeper to perform the movement, and that the pulse rate of the timekeeper was affected by arousal level (Block & Zakay, 1996). When startled, the pacemaker of the timekeeper was sped up such that movement delays were underestimated and EMG timing was compressed. A compression of movement is not typically seen for startle trials in spatially-based movements, arguably because there is no need to use a timing mechanism. Although other researchers have highlighted differences in preparation depending on the goals of the movement (e.g., Carlton, 1994), the use of a startling stimulus allowed us to make inferences about the reason for differences based on the use of an internal timekeeper for timed movements in comparison to spatially targeted movements.

To further investigate differences between spatially and temporally based movements we conducted an experiment comparing the preparation of movements defined with different goals (Experiment 3). It has been suggested that for movements
performed as fast as possible, movement amplitude is modulated by the duration of motor
euron excitation which is reflected in the duration of EMG burst of the agonist muscle
(Gottlieb, Corcos, & Agarwal, 1989a). Conversely, when movements are performed with
a specific movement time goal, movement velocity is modulated by the amplitude or
intensity of motor neuron excitation which is reflected in the initial slope of the rise of
EMG burst of the agonist muscle (Corcos, Gottlieb, & Agarwal, 1989). We expected the
modulation of different control parameters to be prepared in advance, and thus present in
both control and startle trials. Based on our data from Experiment 2, we also expected
that when a timing goal was required, participants would rely on an internal timekeeper,
whose pulse-rate would be accelerated during startle trials.

As predicted, our results indicated that different control parameters were prepared
depending on how the movement was defined. Consistent with previous research,
movement amplitude was modulated by agonist duration while movement velocity was
modulated by agonist rise-time. These effects were also present in startle trials,
confirming that the different control parameters (i.e., agonist duration and rise time) were
prepared and stored in advance. Even though all movements were sped-up by the startling
stimulus; the temporally-based movements showed greater compression as compared to
the spatially-based movements, as did slower movements as compared to faster
movements. These results were consistent with our prediction that an internal timekeeper
for timed movements was disrupted or perturbed by the startling stimulus and that the
preparatory processes for spatially targeted movements are different than those with a
timing goal.
The results of Experiment 2 confirmed that between-limb sequencing can be prepared in advance. However, sequenced bimanual movements may be prepared in a different manner to sequenced unimanual movements as the bimanual movement elements are relatively independent because they do not require the same limb. To extend our examination of motor preparation involving sequenced movements, we evaluated unimanual movements of varying complexities (Experiment 4) including single element movements with different amplitudes and a sequenced two-step movement. Movements were practiced over four days in either a simple or choice RT paradigm so that preparation could be examined when the movement was and was not known in advance. One idea was that multiple element movements would be “chunked” with practice, such that they would be eventually re-coded and controlled by a single motor representation.

In the simple RT paradigm, the two-step movement showed increased RT values early in practice for control trials, in comparison to single element movements. This difference was minimized with practice, a similar result to what has been previously shown for sequenced movements (Klapp, 1995). During startle trials, all movements were triggered at short latencies suggesting at least the initial component of the movement was prepared in advance and stored in a manner such that it was accessible to be triggered by the startling stimulus. Based on an evaluation of movement variability, we concluded that the second component of the two-step movement was also prepared in advance throughout practice. A secondary analysis of a two-component reversal movement showed similar RT effects to the two-step movement (Appendix A). The reversal movement also showed increased RT values relative to a single element movement that were minimized by the end of practice and was triggered at short latencies by the startling
stimulus. However, unlike the two-step movement, the analysis of movement variability suggested that only the initial movement component was prepared in advance even with extensive practice.

In the choice RT paradigm, RT values increased with movement amplitude and number of components. Increased RT for multiple element movements was present for both the two-step and reversal movements, which provided evidence that the number of movement elements is an important consideration of choice RT. As expected, the startling stimulus had little effect on RT as participants were unable to prepare any portion of the movement in advance due to uncertainty of the required response (Carlsen, Chua, Inglis, Sanderson, & Franks, 2004a). The lack of preparation also resulted in habituation to the startling stimulus, as shown by a dramatic decrease in EMG activation in the SCM which is considered a primary indicator of the startle reflex (Carlsen et al., in press).

Theoretical Contributions

The examination of RT differences based on response complexity, practice and stimulus intensity (Experiment 4), were evaluated with respect to current theories regarding the preparation of sequenced movements. It has been previously hypothesized that in a simple RT paradigm, multiple element movements are prepared in advance and then stored in a memory buffer which is continuously cycled to determine the correct order of elements (Klapp, 2003; Sternberg, Monsell, Knoll, & Wright, 1978). Based on this hypothesis, we predicted that a startling stimulus would not affect a multiple element movement because the first movement element is not immediately accessible when the “go” signal occurs. As the startling stimulus triggered multiple element movements at
similar latencies to single element movements, our results do not support the hypothesis of a cycling memory buffer. Instead, the time to prepare a response appeared to be related to the complexity of the motor commands needed to activate the appropriate neuromuscular coordination structures. A movement requiring more complex motor commands is thought to require a more extensive neural network to complete the action, which, in turn, takes longer to activate. Thus, rather than assuming RT differences are due to search/retrieval processes, we believe that these differences are due to initiation/implementation processes.

Our assertion that preparation time is related to the required neural commands is consistent with the theory presented in the seminal paper by Henry and Rogers (1960) examining response latencies for complicated movements. The authors concluded that more complex programs take longer to initiate because “a larger amount of stored information will be needed, and thus the neural impulses will require more time for coordination and direction into the eventual motor neurons and muscles” (pp. 450). Henry and Rogers also hypothesized that time is required to “channel existing nervous impulses from brain waves and general afferent stimuli into the appropriate neuromotor coordination centers, subcenters, and efferent nerves” (pp. 448). To provide a more specific explanation as to how the coordination of neural structures may affect reaction time, we examined existing frameworks that describe movement initiation from a neurophysiological perspective.

Recent models of initiation for voluntary movements involve an accumulator, whereby a response is triggered when activation levels grow over time to reach a threshold level (Hanes & Schall, 2006). Differences in initiation time can be attributed to
differences in rate of activation accumulation (Carpenter & Williams, 1995), differences in threshold levels (Nazir & Jacobs, 1991) or a hybrid of the two (Pacut, 1977). These models may provide an explanation to the results detailed in Experiment 4 including differences in reaction time due to response complexity, practice and stimulus type (Figure 8.1). If we consider a given threshold level for a low complexity movement, it would seem reasonable that a more complex movement requiring more motor neurons would result in a higher threshold level and thus initiation time. Thus, even though all the motor commands are prepared in advance, the complexity of the movement would still affect reaction time. Similarly, practice of a given movement would likely result in a lowering of threshold such that initiation time is reduced, resulting in a decrease in simple RT with practice. The change in threshold level would provide an explanation for the observed results of control trials in the simple RT portion of Experiment 4, namely increased RT for more complex movements and decreased RT with practice (see grey vertical dashed lines in Figure 8.1).

If activation thresholds change with practice and response complexity, it may be surprising that we did not see RT differences for startle trials. However, it has been previously shown that a startling stimulus results in increased activation of the nervous system (Carlsen et al., 2004a; Maslovat, Carlsen, Ishimoto, Chua, & Franks, 2008; Maslovat, Carlsen, Chua, & Franks, 2009). This activation increase would likely alter the accumulation rate such that thresholds are reached in less time as compared to control trials (solid black line in Figure 8.1). A higher rate of activation increase would result in a smaller effect of threshold differences on initiation time, resulting in similar RTs for all conditions (see black vertical dashed lines in Figure 8.1). In this way, the increase in
activation rate associated with the startling stimulus would negate any difference in activation time due to movement complexity or amount of practice and would produce short latency responses for all types of movements (as observed in Experiment 4).
Figure 8.1 Schematic representation of a hybrid accumulator model of movement initiation. A thick dark line represents activation accumulation for startle trials and a thick grey line represent activation accumulation for control trials. Hypothetical activation thresholds (dashed horizontal lines) are shown for low and high complexity movements as well as following practice. Note the large changes in control RT values (grey vertical dashed lines) associated with changes in activation thresholds as compared to startle RT values (black vertical dashed lines).
Motor Preparation and Alternate Forms of Practice

The first four experiments of this dissertation examined preparation changes associated with physical practice, as this is the most common means to improve performance. The recent discovery of a common neural network involved in both covert and overt movements, known as the mirror neuron system (MNS), has resulted in a renewed interest in other forms of practice that have also shown to be beneficial to learning (see Maslovat, Hayes, Horn, & Hodges, 2010; Rizzolatti & Fabbri-Destro, 2010 for reviews). It has been suggested that observation and imagery involve the same preparation processes as those involved in execution but with reduced activation levels or increased inhibition (Jeannerod, 2001). To examine the preparation processes undertaken during observation and motor imagery, we used a startling stimulus to see if an imagined or observed movement could be triggered in a similar manner to movements that are overtly prepared (Experiment 5). On approximately 20% of the trials we recorded a unimanual partial response, which suggested that participants prepared and stored motor commands in a similar manner to those movements intended to be performed, at least on some of the trials. However, imagery trials were more likely to result in partial movements and appeared to “prime” observation trials such that partial movements were observed more often during observation when preceded by imagery trials. This suggests that automatic simulation of a movement via activation of a person’s motor system is not a necessary consequence of watching and there are conditions which are more or less likely to promote simulation.

One condition that appears to be very important in the effectiveness of observational practice is the observer’s experience with the task. There are disparate
findings as to whether observation of movements that are not within the observer’s repertoire (which often typify observational learning situations) results in motor system involvement. To explore this question, we examined observational practice of a model learning a novel skill (Experiment 6). One of the challenges in determining if potential positive effects of observation can be attributed to motor system involvement is to reduce the strategic information that the observer can pick up while watching. Thus, we chose to study the learning of a coordination task that is not readily amenable to picking up a strategy (at least when viewing expert or correct models; Hodges & Franks, 2000, 2001, 2002). In addition to behavioural outcome measures we recorded perceptual/discrimination measures and neural activation patterns (subset of participants only, Appendix B) from both models and observers. As predicted, based on the novelty of the skill, we did not find any positive effects associated with observation in terms of physical performance, but observers did improve in their perceptual discrimination ability of the observed pattern. Both observational and physical practice resulted in a decrease in activation of areas associated with the mirror neuron system, a region of the brain associated with action imitation and understanding. Thus we concluded that while watching a novel coordination movement can improve cognitive-perceptual performance and even lead to cortical changes in areas of the brain associated with the motor system, physical practice is required to improve behavioural performance.

What is Learned?

One goal of this dissertation was to better understand the processes involved in motor skill learning. It is readily apparent that with practice a learner is better able to achieve the goals of the task. While we can observe improvements in motor performance,
the mechanisms underlying improvements are not directly observable and thus must be inferred in conjunction with other measures of the learning process. There are many possible loci for the behavioural improvements observed following practice, including improved perceptual recognition of relevant cues, enhanced response selection, better error detection and correction, more efficient utilization of feedback during movement execution, and more accurate preparation. In the final experiment of this dissertation (Experiment 6), we did find practice-related changes in processes related to pattern discrimination and reorganization of cortical activation patterns. In the other experiments presented in this dissertation, practice-related changes were related to the way movements were prepared.

When a learner is aware of the movement to be performed, they can prepare motor commands associated with the movement in advance, a process known as pre-programming. It is clear from the results of this dissertation that pre-programming improves with practice, such that the learner is able to prepare in advance motor commands that produce more accurate movements (Experiment 1 & 2). This does not preclude improvements in other areas but rather confirms that advance preparation is an important area that is involved in the learning process. As we are often required to make anticipated responses following some imperative stimulus, it is not surprising that improvements occur in advance preparation. As long as the time prior to reacting to a “go” signal is not a limiting factor, an efficient strategy would be try and prepare in advance more accurate motor commands and thus minimize the time required after the “go” signal to perform the correct movement. This would provide performance benefits not only to movements that involve a quick response to a “go” signal (i.e., sprint races),
but also to those movements that are performed without initiation time constraints but require precise movement execution (i.e., reaching and grasping).

It has been suggested that practice not only improves the accuracy of the motor commands but also changes how the movement is prepared, such that the learner is able to prepare more complex movements in advance. Early in learning, participants may only be able to pre-program a single component of a complex movement due to limitations with advance preparation of movement sequencing. However, with practice it is possible that participants are able to recode multiple element movements such that they are prepared and controlled as a single representation or movement “chunk” (Keele & Summers, 1976). This change in preparation is thought to represent a higher, more automatic degree of movement organization such that fewer resources are required to prepare, initiate and execute each specific movement. In this manner, learning can be thought of as acquiring a “hierarchy of psycho-physical habits (Bryan & Harter, 1899) or an organizational process of “higher order encoding” (Johnson, 1973).

One line of evidence for chunking in keypress tasks has involved a reduction in reaction time with practice for multiple component movements, as compared to single component movements (Klapp, 1995). The longer initial reaction time for multiple elements has been attributed to the individual preparation of movement elements which must then be located in the proper sequence by scanning a memory buffer (Klapp, 2003; Sternberg et al., 1978). Because this reaction time difference disappears with practice, it has been suggested that chunking has occurred such that multiple element movements are prepared in advance as a single unit and thus sequencing is no longer required (Klapp, 1995). The use of startle methodology allowed for a novel way to test this hypothesis.
(Experiment 4, simple RT paradigm), as a startling stimulus is thought to trigger movements that have been pre-programmed. For control trials, our data for multiple component movements showed a pattern of practice-related reaction time changes consistent with what has been previously reported (Klapp, 1995). However, during startle trials the two-step movement was triggered at short latency with similar consistency to control trials both before and after practice, leading us to conclude that the two-step movement was prepared as a single movement throughout the experiment. Conversely, the reversal movement showed increased variability during the reversal portion for startle trials both before and after practice, suggesting it was prepared as two components throughout the experiment. Collectively, these results did not provide evidence for movement chunking for unimanual movements.

A consistent finding from a number of experiments described in this dissertation is that RT values for control trials decrease with physical practice. While the reduction in choice RT (Experiment 4) could be at least partially attributable to faster response selection, the reduction of simple RT (Experiment 1 & 4) would likely be due to either faster stimulus identification or an improvement in time to prepare and initiate the movement. Considering the magnitude of RT decrease for these experiments was approximately 20 ms, it is unlikely that this effect was solely due to perceptual mechanisms and thus it appears that the processes involved in movement initiation become faster with practice. A reduction in simple RT with practice may be due to a more efficient organization and coordination of the neural commands necessary to perform the movements, such that the movement can be executed in a shorter time following the imperative stimulus.
We have previously suggested that when a movement is known in advance, the motor commands can be pre-programmed and the initiation time is related to how long it takes to activate the motor neurons to a threshold potential. It is likely that practice reduces the required activation threshold to perform a movement and thus decreases the initiation time (at least for control trials, see Figure 8.1). It has been shown that physical training results in adaptations to the nervous system at a time course that is much faster than observed in the muscular system (e.g., Kidgell & Pearce, 2010). In fact, changes have been seen at various levels of the nervous system including supraspinal centers, descending neural tracts, spinal circuitry and motor end plate connections (see Carroll, Riek, & Carson, 2001, for a review). Results from Experiment 4 confirmed that the practice-related reduction in RT was larger for more complex movements, such that all movements were initiated at similar times for control trials on the last day of practice. This differential rate of reduction may have been due to a floor effect as the simpler movements were closer to the minimal motor neuron activation time and thus may have shown a smaller decrease in RT. Similarly, practice-related changes to a simple RT task would not be expected for startle trials as the increased neural activation would likely increase accumulation rates such that any practice-related changes would be masked by the effects of the startling stimulus (Figure 8.1).

We have shown that for physical practice, learning results in a more accurate pre-programming of motor commands and in a reduction in time to initiate these commands. We did not, however, find physical performance benefits when participants were only able to observe the required movement, even when watching repeated demonstrations performed by a model that was learning the task (Experiment 6). Observers showed
perceptual benefits and changes to neurological activation patterns as a result of watching, but physical practice was necessary to show behavioural improvements. We intentionally chose a bimanual coordination task that the observers were unfamiliar with, and it is possible that this task novelty contributed to the lack of benefits of observation on physical performance. Although we did not test participants in a physical practice reacquisition phase, we hypothesized that the perceptual discrimination benefits would result in time savings to acquire the observed movement pattern, as it is been suggested that a lack of perceptual detection of the intended movement hampers acquisition of a new coordination pattern as participants are unable to correct their movements (Wilson, Snapp-Childs, Coats, & Bingham, 2010).

What is Prepared?

In addition to examining what is learned with practice, a second goal of this dissertation was to better understand what motor commands are stored as a participant prepares to perform a movement. Studies using startle methodology to determine what is prepared in advance often require participants to perform the movement at maximal speed. While this line of research has provided valuable information pertaining to when advance preparation occurs and how these movements are prepared, it does not allow for examination of movements performed at sub-maximal speeds. Through the comparison of spatially and temporally defined movements, it is clear from this dissertation that preparation of a movement is dependent upon how the goals of the task are represented.

Consistent with earlier observations regarding organizing principles for movements with a temporal versus spatial goal (Corcos et al., 1989; Gottlieb et al., 1989a, 1989b), the control parameters appear to be different for these tasks (Experiment
3). For movements of different amplitudes (i.e., speed-insensitive movements), preparation involves pulse width of motor neuron excitation, which results in a change to the duration of the agonist burst. Conversely, when movement timing is manipulated (i.e., speed-sensitive movements), preparation involves pulse intensity of motor neuron excitation, which results in a change to the initial slope of the EMG rise of the agonist burst. The motor commands that modulate the different control parameters appear to be prepared and stored in advance of the movement. This was shown by the movements triggered by the startling stimulus showing similar patterns of agonist duration modulation for spatially based movements and agonist rise-time modulation for temporally constrained movements.

In addition to different control parameters, we have hypothesized that when timing-based movements are prepared participants rely on an internal timekeeper. The pulse rate of the pacemaker of the timekeeper is affected by arousal level and thus is accelerated during startle trials. This effect is seen by a greater temporal compression of movements that are time-dependent as compared to movements performed as fast as possible to a spatial target. We found evidence supporting this timekeeper hypothesis for bimanual movements with a delay between limb initiation (Experiment 2) and for movements with a constrained temporal goal (Experiment 3). It is not surprising that how the goals of a movement are defined would change the processes of motor preparation. Although we are often seeking consistent “rules” to explain performance, it is unlikely a single control variable would be found for all movements (Stein, 1982). Rather, our nervous system appears to be flexible in the ability to modulate different variables to perform different types of movements.
While physical practice is the most common means to improve performance, it is now well-accepted that motor imagery and observation can also result in motor skill improvements. What is less understood is how improvement occurs in the absence of physical performance. One suggestion, supported by neurophysiological data, is that the processes that occur during overt movements are simulated during these covert processes, with the only difference being that movement execution is inhibited (Jeannerod, 2001). Thus imagery and observation do not simply aid in assisting the performer understand movement strategy, but rather have an effect at the level of motor preparation. We found support for the hypothesis that motor preparation occurs during imagery and observation (Experiment 5), as a startling stimulus triggered a response in the imagined or observed hand on approximately 20% of the trials. However, no response was seen on 80% of the startle trials and the observation trials were less likely to lead to a partial response as compared to imagery trials. The reason why a response did not occur for all trials may relate to the excitation level of the system during imagery and observation. Movement inhibition during imagery and/or observation could result in a decrease in neural activation such that not even a startling stimulus causes motor neurons to reach threshold potential, at least on every trial. As some variability would be expected in the neural activation level, some trials may show a partial response due to a sufficient number of motor neurons reaching threshold levels, while others may not.

Limitations and Future Directions

The current dissertation utilized different experimental protocols (simple RT, choice RT, startle methodology, learning paradigms), examined different types and complexities of movements (unimanual, bimanual; discrete, continuous; single
component, multiple component), and analyzed various dependent measures (behavioural, perceptual, electrophysiological) to provide a comprehensive investigation into motor preparation. However, our results may be somewhat limited by the methodology we employed. Our studies have largely focused on a single aspect of performing a movement, namely response preparation. While we are confident that we have accurately measured differences in preparation that occur with practice, we are not able to evaluate changes that may have also occurred in other areas such as stimulus identification or response selection. In addition, some of the differences between our results and previous work may be due to differences in the task used. For example, many of the studies showing evidence for chunking have involved keypress tasks which are performed much quicker than arm movements. It is possible that shorter movements are more prone to be chunked with practice, as it would require a high amount of cognitive resources to prepare and initiate each movement element individually.

To further study the processes involved in motor preparation it will be necessary to continue to complement behavioural outcome measures with neurophysiological measures to help understand how the nervous system is involved in the production of the observed response. The use of procedures such as transmagnetic stimulation (TMS) and transcranial direct current stimulation (tDCS), which can increase or decrease cortical excitability of a given area, would allow for determination as to whether specific brain regions are essential, beneficial, or unnecessary for the performance of a task. With respect to imagery and observation, more investigation is required to determine what is occurring at various levels of the nervous system during these activities. A better understanding of the inhibitory processes that are thought to occur during imagery and
observation may guide the development of new methodologies that will allow
investigation into preparatory processes associated with these alternate forms of practice.

Continued research examining the process of response preparation and the changes that occur with practice would provide valuable information to those interested in the teaching and learning of motor skills. While amount of practice may be the predominant factor in the determination of skilled performance, gaining a greater understanding of when, if, and how preparation occurs may allow for more efficiency in the time spent practicing. Determining the limits of advance preparation and whether these limits change as a skill is acquired would affect the instructions given to the learner as well as the practice conditions used to maximize performance. Understanding the processes involved in imagery and observation may also increase their effectiveness as a means to increase practice time or as an alternative for those not able to physically practice the task.

Concluding Remarks

This dissertation adds to our understanding of the processes associated with motor preparation, and how these processes change with practice. The use of a startling stimulus within a learning paradigm provided a novel methodology to probe preparation processes at various stages of skill acquisition. The combination of studies involving tasks of varying parameters and complexities allowed for a comprehensive investigation into response preparation. In addition to providing information as to how specific movements are prepared, our results confirm that improvements in performance can be at least partially attributed to changes in the motor preparation process. With physical practice, participants are better able to prepare in advance the motor commands associated with a
movement, such that they are more likely to achieve the goals of the task. The time taken to initiate movements appears to be related to the complexity of the neural commands, and this initiation time is reduced with practice. The content of the pre-programmed commands is dependent upon how the goals of the task are represented, with specific differences noted between spatially targeted movements performed as fast as possible compared to temporally constrained movements.

We found evidence that motor preparation can occur during imagery and observation, with imagery appearing to result in a greater likelihood of movement simulation. We also showed comparable changes in cortical activation patterns associated with both physical and observational practice of a novel coordination skill, despite a lack of learning as measured by task attainment. Collectively, while the results of this dissertation highlight that there are similarities between covert and overt movements, they also emphasize that there are differences not only between physical and alternative forms of practice, but also between imagery and observation. While imagery and observation have been shown to provide learning benefits, it appears that physical practice is still the best method for improving motor preparation processes and overall performance.
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Appendix A

Motor Preparation of a Reversal Movement
Introduction

In Experiment 4, we investigated the role of practice for motor preparation of unimanual movements of various complexities. We examined three movements that differed in complexity of the movement element (short versus long movement) and number of movement elements (two-step movement). We studied the two-step movement to determine if preparation changed with practice such that a multiple component element could be recoded into a single encapsulated unit; however the results indicated that the entire two-step movement was prepared in advance throughout the experiment.

Participants in Experiment 4 also performed a unimanual reversal movement that involved movement out to a 20° target followed by a change of direction back to the starting position. In the current study we report our analysis of the preparation processes associated with this reversal movement, and how these processes changed with practice. We limited our analysis of the reversal movement to a comparison with the short movement data presented in Experiment 4. We chose this comparison as the initial movement element was identical in both conditions (i.e., extension to a 20° target), yet the reversal movement also included flexion movement back to the home position.

We included a reversal movement because it involves two-targets, yet the muscle activation pattern is quite different to that of the two-step movement. To perform the first component of a two-step movement, an initial agonist burst provides the impulsive force to start the movement, an antagonist burst provides the braking force to slow the movement, and then a second agonist burst clamps the limb to stop at the correct position (see Berardelli et al., 1996 for a review). This is in contrast to a reversal movement whereby the antagonist activity of the first movement not only slows the first movement...
component but also initiates the second component and thus functions as the agonist muscle for the reversal movement. This dual role of the antagonist muscle utilizes the elastic properties of the muscles and saves mechanical energy, as evidenced by movement time to the first target being sped up relative to a single movement of equal amplitude i.e., the “two-target advantage”; Adam, Paas, Eyssen, Slingerland, Bekkering, & Drost, 1995; Adam, Vander Bruggen, & Bekkering, 1993; Khan, Lawrence, Buckolz, & Franks, 2006).

The difference in muscle activation patterns between the two-step and reversal movements has been taken as evidence for different control processes, with preparation of the reversal movement being simplified by a single force performing two functions (Adam et al., 2000). However, it is currently unclear whether a reversal movement is prepared as a single unit of action or as a sequenced movement. A comparison of simple reaction times (RTs) has shown an increase for an extension-flexion reversal movement versus an extension movement only, which has been attributed to increased programming that must occur after the “go” signal due to movement sequencing (Franks, Nagelkerke, Ketelaars, & Van Donkelaar, 1998; Khan et al., 2006; Khan, Mourton, Buckolz, & Franks, 2008a). However, it has been argued that this is not a valid comparison as the RT differences are confounded by different control mechanisms and thus not necessarily directly attributable to a sequencing requirement (Ketelaars, Garry, & Franks, 1997). More recently, evidence for advance preparation of the entire reversal movement has been provided by showing that participants are unable to inhibit the reversal portion of a movement when the movement cue changes from a reversal to a single extension movement at movement onset (Khan, Tremblay, Cheng, Luis, & Mourton, 2008b). It is
also possible that the preparation of a reversal movement depends on the amount of practice undertaken and whether or not the movement has been “chunked” into a single element. The purpose of the current study was to determine if a reversal movement was prepared as a single unit or a sequenced action, and whether this preparation changed as a result of extensive practice.

For the simple RT paradigm, we predicted that the reversal movement would have a longer control RT than the short movement, at least early in practice. This was based on the results of previous research (Franks et al., 1998; Khan et al., 2006, 2008a) and the theory that a sequenced movement is initiated at a longer RT than a single component movement (Klapp, 1995, 2003). This prediction is also consistent with the results of Experiment 4 which led to the hypothesis that RT is determined by the complexity of the neural commands required to produce the movement (as opposed to a sequencing requirement). We also expected that the reversal movement would be triggered by the startling stimulus at similar latencies to those observed for the short movement, as this was shown previously for the two-step movement. It is apparent from Experiment 4 that RT differences do not fully allow us to make conclusion regarding advance preparation and should be complemented by a within-trial variability analysis. We predicted that movement consistency would be similar for control and startle trials for the initial movement component. Examination of the variability of the reversal portion of the movement would determine if the entire movement was prepared in advance (similar to what was shown for the two-step movement) or if only the extension movement was prepared before the “go” signal with the reversal component initiated and integrated in an on-line manner.
For the choice RT paradigm where participants performed one of five possible movements (short, long, two-step, flexion, reversal), we expected that the reversal movement would have a longer control RT as compared to the short movement. This was based on the results from Experiment 4 suggesting that the complexity of the first movement element is not the only determinant of RT, and that number of movement components must also be considered. Due to a lack of advance preparation, we did not expect the startling stimulus to trigger the reversal movement at latencies such as those observed in the simple RT paradigm and expected higher variability in the initial movement component between startle and control trials.

Methods

Participants in Experiment 4 also performed reversal movements in either a simple or choice RT paradigm during the four days of testing. This movement was randomly presented, along with the other three movements, and was cued via a short arrow pointing forward above a short arrow pointing backwards (\(\rightarrow\rightarrow\leftarrow\leftarrow\)), representing a reversal movement from the 20° target back to the home position without pausing. As with the other movements, participants performed 15 reversal movements per block for a total of 45 trials per day. On the first and last day of testing, two startle trials were randomly presented per block for a total of six startle trials per day.

For the simple RT paradigm, 32 of the 1920 reversal movements were discarded (1.6%) due to displacement reaction time less than 90 ms (i.e., anticipation, 13 trials) or in excess of 500 ms (2 trials), incorrect movements (11 trials), and startle trials in which no detectable startle response (SCM activity) was observed (6 trials). For the choice RT
paradigm, 60 of the 1920 reversal movements were discarded (3.1%) due to incorrect movements (57 trials) and displacement reaction time longer than 900 ms (3 trials).

Dependent Measures and Statistical Analyses

Premotor RT and within-subject movement consistency of the first 100 ms were separately analyzed for the simple and choice conditions via a 2 Day (Day 1, Day 4) x 2 Movement (short, reversal) x 2 Stimulus Type (control, startle) repeated measures analysis of variance (ANOVA). Movement consistency for the second component of the reversal movement (VAR2) was analyzed via a 2 Day (day 1, day 4) x 2 Stimulus Type (control, startle) repeated measures ANOVA. For the repeated measure ANOVAs, the Greenhouse-Geisser Epsilon factor was used to adjust the degrees of freedom for violations to sphericity. Uncorrected degrees of freedom are reported, with the corrected p values. Partial eta squared (ηp²) values reported as a measure of effect size. The alpha level for the entire experiment was set at .05, and significant results were examined via Tukey’s honestly significant difference (HSD) test and simple effects tests to determine the locus of the differences.

Results

To represent overall performance of the movements, we created ensemble averages for the last testing day, showing rectified raw EMG activation (including SCM for startle trials) and displacement. This was achieved by normalizing each trial in time to displacement onset (which was considered time 0) and normalizing EMG activation to a percentage of the maximal value within a trial. These averages represent data from all trials from all participants (i.e., 450 trials for control, 60 trials for startle) and are shown for control and startle trials for the short and reversal movements in Figure A.1, with
results of the simple RT paradigm shown in the top 4 panels and the results of the choice RT paradigm shown in the bottom 4 panels. A summary of the results for the main dependent measures, including mean and standard deviations, are provided in Table A.1.
Table A.1 Experimental results for each stimulus type, day and movement, showing means and standard deviations (bracketed). Simple RT values are shown on the top two tables, choice RT values are shown in the bottom two tables. Note that VAR2 only has values for the reversal movement.

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<td>85.5 (7.5)</td>
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<td>1.66 (0.77)</td>
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<td>Premotor RT (ms)</td>
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**Figure A.1** Group ensemble averages for the short and reversal movements on day 4 for simple RT (top 4 panels) and choice RT (bottom 4 panels), separated by control (left panels) and startle (right panels) values. Agonist and antagonist values (grey lines) are rectified raw EMG, normalized to a percentage of the maximal value within each trial, with left and right SCM (black lines) shown on startle trials. All values are normalized to displacement onset (dark black line) which was considered relative time 0.
Simple RT Results

Mean premotor RT values for the simple RT paradigm are shown for control and startle trials for day 1 and 4 in Figure A.2. As predicted by Klapp (1995) and similar to what we found in Experiment 4 for the two-step movement, RTs for control trials were longer for the reversal movement on day 1 and this difference was minimized with practice. For startle trials, RT values were lower than control trials, and no changes occurred with practice nor were there differences observed between the movements. These results were confirmed by a number of main effects and interaction effects.

Although there was a main effect for day, $F(1, 9) = 20.58, p = .001, \eta_p^2 = .70$, this effect interacted with both stimulus type, $F(1, 9) = 19.05, p = .002, \eta_p^2 = .68$, and movement, $F(1, 9) = 5.37, p = .046, \eta_p^2 = .37$. The Day x Stimulus effect was due to a reduction in control trials with practice (from 126 ms to 105 ms) but no change for startle trials (from 85 ms to 83 ms). The Day x Movement effect was due to a difference between the reversal ($M = 108$ ms) and short ($M = 104$ ms) on day 1, but no difference on day 4 (reversal $M = 94$ ms; short $M = 93$ ms). There was also a main effect for stimulus, $F(1, 9) = 69.21, p < .001, \eta_p^2 = .89$, as startle trials were performed at faster RT values. These results combined in a significant three-way Day x Stimulus X Movement interaction, $F(1, 9) = 6.47, p = .032, \eta_p^2 = .42$, due to a difference between the short ($M = 130$ ms) and reversal ($M = 123$ ms) movement for day 1 control trials only. Control trials on day 4 (short $M = 105$ ms, reversal $M = 104$ ms), were performed at similar latencies, as were startle trials on both day 1 (short $M = 85$ ms, reversal $M = 85$ ms) and day 4 (short $M = 81$ ms, reversal $M = 83$ ms).
Figure A.2 Mean premotor RT values (SEM) for simple RT paradigm, separated by day and condition. An asterisk (*) denotes a significant difference for day 1 control trials between the short and reversal movements.
The analysis of variability of the first 100 ms revealed no significant effects, confirming that there was no difference between startle and control trials for either movement on either testing day. This result is consistent with the expectation that the initial movement component was prepared in advance. The analysis of variability for the second movement component of the reversal movement showed a main effect for stimulus, $F(1, 9) = 43.57, p < .001, \eta^2_p = .83$, whereby startle trials were performed with more variability ($M = 4.28^\circ$) as compared to control trials ($M = 3.03^\circ$). This did not change with practice as the effect of testing day did not reach statistical significance ($p = .616$).

**Choice RT Results**

Mean RT values are shown for control and startle trials on day 1 and day 4 in Figure A.3. Overall, premotor RT was higher for the reversal movement as compared to the short movement for both control and startle trials, and this difference was maintained with practice. This result was confirmed by a main effect for movement, $F(1, 9) = 33.69, p < .001, \eta^2_p = .79$, due to the reversal movement having a significantly longer RT ($M = 353$ ms) as compared to the short movement ($M = 332$ ms). However, this effect was dependent on the stimulus type as shown by a Stimulus x Movement interaction, $F(1, 9) = 19.57, p = .002, \eta^2_p = .69$. Post-hoc analyses confirmed that the startling stimulus had no significant effect on RT for the short movement (increased by 3 ms) but significantly reduced RT for the reversal movement (decreased by 20 ms). Both control and startle trials showed a significant increase in RT for the reversal movement compared to the short movement, although this difference was greater for control (33 ms) as compared to startle (10 ms) trials. Participants also reduced their RT with practice from day 1 ($M =$
393 ms) to day 4 ($M = 292$ ms), as confirmed by a main effect for day, $F(1, 9) = 46.77$, $p < .001$, $\eta_{p}^2 = .84$. 
Figure A.3 Mean premotor RT values (SEM) for choice RT paradigm, separated by day and condition. An asterisk (*) denotes a significant difference between the short and reversal movement for control and startle trials on day 1 and 4.
Analysis of variability for the first 100 ms showed a main effect for stimulus, $F(1, 9) = 6.12, p = .035, \eta_p^2 = .41$, confirming that startle trials were more variable ($M = 2.1^\circ$) than control trials ($M = 1.5^\circ$). A main effect for Day, $F(1, 9) = 11.47, p = .008, \eta_p^2 = .56$, confirmed participants improved their consistency from day 1 ($M = 2.2^\circ$) to day 4 ($M = 1.4^\circ$). There was also a significant main effect for movement, $F(1, 9) = 8.88, p = .015, \eta_p^2 = .50$, which was due to the reversal movement having more variability ($M = 1.9^\circ$) than the short movement ($M = 1.7^\circ$). Analysis of variability for the second component of the reversal movement showed a main effect for day $F(1, 9) = 6.14, p = .035, \eta_p^2 = .41$, whereby participants improved their consistency of the reversal component of the movement from day 1 ($M = 4.4^\circ$) to day 4 ($M = 3.2^\circ$). No main effect for stimulus was found, nor was there a Stimulus x Day interaction confirming that the startling stimulus did not have an effect on between-trial movement variability on either testing day.

Discussion

Simple RT

The purpose of this experiment was to examine how a reversal movement is prepared, and to determine whether preparation changed with practice. Changes to RT with practice for control trials in the simple RT paradigm (Figure A.2) were similar to those reported in Experiment 4 for the two-step movement, whereby the reversal movement was performed with longer RT values compared to the short movement early in practice but not after four days of practice. The increased RT of the reversal movement relative to a single element movement has been used as evidence for sequencing that must occur after the “go” stimulus (Franks et al., 1998; Khan et al., 2006, 2008a), typically attributed to scanning of a memory buffer to locate the proper movement.
element (Klapp, 2003; Sternberg, Monsell, Knoll, & Wright, 1978). However, we have reason to believe that mechanism is not responsible for the delay in movement initiation in the current experiment. For startle trials, RT values for the reversal movement were similar to the short movement and were at a latency consistent with previous experiments suggesting that such short reaction times are due to triggering of a pre-programmed response (e.g., Carlsen, Chua, Inglis, Sanderson, & Franks, 2004a; Maslovat, Carlsen, Ishimoto, Chua, & Franks, 2008). This result suggests that participants prepared and stored in advance at least the initial component of the reversal movement and that it was immediately accessible to be triggered by the startling stimulus. This is consistent with the results of the two-step movement from Experiment 4 and does not support the view of a memory buffer which is constantly cycling to determine the proper order of movement elements.

We also examined within-subject movement variability between startle and control trials to determine if the triggered movement was performed with similar consistency in both types of trials. While variability of the first 100 ms movement segment was similar between startle and control trials, the second component was more variable for startle trials on both days of practice. This result would indicate that while the initial portion of the movement was prepared in advance, the reversal component was not and this did not change even with extensive practice. This result is in contrast to the work by Khan et al. (2008b) suggesting the entire reversal can be prepared in advance; however it is consistent with the earlier work by Khan et al. (2006), showing that even in a simple RT paradigm reversal movements can be prepared in an online manner. Thus it appears that the reversal movement is prepared in a different manner to a two-step
movement, as our previous results indicated that the two-step movement was entirely prepared in advance through practice, yet the current results indicate that the reversal movement remained prepared as two separate movement elements. The reasons behind this difference in preparation are unclear. It is possible that participants focused on the initial target and were less concerned with accurate performance of the reversal movement back to the home position. This may have resulted in a mode of control that emphasized the initial movement and did not promote full advance preparation. However, further research would be required to determine the locus of this effect, and if advance preparation of a multiple component movement can be promoted or hindered by strategy or instructions regarding the relative importance of the different movement components.

**Choice RT**

For the choice RT paradigm, the reversal movement had longer RT values as compared to the short movement for both control and startle trials, and these differences were maintained with practice (Figure A.3). Similar to the results of Experiment 4, it appears that complexity of the initial movement element is not the only determinant of choice RT and sequencing requirements must also be considered. As expected, the startling stimulus did not trigger the reversal movement at short latencies and initial movement variability was higher for startle as compared to control trials. We attribute both of these results to a lack of advance preparation. Although initial movement variability was higher for startle trials, the startling stimulus did not affect variability of the second movement component. This result is consistent with analysis of the two-step movement in Experiment 4, lending further support to the suggestion that by the time the
participants initiated the second movement element they had overcome any interference by the startling stimulus resulting in a similar movement consistency.

Theoretical Contributions

It is worthwhile to examine the results of the reversal movement in the theoretical framework we presented in Experiment 4 regarding the preparation of complex movements. We hypothesized that in a simple RT paradigm the longer time for movement initiation associated with sequenced movements during control trials may relate more to the neural network required to produce the movement than searching of a memory buffer for the appropriate movement element. Our current results support this hypothesis as the reversal movement would require greater neuromotor coordination than the short movement, as the antagonist muscles of the first movement would be required to change roles such that they function as agonist muscles on the reversal portion. Even if participants only prepared in advance the initial component of the reversal movement, it would be expected that more intricate motor commands would be required to integrate the reversal component into the movement. Although the reversal movement was performed with a longer RT ($M = 130$ ms) compared to the short movement ($M = 123$ ms), it was not as long as the two-step movement from Experiment 4 ($M = 138$ ms). These results are consistent with the explanation that the complexity of neural commands dictate reaction times as the most complex activation would be required for the two-step movement (which was fully prepared in advance), followed by the reversal movement (which was only partially prepared in advance but had an additional movement component), followed by the single movement element.
The results of the startle trials provided additional evidence that the initial movement component is immediately available to the performer and that a memory buffer need not be scanned during the production of sequenced movements. Similar to the results of the two-step movement from Experiment 4, the initial component of the reversal movement was performed on startle trials at a similar latency to that observed for single element movements. Thus it appears that whether only the initial movement element or the entire movement is prepared in advance, motor commands are stored in such a manner that they can be triggered by the startling stimulus.

We also hypothesized that in a choice RT paradigm when advance preparation could not occur, complexity of the initial movement element would not be the only determinant of RT and sequencing requirements must also be considered. Consistent with this hypothesis (and the previously reported result for the two-step movement), we found longer RTs for the reversal movement as compared to the short movement. Collectively, the results of the current experiment provide additional confirmation that the relationship between RT and movement complexity may relate more to the neural activation required to perform the movement rather than specific sequencing requirements.
Appendix B

Neurological Changes Associated with Observational Practice
Introduction

In addition to the behavioural and perceptual measures reported in Experiment 6, we also measured neurological changes associated with physical and observational practice for a subset of five participants (three from the physical practice group, two from the observational practice group). These participants were scanned with functional Magnetic Resonance Imaging (fMRI) at two points during the experiment: between the first baseline testing session and first acquisition session and between the second acquisition session and the final testing session. fMRI data were collected while participants watched six different videos of the phase patterns displayed via rear-projection from an LCD projector to a screen in front of the participants. Each video was 270 s in length and contained six 20 s segments of 0°, 90°, and 180° phase patterns presented as 1 Hz pendula (2 segments for each phase pattern). The phase patterns within each block were presented in a random order (a flow diagram showing a sample of the order of events seen by a participant is shown in Figure B.1). Each video began with a blank screen (30 s), followed by six alternations between a phase pattern (20 s) and stationary green lines (20 s).
Figure B.1 Sample of events seen by participants during fMRI scanning runs. Participants watched a total of six videos of 270 seconds in duration.
**Data Analysis**

fMRI data were collected on a research-dedicated Phillips 3-T system fitted with a SENSE head coil. Conventional spin-echo, T1-weighted sagittal localizers were used to view the positioning of the participant’s head and to set the functional image volumes to be acquired in line with the AC–PC plane. Functional image volumes were collected with an echo-planar imaging gradient-echo pulse sequence sensitive to the BOLD contrast (TR = 2000 ms, 90° flip angle, FOV = 240 x 240 mm, 128 x 128 matrix, 62.5 kHz bandwidth, 3.00 x 3.00 mm final measured in-plane resolution, 3.00 mm slice thickness, 1.00 mm slice gap, 36 interleaved transverse slices). A transistor-transistor logic (TTL) pulse from the scanner started the experimental program to allow temporal synchronization of the scanner and the videos for analysis purposes. Each functional run started with five dummy scans (to allow time to achieve steady-state magnetization) which were followed by 135 functional scans. Six functional runs were collected in total, one for each video sequence (see above). After participants completed the functional runs, a high-resolution T1-weighted structural image was acquired with a 3-D gradient echo pulse sequence (TR = 25 ms, 90° flip angle, FOV 256 x 256 mm, 256 x 256 matrix, 1.00 x 1.00 mm in-plane resolution, 1.00 mm slice thickness, 170 slices).

A block design fMRI approach was employed for data analysis. Statistical Parametric Mapping software (SPM2, Wellcome Institute of Cognitive Neurology, London, UK) was used to correct the EPI images for slice timing distortion and motion (e.g., Friston, Williams, Howard, Frackowiak, & Turner, 1996). Subsequent to this, the EPI images were spatially normalized into MNI stereotaxic coordinates using the EPI template provided with SPM2 (e.g., Friston, Ashburner, Frith, Poline, Heather, & Frackowiak, 1995a). Finally, the
normalized EPI images were spatially smoothed using an isotropic 8 mm Gaussian kernel. For each participant, the processed EPI images were analyzed via multiple regression using a fixed-effects general linear model (e.g., Friston, Ashburner, Frith, Poline, Heather, & Frackowiak, 1995b). In particular, the responses for the 90° video segment were examined, with each participant's model including two principal regressors: one for each instance of the 90° phase pattern during the pre-test and one for each instance of the 90° phase pattern during the post-test. Regressors were based on the canonical hemodynamic response function, temporal derivatives of the event-related responses were included as additional regressors, and low-frequency scanner and/or physiological noise was modeled via linear, quadratic, and cubic regressors of non-interest.

For analysis, we collapsed the data from the six videos of each fMRI session. We then contrasted the mean response during observation of the 90° pattern during the pre-test and post-test session. As we were most interested in activation changes associated with the mirror neuron system we have limited our analyses to those regions of interest. A recent meta-analysis of brain areas active in imitation has shown key areas include Brodmann area 6 (pre-motor cortex), Brodmann area 7 (superior parietal lobule), and Brodmann area 40 (inferior parietal lobule) (Molenberghs, Cunnington, & Mattingly, 2009). All contrasts reported below were based on a threshold of p < 0.001 (uncorrected), with a minimum spatial extent (k) of eight contiguous voxels. Voxel coordinates are given in the stereotaxic coordinates of Talairach and Tournoux (1988). All reported voxel coordinates were converted to Talairach coordinates using a modified version of the mni2tal MATLAB script (www.harvard.edu/~slotnick/scripts.htm).
Results

The results of the fMRI analyses for the regions of interest are shown for each participant in Tables B.1 (areas of decreased activation) and B.2 (areas of increased activation), and summarized in Figure B.2. All three physical practice participants and one observational practice participant showed decreased activation from pre-test to post-test in all three regions of interest (Brodmann areas 6, 7 and 40); while the remaining observational practice participant showed decreased activation in the inferior parietal lobule only (Brodmann area 40). Thus, all participants decreased activation in mirror neuron areas following practice. Conversely, there was no consistent evidence of increased activation in any of our participants regardless of practice condition (Table B.2). Two participants showed increased activation in parietal areas (one observational practice, one physical practice), the remaining three participants showed no increase in activation in the regions of interest. There was no evidence of increased activation in the premotor cortex (cf., Molenberghs et al., 2009).
Table B.1 Voxel cluster statistics for areas showing significant *decreased* activation following practice, by participant.

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Reported coordinates and t values for the cluster maxima. k = # of voxels in the cluster.

BA = Brodmann’s area, L = left, R = right.
Table B.2 Voxel cluster statistics for areas showing significant *increased* activation following practice, by participant.

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Reported coordinates and t values for the cluster maxima. k = # of voxels in the cluster.

BA = Brodmann’s area, L = left, R = right.
Figure B.2 A schematic summary of selected brain regions showing decreased (top two panels) or increased (bottom two panels) activation. Regions of interest include Brodmann Area (BA) 6 (pre-motor cortex), 7 (superior parietal lobule), and 40 (inferior parietal lobule). Numbers in black circles indicate the number of participants (out of five) that showed a significant change in activation in the given area.
We were interested if the individual neurophysiological activation differences were correlated to the behavioural changes observed in each participant. For the physical practice group, all three physical practice participants showed substantial decreases in error between the pre-test and post-test (44°, 23°, and 55° reduction in error respectively), and corresponding decreases in activation in all regions of interest. For the observational practice group, one participant showed an increase in error between the pre-test and post test (30° more error on the post-test) while the second participant showed a reduction in error of a similar magnitude (39°) to the physical practice participants. However, examination of neurophysiological data showed more areas of decreased activation for the observation participant who performed worse in the post-test (all three regions of interest), as compared to the observation participant who performed better in the post test (inferior parietal lobule only). Thus, for the observational practice participants at least, the observed neurophysiological changes did not appear to be related to the physical performance changes.

Discussion

Although we only tested a small subset of our sample with respect to neurophysiological changes as a function of practice, these data provided additional insight into the processes that occurred during observational practice. Similar to previous research (Cross, Hamilton, & Grafton, 2006), both observational and physical practice resulted in changes in activation in the mirror neuron system, suggesting common neural substrates for both processes. However, in contrast to the findings of Cross et al., our results primarily show a decrease in activation of MNS areas with practice, rather than an increase. Decreased activation with practice has been shown in previous experiments (e.g., Vogt et al., 2007) and may reflect an increased understanding of the goals of the movement. For example it has
been shown that motor experience with an object reduces the activation in motor cortex regions during observation, possibly due to reduced implicit analysis (Handy, Tipper, Schaich Borg, Grafton, & Gazzaniga, 2006). In addition, when participants are scanned while performing a 90º relative phase pattern, brain activation decreases are found in the prefrontal and parietal cortices as a function of learning (Debaere, Wenderoth, Sunaert, Van Hecke, & Swinnen, 2004; Remy, Wenderoth, Lipkens, & Swinnen, 2008). If the function of the MNS is one of action understanding, then it would be reasonable to expect decreased activation once the movement is understood. Thus observation may have aided in the understanding of the movement pattern (further confirmed by the perceptual discrimination data) even though this knowledge did not translate to improved physical performance.