Investigating Motor Preparation in Synchronous Hand and Foot Movements Under Reactive vs. Predictive Control

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Thesis submitted to the University of Ottawa

in partial fulfillment of the requirements for

the degree of Master of Science in Human Kinetics

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Statement of Contributors

All the work contained in this document was carried out by the author in collaboration with Dr. Anthony Carlsen, and with input from Dr. Yves Lajoie and Dr. Dana Maslovat.

Acknowledgements

I would like to begin by thanking my supervisor, Dr. Tony Carlsen, for his guidance, patience, and encouragement. I could not have asked for a better thesis supervisor. I would also like to thank my committee members, Dr. Yves Lajoie and Dr. Dana Maslovat, for their time and feedback throughout this process. Additionally, I would like to thank all the members of the motor control labs for their support and friendship.

To Mom, Dad and Alex, thank you for your unwavering support, encouragement, understanding and patience. I would not be where I am today without the three of you by my side.

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Abstract

Synchronizing hand and foot movements under reactive versus predictive control results in differential timing structures between the responses. Under reactive control, where the movement is externally triggered, the electromyographic (EMG) responses are synchronized, resulting in the hand displacement preceding the foot. Under predictive control, where the movement is self-paced, the motor commands are organized such that the displacement onset occurs relatively synchronously, requiring the EMG onset of the foot to precede that of the hand. The current study used a startling acoustic stimulus (SAS), which is known to involuntarily trigger a prepared response, to investigate whether these results are due to differences in the pre-programmed timing initiation structure of the responses. Participants (n=17) performed isolated and synchronous movements of the right heel and right hand under both reactive and predictive modes of control. The reactive condition involved a simple reaction time (RT) task where participants performed the required movement in response to a visual go-signal. The predictive condition involved an anticipation-timing task where participants initiated the required movement coincidently with a sweeping clock hand reaching a target. On a subset of trials, a SAS (114 dB) was presented 150 ms prior to the imperative stimulus. Results from the SAS trials revealed that while the differential timing structures between the responses was maintained under both reactive and predictive control, the EMG onset asynchrony under predictive control was significantly smaller following the SAS. Additionally, there was no difference in the effect of the SAS when the movements were performed in isolation versus synchronously. Together, these results suggest that the timing between the responses, which differs between the two control modes, is pre-programmed; however, under predictive control, an increase in cortical activation from the SAS may have shortened the between-limb delay.

List of Abbreviations

CNV: Contingent negative variation

ECR: Extensor carpi radialis

EEG: Electroencephalography

EMG: Electromyography

LME: Linear mixed effects

LRP: Lateralized readiness potential

MRCP: Movement-related cortical potential

RM ANOVA: Repeated measures analysis of variance

RP: Readiness potential

RT: Reaction time

SAS: Startling acoustic stimulus

SCM: Sternocleidomastoid

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Chapter 1: Literature Review

1. Introduction

On a daily basis, humans often perform synchronous multi-limb movements that can occur under a reactive or a predictive mode of control. For example, a driver may need to react quickly in an emergency and simultaneously hit the brake and turn the steering wheel to avoid a collision, or a pianist may simultaneously press a piano key and a pedal in order to generate the desired musical sound. One of the primary aims within the field of motor control is to better understand the processes that underlie the control of voluntary movement, including how movements are prepared and executed. One methodology used in motor control laboratories to investigate response preparation involves the use of a startling acoustic stimulus (SAS). It has been shown that pairing a simple reaction time (RT) task with a SAS results in the intended movement being triggered at extremely short latencies (Carlsen et al., 2012). This robust phenomenon is thought to arise from the involuntary release of a prepared response and has allowed researchers to determine what aspects of a response can be prepared in advance.

Synchronous movements of the hand and foot have previously been investigated under two modes of control: (1) reactive, which is a simple RT situation where the synchronous movement is executed in response to an external stimulus and (2) predictive, which is when individuals execute the synchronous movement at their own pace (Bard et al., 1991). Under reactive control, the response of the hand precedes that of the foot, which indicates that a single triggering signal is used to simultaneously release the motor commands to both effectors. However, under predictive control, the foot response tends to precede the hand response, which suggests that two distinct motor commands are released and that the command to the foot is released first (Bard et al., 1992; LaRue, 2007). Currently, the preparatory status of these reactive and predictive responses is unclear. The purpose of this study was to investigate the preparatory state of motor commands for synchronous hand and foot movements under reactive versus predictive modes of control.

As such, the following literature review will first summarize the relevant background information regarding RT and how it is commonly used in the laboratory to study response programming (i.e., motor preparation). Next, the behavioural and neurophysiological evidence of response programming will briefly be discussed. The use of a SAS and the StartReact paradigm will then be highlighted as a tool to probe for response programming. Finally, the literature review will conclude with a discussion of synchronous hand and foot movements that are executed under both reactive and predictive modes of control.

2. Information Processing Model

The study of motor control aims to provide insight into both how the central nervous system is organized to produce skilled and coordinated movements, and how sensory information from the environment and the body are used in the control of movement (Schmidt & Lee, 2011). An information processing model has long been used across behavioural neuroscience fields such as motor control, and it appears to have strong explanatory and predictive power regarding how the brain processes sensory information to control various actions. This type of model typically involves three distinct stages of processing that occur between the onset of a stimulus and the onset of a motor response (Schmidt & Lee, 2011). The first stage, often termed stimulus identification, involves detecting and identifying the relevant sensory information from the environment. The second stage is response selection, where the individual must select the appropriate response based on the stimulus that was identified in the first stage. The third stage, termed response programming, involves organizing and preparing the selected response and then initiating that prepared response (Keele, 1968).

2.1 Reaction Time

Since the stages of information processing are modelled as occurring within the brain, they cannot be directly observed and thus need to be inferred from overt actions under various experimental conditions (Schmidt & Lee, 2011). The most common approach to studying the different stages of information processing in the laboratory is to consider the duration of the aforementioned central processes. This can be done using a RT paradigm, as RT is defined as the time between the presentation of a stimulus and the initiation of a response (Donders, 1969). More specifically, the stages of information processing are thought to occur during the RT interval; therefore, changes in RT are assumed to reflect changes in the amount of time needed to complete a particular information processing stage (Donders, 1969). Using electromyography (EMG), the RT interval can be divided into two components: premotor RT and motor time. Premotor RT is defined as the interval of time between the presentation of the imperative stimulus and the onset of activity in the muscle, and is often used as an indication of central processing time (Botwinick & Thompson, 1966; Weiss, 1965). On the other hand, motor time is defined as the interval of time between the initial activation of the muscle and when it actually starts to move, and is thought to represent peripheral effects, such as the muscular processes required to overcome the inertia of the limbs (Botwinick & Thompson, 1966; Weiss, 1965).

One common RT paradigm used to gain insight into the stages of information processing is a simple RT paradigm. In this type of RT task, there is one stimulus and participants are required to respond with a known response. Since there is only one possible response, it is unnecessary to perform the response selection stage during the

RT interval in a simple RT task (Donders, 1969). More specifically, when the required response is known in advance, like in a simple RT task, response programming can occur before the go-signal (i.e., before the stimulus identification stage), and this is referred to as response pre-programming (Donders, 1969; Keele, 1968). As a function of response pre-programming, RT latencies measured in a simple RT task are typically shorter than the latencies measured in other RT paradigms where the required response is not known in advance of the go-signal (Donders, 1969).

3. Response Programming

Response programming involves both the organization and preparation of the appropriate motor commands, and the initiation of that prepared response (i.e., the motor program). Initially, a motor program was defined as a pre-structured set of muscle commands that allows the movement to be executed uninfluenced by feedback (Keele, 1968). However, more recently a motor program has been conceptualized as an abstract representation of a class of movements that contains a set of invariant features that can be parametrized to produce a specific movement (Summers & Anson, 2009).

3.1 Behavioural Evidence

A number of different methodologies have been used to examine response programming including, but not limited to, a simple RT paradigm requiring movements of differing complexity (Henry & Rogers, 1960) and a movement blocking paradigm (Wadman et al., 1979). In their experiment, Henry and Rogers (1960) investigated the effects of increasing movement complexity on RT by increasing the number of movement components in a simple RT task. In the simplest condition, participants were required to lift their finger from a key as quickly as possible in response to an auditory go-signal. In the intermediate condition, participants were asked to lift their finger from the key as quickly as possible and then reach forward and upward to grasp a suspended tennis ball. In the most complex condition, participants were required to: first, lift their finger from the key as quickly as possible; second, reach upward to the right to strike a suspended tennis ball; third, reverse their movement direction to push a button; and then finally, reach upward to the left to grasp a second suspended tennis ball. The authors found that RT increased as the number of movement components increased (i.e., movement complexity increased). Given that the stimulus to initiate the movement and the number of response alternatives were held constant, the authors argued that more complex movements require more time to prepare the required response.

Another paradigm that has been used to examine response programming is a movement blocking paradigm (Wadman et al., 1979). Using this paradigm, Wadman and colleagues (1979) had participants perform rapid elbow extension movements to a target, while recording the muscle activity of the triceps (agonist) and biceps (antagonist) using EMG. Additionally, on a subset of trials, participants were unexpectedly blocked from making the movement. Their results showed that a typical triphasic EMG pattern (agonist - antagonist - agonist) was recorded on unblocked trials. Interestingly, results from the blocked trials showed that a similar pattern of muscle activation was recorded, even though the arm did not move when blocked. Following the first 100 ms, the EMG pattern began to diverge in response to proprioceptive feedback. These results suggest that the sequence of muscle contractions was pre-programmed and executed uninfluenced by proprioceptive feedback.

3.2 Neurophysiological Evidence

In addition to the behavioural methods outlined above, neurophysiological methods have been used to better understand response programming. For example, electroencephalography (EEG), a non-invasive neuroimaging technique, has been used to examine the preparatory processes that precede voluntary movement (Leuthold et al., 2004). EEG uses electrodes placed over the scalp to record the electrical potentials generated by the synchronized firing of a large group of cortical neurons (Woodman, 2010). In order to gain an electrophysiological window into the preparatory processes, EEG waveforms can be time-locked to movement EMG onset and then averaged over a large number of trials (Woodman, 2010). The resulting waveform, termed a movement-related cortical potential (MRCP), can then be used to investigate the nature of motor preparation.

In the EEG literature, voluntary unimanual movements under both self-paced and externally cued conditions have been shown to be preceded by a slowly increasing bilaterally recorded negative potential that can begin as early as 1.5 seconds prior to movement onset (Deecke et al., 1976; Walter et al., 1964). When the movement is initiated under self-paced conditions, the MRCP is referred to as the readiness potential (RP) or Bereitschaftspotential (Deecke et al., 1976). Initially, this activation is symmetrically distributed over the precentral, central, and parietal areas of the cortex. However, greater cortical activation is recorded in the motor cortex contralateral to the responding hand just prior to movement initiation (Deecke et al., 1976). This asymmetric lateralization of the RP, termed the lateralized readiness potential (LRP), is thought to reflect an increase in cortical activation associated with response preparation (Ulrich et al., 1998). In contrast, when a unimanual movement is initiated in response to a go-signal that is preceded by a warning signal, the MRCP that develops during the foreperiod (i.e., the time between the warning signal and the go-signal) is referred to as the contingent negative variation (CNV) (Walter et al., 1964). This waveform is comprised of two components: an early component that emerges following the warning signal and a later component that immediately precedes the go-signal (Rohrbaugh et al., 1976; Rohrbaugh & Gaillard, 1983). The early CNV component, which is maximal over the frontal cortex, is thought to reflect the orienting processes associated with the warning signal, whereas the late CNV component, which is maximal over the centroparietal areas, is thought to reflect motor preparation (Rohrbaugh & Gaillard, 1983; Ulrich et al., 1998).

In order to examine the nature of motor preparation, a number of studies have analyzed the onset of the LRP and the amplitude of the late CNV within a pre-cuing paradigm (Leuthold et al., 1996, 2004; MacKay & Bonnet, 1990; Ulrich et al., 1998). For example, Leuthold and colleagues (1996) examined the onset of the LRP when the go-signal was preceded by a precue that provided advance information about both response parameters (response finger and movement direction), only one response parameter (left vs. right index finger or extension vs. flexion), or no information about the upcoming response. The authors found that the LRP emerged well in advance of the go-signal when the precue specified both the response finger and movement direction or the response finger alone, but not when movement direction alone was precued or no information regarding the upcoming response was provided. These results suggest that the precued information regarding both response parameters or the response finger alone were used in advance of the go-signal to increase the level of cortical activation in the corresponding motor cortex (Leuthold et al., 1996). In a similar study, MacKay and Bonnet (1990) examined the amplitude of the late CNV when the go-signal was preceded by a precue that specified either both response parameters (movement direction and response force), only one parameter, or no information about the forthcoming response. The authors found that the amplitude of the late CNV increased with the amount of advance information provided about the upcoming movement. Taken together, these studies indicate that motor preparation occurs well in advance of the go-signal when certain aspects of the upcoming response are known, as demonstrated by the onset of the LRP and the increase in the late CNV amplitude.

3.3 Cortical Cell Assemblies

While the studies discussed above demonstrate that pre-programming can occur, there has been little neural evidence to support the existence of motor programs. The cortical cell assembly model, put forward by Wickens and colleagues (1994), proposed that a motor program could be thought of as a network of cortical pyramidal neurons with strengthened synaptic connections (i.e., a cell assembly). According to this view, response preparation involves activating the desired cell assembly to a level that is held just below threshold. Following the presentation of the imperative stimulus, the additional input of activity activates the cell assembly, which then activates the corticospinal connections and results in movement execution (Wickens et al., 1994).

4. Startling Acoustic Stimulus (SAS)

Building on the behavioural and neurophysiological evidence described above, researchers have used a loud acoustic stimulus that elicits a startle reflex (i.e., a SAS) to investigate the nature of advance response preparation. Numerous studies have shown that when a SAS is presented in a simple RT task, the intended response is elicited at a significantly shorter latency in comparison to the control (non-SAS) trials (Carlsen et al., 2004a, 2012; Valls-Solé et al., 1999). Currently, this significant reduction in RT is thought to occur as a result of the SAS directly increasing the activation of initiation processes via a reticulo-thalamo-cortical pathway (Carlsen et al., 2012). From the perspective of the cortical cell assembly model, this increase in activation then provides the necessary input to the desired cell assembly to trigger the release of the prepared and cortically stored response without the usual cortical processing (Carlsen et al., 2012; Carlsen & Maslovat, 2019).

4.1 The Startle Reflex

The startle reflex, a protective response to an intense and unexpected stimulus, is characterized by a generalized flexion response that consists of bilateral blinking, facial grimace, head and neck flexion, shoulder elevation, and trunk flexion (Yeomans & Frankland, 1995). When a SAS is used, the auditory input is sent directly from the cochlear nucleus to the giant neurons within the nucleus reticularis pontis caudalis, which activates the motor neurons in the spinal cord through the reticulospinal tract and results in the involuntary startle response (Yeomans & Frankland, 1995). Since this short pathway bypasses the usual cortical processing in the auditory cortex, it leads to extremely short startle response onset latencies (Yeomans & Frankland, 1995). In order to confirm that a startle response has actually occurred, a number of indicators can be used. For example, EMG activity in the orbicularis oculi and sternocleidomastoid (SCM) muscles are often used as startle response indicators as these EMG responses have been shown to be the most consistently recorded (Brown et al., 1991). However, SCM activation is considered to be the more reliable startle indicator as it is the most resistant to startle habituation (Brown et al., 1991; Carlsen et al., 2011).

4.2 The StartReact Effect

As previously mentioned, the presentation of a SAS in a simple RT task can often result in the intended movement being triggered at extremely short latencies (Carlsen et al., 2012). This phenomenon, termed the StartReact effect, is thought to arise from the early and involuntary release of a prepared response in association with the startle reflex (Carlsen et al., 2012). For example, to determine whether a SAS leads to the early release of a prepared response, Carlsen et al. (2004a) examined the effect of a SAS on different elbow extension movements. In their experiment, participants performed either a 20°, 40° or 60° elbow extension movement in response to an auditory go-signal, where the go-signal was occasionally replaced with a SAS. Similar to previous findings, the results showed that RT latencies were significantly shorter on SAS trials than on control trials, while the movement kinematics and EMG patterns remained largely unchanged between the two conditions. Researchers have subsequently used a SAS in various voluntary motor tasks to gain insight into when pre-programming occurs, in what situations pre-programming occurs, and what aspects of a movement can be pre-programmed (Carlsen et al., 2004b; MacKinnon et al., 2007; Maslovat et al., 2008; Queralt et al., 2008).

To investigate in which situations pre-programming can occur, Carlsen et al. (2004b) examined the effects of presenting a SAS in a simple RT task versus a choice RT task. In their simple RT task, participants were required to perform a 20° right wrist extension movement. In the choice RT task, either 2 or 4 stimulus-response alternatives were presented. In the 2-choice condition, participants performed either a 20° right wrist flexion or right wrist extension movement. In the 4-choice condition, participants performed either a 20° wrist flexion or extension movement with either hand. In both choice conditions, the required response was provided by a visual go-signal. Additionally, on 12% of the right wrist extension trials, regardless of whether it was a simple RT trial, 2-choice RT trial or 4-choice RT trial, a SAS was delivered in conjunction with the visual go-signal. The authors found that the presentation of a SAS led to significantly shorter RTs in the simple RT task, but not in the choice RT tasks. These results indicate that a SAS decreases RT only when the required response is known in advance of the go-signal (i.e., in a simple RT task) and is therefore pre-programed (Carlsen et al., 2004b).

However, even within a simple RT task, a SAS has also been used to show that response pre-programming also depends on the temporal predictability of the go-signal (Carlsen & MacKinnon, 2010). In their experiment, participants were required to perform a right wrist extension movement in response to a visual go-signal under four different cueing conditions. In the “variable foreperiod” condition, the go-signal was presented 2 to 3 seconds after the warning signal. In the “fixed foreperiod” condition, the go-signal was always presented 3 seconds following the warning signal. In the “countdown” condition, four squares appeared sequentially from left to right on a computer monitor at 1000 ms intervals, and participants were asked to time the initiation of their response to coincide with the appearance of the fourth square. Finally, in the “clock” condition, an analog clock face without any numbers was displayed on the monitor. At the start of a trial, the clock hand began at the 12 o’clock position and made one revolution in a clockwise direction in 4 seconds. Participants were instructed to initiate their response when the clock hand reached the 9 o’clock position, which was indicated by a red arrow. The first two conditions were considered to have low temporal resolution since participants were unaware of either foreperiod durations and thus had to react to the go-signal. In contrast, the latter two conditions were considered to have high temporal resolution since participants were able to anticipate when the go-signal would occur. Additionally, on certain trials, a SAS was presented 150, 500, or 1500 ms prior to the go-signal. Results showed that when the SAS was presented 1500 ms prior to the go-signal, the proportion of trials in which the response was elicited was significantly greater in the variable foreperiod (57.5%) and fixed foreperiod (68.1%) conditions compared to the countdown (10%) and clock (0%) conditions. When the SAS was presented 500 ms prior to the go-signal, the authors found that the proportion of trials where the response was elicited early rose to approximately 90% in the variable foreperiod and fixed foreperiod conditions, 47.5% in the countdown condition and only 17.5% in the clock condition. Interestingly, when the SAS was presented 150 ms prior to the go-signal, the response was elicited early in more than 90% of the trials irrespective of the cueing condition. Together, these results indicate that when the temporal predictability of the go-signal is low, the response is often fully programmed and ready for initiation at least sometime between 2 seconds and 1 second prior to the go-signal. In contrast, when the temporal predictability of the go-signal is high, participants appear to wait until just prior to when the response is needed (i.e., < 200 ms prior to the go signal) to program the response (Carlsen & MacKinnon, 2010). Similar results have been reported in a stepping task, where the response was progressively programmed sometime between 1400 ms and 100 ms prior to the go-signal (MacKinnon et al., 2007), and in a stop-signal anticipation-timing task, where no overt response was elicited when the SAS was delivered 200 ms prior to the target (Carlsen et al., 2008).

In addition to examining when and under what circumstances pre-programming occurs, a SAS can also be used to investigate what aspects of a movement can be pre-programmed. For example, Maslovat and colleagues (2008) examined the effects of a SAS on a synchronous bimanual movement of different amplitudes. When participants were required to simultaneously perform a 20° elbow extension movement with their right arm and a 10° elbow extension movement with their left arm in response to an auditory go-signal, the presentation of a SAS led to the early elicitation of the asymmetrical bimanual movement (Maslovat et al., 2008). The authors reported that RT was significantly shorter on SAS trials compared to control trials, and that the movement kinematics and EMG patterns were similar between the two conditions. These results indicate that different movement amplitudes can be pre-programmed for each limb. In a follow-up study, Maslovat et al. (2009) used a SAS to probe for advance preparation in an asynchronous bimanual movement of equal amplitudes. In their experiment, participants were required to perform a 20° bimanual elbow extension movement, where the initiation of the left arm was delayed by 100 ms relative to the initiation of the right arm. Similar to the results of the asymmetrical bimanual movement, the authors reported that the SAS triggered the asynchronous bimanual movement, and that RT latencies were significantly shorter on SAS trials compared to control trials (Maslovat et al., 2009). However, contrary to the typical results seen in StartReact experiments, Maslovat and colleagues (2009) found that the triggered movement differed between the conditions in that the between-limb delay and within-arm EMG patterns were significantly shorter in the SAS trials compared to the control trials. To explain these findings, the authors hypothesized that when a timing component is added to the movement, the use of a SAS may have impacted the internal timer. Collectively, these studies indicate that both asymmetrical bimanual movements (i.e., bimanual movements of different amplitudes) and asynchronous bimanual movements (i.e., bimanual movements with an overt between-limb timing requirement) can be prepared in advance.

Thus, considering the studies discussed above, it is clear that a SAS serves as an invaluable tool to elucidate the nature of response pre-programming.

5. Synchronous Movements of the Hand and Foot

Synchronous movements of the hand and foot have previously been studied under two modes of control: reactive (i.e., externally triggered) and predictive (i.e., self-paced) control. For example, Bard et al. (1991) had participants raise their right index finger and right heel simultaneously under both reactive and predictive modes of control. In the reactive condition, participants were required to simultaneously raise their finger and heel as quickly as possible in response to an auditory go-signal. In the predictive condition, participants were required to raise their finger and heel at the same time in a self-paced movement without an auditory go-signal. Results from the reactive condition showed that the extensor digitorum longus muscle and internal gastrocnemius muscle were activated at approximately the same time, as there was no significant difference in premotor RT. Additionally, the authors reported that the finger response preceded the heel response by ~25 ms. These results are similar to previous findings, demonstrating that under reactive conditions, the motor commands are sent simultaneously to both muscle groups, and that the finger consistently moves before the heel as a result of the shorter efferent pathway and smaller limb mass (Paillard, 1946). As a function of the smaller limb mass, the finger requires less time to generate enough force to overcome the inertia and initiate the movement. Interestingly, results from the predictive condition showed that the internal gastrocnemius muscle was activated well in advance of the extensor digitorum longus muscle (~30 ms earlier), and that the ensuing heel response was initiated much closer in time to the finger motor response, but still ~7 ms earlier. When the response of the foot precedes that of the hand, it is referred to as a negative asynchrony. This negative asynchrony has been argued to be driven by anticipated sensory feedback, such that the motor commands are planned, organized and scheduled based on the anticipated sensory consequences of the planned movement (Bard et al., 1991). In other words, it was suggested that the heel response precedes the finger response so that the afferent sensory information derived from each effector arrives simultaneously at the central level (Bard et al., 1991; Blouin et al., 2004). Thus, it appears that under predictive control, synchrony is evaluated based on the arrival of sensory feedback at the central level rather than the actual time of execution of the responses.

Further support for the role of somatosensory feedback in movement synchronization comes from a comparative follow-up study with a deafferented patient (Bard et al., 1992). The authors replicated their experiment with a deafferented patient and found that the patient behaved similarly to healthy individuals in the reactive condition, as their finger response preceded the heel response. However, in contrast to healthy individuals, the deafferented patient also initiated the finger response prior to the heel response in the predictive condition. These results indicated that the deafferented patient adopted the same reactive control mechanism (i.e., used a common triggering signal to simultaneously release the motor commands to both limbs) to control synchronicity in both reactive and predictive conditions. Moreover, these results provide further evidence for the role of somatosensory feedback in the timing of motor commands because without proprioceptive feedback, the deafferented patient was unable to use the afferent information derived from the finger and heel to adopt the anticipatory strategy that is consistently used by healthy individuals in the predictive condition (Bard et al., 1992).

It has been suggested that the evaluation and comparison of reafferent information occurs at the cerebellar level (Bard et al., 1992; Blouin et al., 2004). This comparative process is thought to occur within an internal model where the efference copy, an internal copy of the motor commands, is sent to the cerebellum at the same time as the motor commands are sent to the effectors (Ivry & Keele, 1989; Wolpert et al., 1995). The efference copy allows the cerebellum to predict the sensory consequences of a voluntary movement (i.e., to generate the “image of goal achievement”) before the reafferent information is received (Bard et al., 1992). The efference copy is then compared to the reafferent information, and any discrepancies between the predicted and actual sensory consequences of the movement are used to update and adjust the motor commands accordingly to result in the desired movement (Bard et al., 1992; Ivry & Keele, 1989).

In summary, these studies indicate that participants unconsciously adopt different modes of control depending on the movement initiation contexts (i.e., reactive vs. predictive). Moreover, the results suggest that reafferent information contributes to the timing of motor commands in the predictive condition.

Chapter 2: Research Article

Investigating Motor Preparation in Synchronous Hand and Foot Movements Under Reactive vs. Predictive Control

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1. Introduction

On a daily basis, humans often perform synchronous multi-limb movements that can occur under a reactive or a predictive mode of control. For example, a driver may need to react quickly in an emergency and simultaneously hit the brake and turn the steering wheel to avoid a collision, or a pianist may simultaneously press a piano key and a pedal in order to generate the desired musical sound. Synchronous movements of the hand and foot have previously been investigated in the laboratory under two modes of control: (1) reactive, which is a simple reaction time (RT) situation where the synchronous movement is executed in response to an external go-signal and (2) predictive, which is when individuals execute the synchronous movement at their own pace (Bard et al., 1991). When the synchronous movement is performed under reactive conditions, the EMG activity is synchronized but the response of the hand precedes the response of the foot as a result of differences in nerve conduction time. However, when it is performed under predictive conditions, the EMG response of the foot precedes that of the hand so that the limb displacement is essentially synchronized (Bard et al., 1991; Blouin et al., 2004). While these control modes result in differential timing structures between the responses, the preparatory status of these reactive and predictive responses is unclear. The purpose of the current study was to investigate whether the distinct reactive and predictive EMG responses are due to differences in the pre-programmed timing initiation structure of the responses. Specifically, it was of interest whether the two movements in a synchronous hand and foot task are prepared and initiated as a single “package” with a timing structure that depends on the mode of control, or whether the responses are prepared as individual components and triggered separately.

One methodology used in motor control laboratories to investigate response preparation involves the use of a startling acoustic stimulus (SAS). It is well documented that when a SAS is delivered in place of or in conjunction with the go-signal in a simple RT task, it can trigger the intended response at extremely short latencies (Carlsen et al., 2012). This robust phenomenon, termed the StartReact effect, is thought to arise due to the involuntary release of a prepared response in association with the startle reflex (Carlsen & Maslovat, 2019). Based on this, it has been argued that a SAS can be used to investigate what has been prepared in advance.

The purpose of this study was to determine if preparation of synchronous hand and foot movements differs depending on the mode of control: reactive versus predictive control. To address this question, a SAS was presented prior to the imperative stimulus on a subset of trials to determine what is pre-programmed under both modes of control. It was hypothesized that the responses would be prepared and triggered independently such that the startle would result in synchronous EMG responses from the hand and foot, irrespective of the mode of control. It was also hypothesized that the presence of a startle would lead to earlier EMG onset times regardless of the control mode.

2. Methods

2.1 Participants

Seventeen adults (7 male, 10 female; mean age = 26.4 years, SD = 7.6) with normal or corrected-to-normal vision, and with no self-reported history of sensory or motor dysfunctions were recruited to participate in this study. Prior to taking part, all participants provided informed consent and completed the modified version of the Edinburgh Handedness questionnaire (Oldfield, 1971; Appendix A) to confirm that they were right-handed or ambidextrous (mean handedness score = 78.3, SD = 31.8). Participants then completed 2 testing sessions over 2 days. The sessions were unequally spaced in time due to the availability of the participants; however, they were spaced at least 1 day apart (mean = 2.9 days, SD = 2.1). Each session consisted of 128 trials and lasted approximately 45 minutes. All ethical standards and safety monitoring procedures were met according to the University of Ottawa's Faculty of Health Sciences and Science Research Ethics Board, and all procedures adhered to the 7th revision of the Declaration of Helsinki.

2.2 Apparatus and Tasks

Testing took place in a secluded room where participants interacted with a custom-made finger switch, footswitch and monitor set-up. Participants sat at a table facing a 24-inch LCD computer monitor (Asus VG248QE; 144 Hz refresh) with their right forearm resting on the table in a pronated position and both feet flat on the floor. The participants were positioned such that their right elbow was flexed at approximately 90° and the shoulder abducted approximately 30°. A cloth barrier was placed approximately 20 cm to the left of the participant's right arm to obstruct the view of their right arm and the tabletop obstructed the view of their legs.

Participants performed a synchronous task where they were asked to simultaneously raise their right heel and extend their right wrist (Figure 1). Each movement was also performed in isolation and used as control. Participants began from a pronated hand position (palm facing down) with the proximal phalanx of the third digit of the right hand holding down a custom-made finger switch, and from a neutral foot position with their right heel resting on a footswitch (Lafayette model 35603). Participants were instructed to extend their right wrist while holding the digits straight and rigid, to lift the hand off the finger switch. At the same time, they were asked to lift their heel off the footswitch using plantar flexion, leaving the distal part of the foot in contact with the ground. A wrist extension movement was chosen instead of a finger extension / abduction movement as individual finger movements have been shown to be resistant to the early response triggering effects of a SAS (Carlsen et al., 2009).

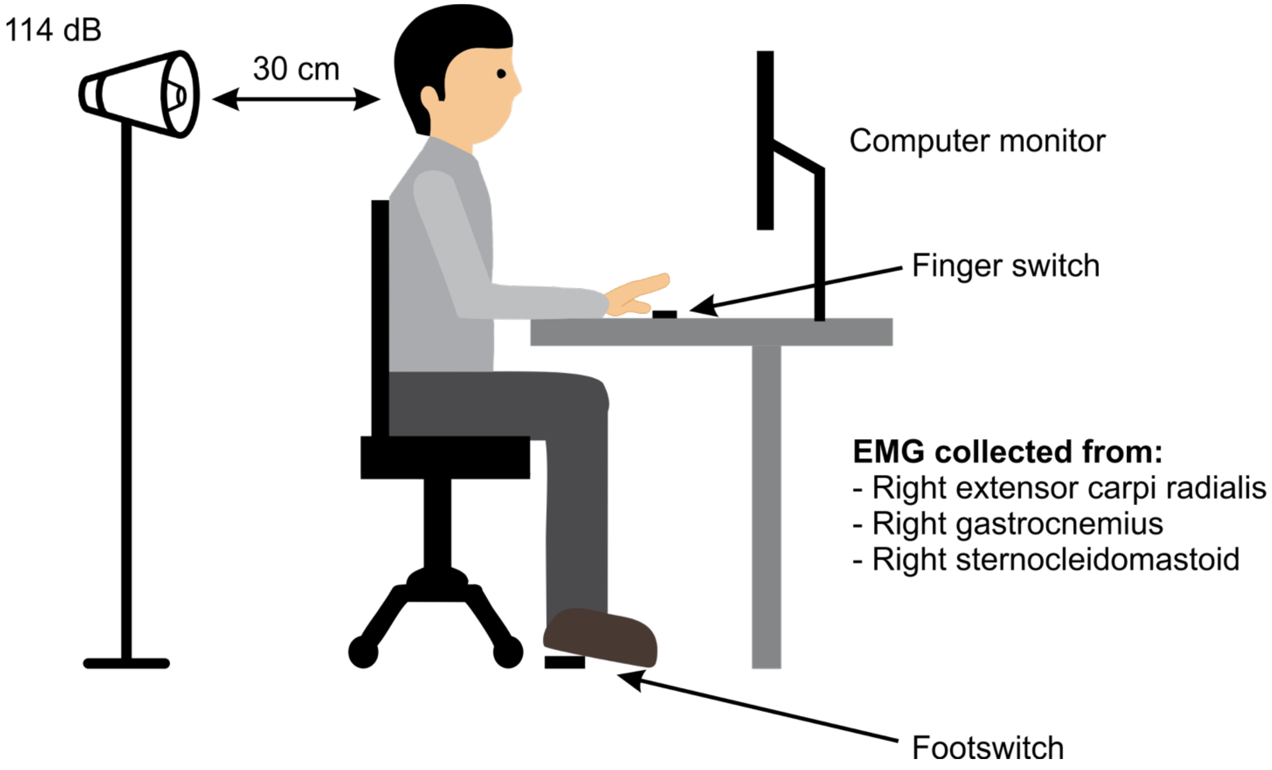

Figure 1. Experimental set-up. Participants sat with their right third finger holding down a finger switch and with their right heel resting on a footswitch. From this position, participants performed a synchronous movement where they were asked to simultaneously lift their right heel and right hand off the switch under both reactive and predictive modes of control. Each movement was also performed in isolation under both control modes. On a subset of trials, a SAS was delivered via a speaker located 30 cm directly behind the participant's head.

All tasks (i.e., the synchronous task and each isolated task) were performed under both reactive and predictive modes of control, with each control mode performed on separate days. In the reactive condition, participants were instructed to perform the required movement as quickly as possible in response to a visual go-signal. The predictive condition involved an anticipation-timing task where participants were instructed to coincide the required movement with a sweeping clock hand reaching a target. This type of task was chosen instead of a self-paced task as it is not possible to deliver a SAS at a specific time point relative to the unknown initiation time in a self-paced task. Additionally, an anticipation-timing task has been shown to produce similar patterns of synchronization between the hand and foot as a self-paced task (LaRue, 2007). Feedback regarding RT or movement initiation timing error (ms) with respect to the target was provided on the monitor at the end of each reactive or predictive trial, respectively. In the reactive condition, participants were awarded points for fast RTs (+1 point for every ms below 170 ms for a maximum of +25 points per trial) and were penalized points for slow RTs (-1 point for every ms above 270 ms for a maximum of -25 points per trial). Similarly, in the predictive condition, participants were awarded points for small movement initiation timing errors (+1 point for every ms below ±40 ms up to a maximum of +25 points per trial) and were penalized points for large movement initiation timing errors (-1 point for every ms in excess of ±80 ms away from the target up to a maximum of -25 points per trial). These points served as a motivator and were not analyzed.

2.3 Startling Acoustic Stimulus (SAS)

Within each testing session a SAS (white noise, 114 dB, 25 ms) was presented 150 ms prior to the visual go-signal or target on 25% of the trials. This time point was chosen based on a previous study by Carlsen and MacKinnon (2010), which showed that at 150 ms prior to the imperative stimulus, the extent of motor preparation was similar between a reactive condition and a predictive condition. Prior to starting the experiment, participants were informed that a loud acoustic stimulus would be presented on some trials and were instructed to disregard the sound as it was irrelevant to the task. A custom written program in LabView (National Instruments Inc.) controlled the presentation of the SAS and the order of the trials. The SAS was presented pseudo-randomly such that the first three trials of a testing block were never SAS trials and the SAS was never presented on two consecutive trials. The SAS was generated using digital to analog hardware (National Instruments PCIe-6321) and was amplified and presented through a loudspeaker (MG Electronics M58-H, frequency response 300 Hz – 11 kHz, <1 ms rise time) placed 30 cm behind the participant’s head. The acoustic stimulus intensity was measured and calibrated using a sound level meter (Cirrus Research Optimus, CR:162C; A-weighted, impulse setting).

2.4 Experimental Procedure

Within each testing session, participants performed the synchronous task and each isolated task under either reactive or predictive control. Participants performed the control modes on separate days. Each session consisted of three testing blocks, one for each task. The blocks with an isolated task (i.e., wrist extension only, heel raising only) consisted of 32 trials, whereas the block with the synchronous task consisted of 64 trials. The order in which participants performed the tasks and the control modes were counterbalanced across participants.

Prior to each testing block, participants performed 4 practice trials to familiarize themselves with the task and the control mode. The practice trials were identical to the testing trials; however, a SAS was not delivered on any of these trials. The practice data were not analyzed.

2.4.1 Reactive Trials

Regardless of the task, all reactive trials began with the words “Get Ready!” being displayed on the computer monitor for 1000 ms, followed by a visual warning signal (white square with a black border; 3 cm x 3 cm). Following a random foreperiod of 1800 ms to 2200 ms (i.e., mean foreperiod of 2 sec), the white square turned green as the visual go-signal (Figure 2A). Participants were required to perform the requisite movement as quickly as possible in response to the go-signal. After each trial, the participant’s RT feedback, the amount of points gained or lost on the trial, and the total amount of points awarded were displayed on the monitor until the beginning of the next trial (3.5 seconds). Each trial lasted approximately 7.5 seconds and participants were given the option to rest in between blocks to minimize fatigue and maximize engagement in the tasks.

2.4.2 Predictive Trials

In the predictive condition, an analog clock face (100 mm diameter) without any numbers was displayed on the computer monitor (Figure 2B). At the start of each trial, the clock hand (black; 50 mm in length) was positioned at the topmost position (i.e., 12 o’clock). During each trial, the clock hand rotated at a constant speed so that it made one revolution in 3 seconds.

Similar to the reactive trials, all predictive trials began with the words “Get Ready!” being displayed on the computer monitor for 1000 ms. Immediately following the disappearance of the phrase “Get Ready!”, the clock hand then moved from the topmost position in a clockwise direction and made one full revolution. Participants were instructed to initiate the required movement coincidently with the clock hand reaching the 8 o’clock (2000 ms) position on the clock face, which was indicated by a red arrow (20 mm in length). The red arrow was displayed just outside of the clock face and pointed directly at the 8 o'clock position for the entire duration of the trial. Following each trial, feedback regarding movement initiation timing error (ms) with respect to the target, the amount of points earned or lost on the trial, and the total amount of points earned were displayed on the monitor for 3.5 seconds (i.e., until the beginning of the next trial). Again, each trial lasted approximately 7.5 seconds and participants were given the option to rest in between blocks. By the end of each testing session, all participants completed a total of 128 trials (24 control and 8 SAS per isolated task, and 48 control and 16 SAS per synchronous task).

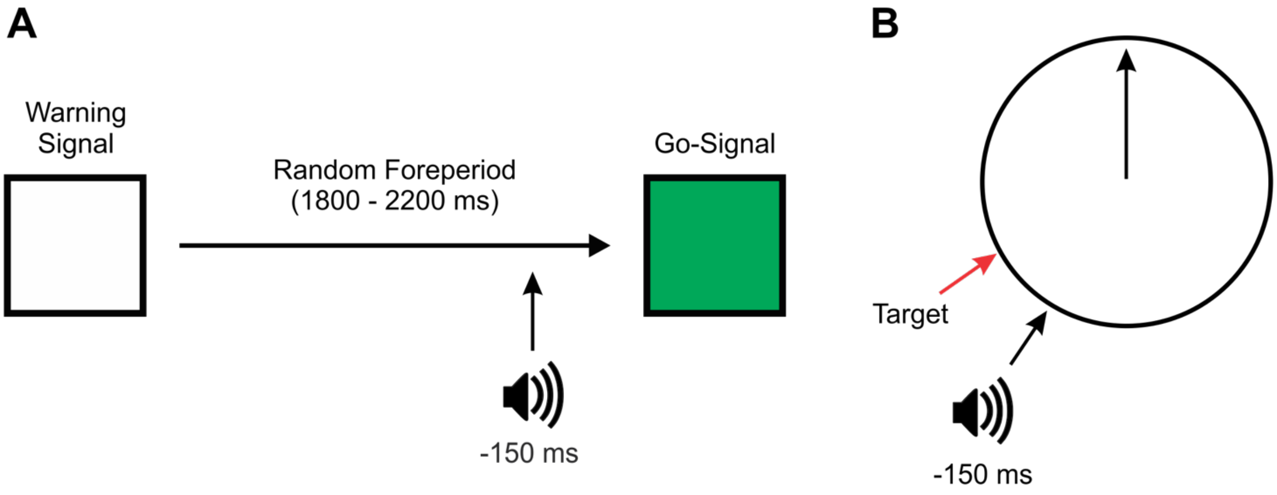

Figure 2. Visual display. **A** Visual display for the reactive trials. The reactive condition involved a simple RT task where participants performed the required movement in response to a visual go-signal. **B** Visual display for the predictive trials. The predictive condition involved an anticipation-timing task where participants were required to coincide the requisite movement with a sweeping clock hand reaching a target. A SAS (114 dB) was presented 150 ms prior to the imperative stimulus on 25% of the trials.

2.5 Recording Equipment

Surface EMG data were collected from the muscle bellies of the right extensor carpi radialis (ECR), the right medial gastrocnemius, and the right SCM (startle indicator) using the Delsys Trigno Wireless EMG system (fixed 48 ms delay). The EMG sensors (Delsys Trigno Avanti Sensor) were placed parallel to the muscle fibres, and then attached to the skin using double-sided adhesive tape. Prior to electrode application, the recording sites were cleaned using an abrasive gel (Nuprep) and alcohol pads to minimize electrical impedance. The finger switch and the footswitch were used to detect movement onset of the right hand and the right foot, respectively. The finger switch required ~0.38 N to close and showed a voltage of 5 V when closed and 0 V when opened. Similarly, the footswitch required ~18 N to close and showed a voltage of 5 V when closed and 0 V when opened. All data were digitally sampled at 1000 Hz (National Instruments PCIe-6321) using a customized LabVIEW (National Instruments Inc.) program and stored for offline analysis. For each trial, data collection was initiated by the computer program 2200 ms prior to the imperative stimulus and continued for 3200 ms.

2.6 Data Analysis

2.6.1 Electromyography (EMG)

EMG burst onsets in the right ECR, right gastrocnemius, and right SCM were identified using a threshold method. Based on this method, EMG burst onset was defined as the point at which the rectified and filtered EMG activity increased to more than 2 standard deviations above baseline and remained elevated for at least 20 ms (Hodges & Bui, 1996). The EMG traces were displayed on a computer monitor and the onset markers, which were computed using a custom LabVIEW algorithm, were then visually inspected and manually adjusted to correct for any errors due to the strictness of the algorithm. Peak EMG amplitude was defined as the largest EMG amplitude recorded within 100 ms following EMG burst onset. For the SAS trials, a startle response was considered to have been elicited if the EMG activity in the SCM muscle occurred within 25-120 ms following the presentation of the SAS (Carlsen et al., 2011). SAS trials where an EMG burst was observed in the SCM muscle were labelled as SCM+ trials, whereas SAS trials with no observable SCM burst were labelled as SCM- trials.

2.6.2 Dependent Measures

EMG onset time was defined as the time between the visual go-signal and EMG burst onset in the movement effector for the reactive condition and as the time of agonist EMG burst onset with respect to the target in the predictive condition. Displacement onset was defined as when the associated movement was detected (i.e., when the voltage changed from 5 V to 0 V). Post-SAS EMG onset was defined as the time of agonist EMG burst onset following the presentation of a SAS regardless of the control mode. EMG onset asynchrony was defined as the difference in EMG onset time between the right ECR muscle and right gastrocnemius muscle. Displacement onset asynchrony was defined as the difference in displacement onset between the wrist extension movement and the heel raising movement. These asynchronies were calculated on each synchronous trial. Asynchrony values were negatively signed when the foot preceded the hand and positively signed when the hand preceded the foot.

2.6.3 Data Reduction

The data from all participants were included in the analyses of this study. Trials in which an error occurred were discarded from analysis. These included RT trials where participants anticipated the go-signal (RT < 50 ms, 56 trials) or were inattentive (RT > 400 ms, 40 trials), anticipation-timing trials where the movement was initiated either well before the target (timing error < -250 ms, 4 trials) or too long after the target (timing error > 100 ms, 10 trials), and trials with movement errors (37 trials). Movement errors included: a lack of movement, moving the incorrect effector or moving only one effector in the synchronous task. SAS trials where participants anticipated the presentation of the SAS (RT < -100 ms, 15 trials), were inattentive (RT > 250 ms, 7 trials), or moved too long after the target (timing error > 100 ms, 13 trials) were also discarded. Synchronous task performance was also examined to ensure that participants were actually performing the movement synchronously under both modes of control and in both control and SAS trials. In the reactive condition, a movement was considered too asynchronous if EMG onset asynchrony was more or less than 2 standard deviations away from the group's mean irrespective of the stimulus type (control or SAS). In the predictive condition, a movement was considered too asynchronous if displacement onset asynchrony was more or less than 2 standard deviations away from the group's mean regardless of the stimulus type. For the reactive condition, this led to the removal of 31 trials, whereas for the predictive condition 42 trials were discarded. Additionally, 103 trials were discarded when motor time for the hand was more or less than 2 standard deviations away from the group's mean regardless of the stimulus type and control mode. Similarly, 81 trials were discarded when motor time for the foot was more or less than 2 standard deviations away from the group's mean regardless of the stimulus type and control mode. Based on the exclusion criteria, 10.1% of the total trials were discarded (439 of 4352 trials).

2.7 Statistical Analysis

The proportion of SAS trials in which an SCM response was observed was analyzed using a 2 Control Mode (reactive, predictive) x 3 Task (wrist extension, heel lift, synchronous) repeated measures analysis of variance (RM ANOVA) to determine if the control mode or task led to a difference in the incidence of a startle response.

EMG onset asynchrony, displacement onset asynchrony, EMG onset time and post-SAS EMG onset were analyzed using linear mixed effects (LME) analyses. For the synchronous tasks, EMG onset asynchrony and displacement onset asynchrony were each analyzed using LME analysis where Control Mode (reactive, predictive) and Trial Type (control, SCM+, SCM-) were specified as interacting fixed factors and participant was specified as a random effect (e.g., [model = premotor RT asynchrony ~ Control Mode * Trial Type + (1 | participant)]). To determine the effect of a SAS on the isolated and synchronous tasks, EMG onset time was analyzed for each control mode and each limb separately using LME analysis where Trial Type (control, SCM+, SCM-) and Task (isolated, synchronous) were specified as interacting fixed factors and participant was specified as a random effect. Additionally, to examine the effect of a startle on the control modes, and the isolated and synchronous tasks, post-SAS EMG onset was analyzed for each limb separately using LME analysis where SCM Response (SCM+, SCM-), Task (isolated, synchronous), and Control Mode (reactive, predictive) were specified as interacting fixed factors and participant was specified as a random effect. LME analyses were performed with R statistical software (R Core Team, 2020) using the lme4 package (Bates et al., 2015) and the lmerTest package (Kuznetsova et al., 2017). The significance value for all statistical tests was set at $p < 0.05$. Post-hoc multiple pairwise comparisons were performed using the emmeans package (Lenth, 2020) in R with Tukey's correction for multiple comparisons to find the locus of any differences.

3. Results

3.1 Startle Indicator

Figure 3 shows the mean proportion of SAS trials that resulted in an observed startle reflex as indicated by a burst of EMG activity in the SCM muscle. Repeated measures ANOVA revealed that there was no significant main effect of Control Mode (F(1,16) = 3.624, p = 0.075, $\eta^2_p = 0.185$), Task (F(2,32) = 0.654, p = 0.527, $\eta^2_p = 0.039$), and no significant interaction between Control Mode and Task (F(2,32) = 0.218, p = 0.805, $\eta^2_p = 0.013$).

These results indicate that there was no difference in the incidence of eliciting a startle reflex across tasks and control modes.

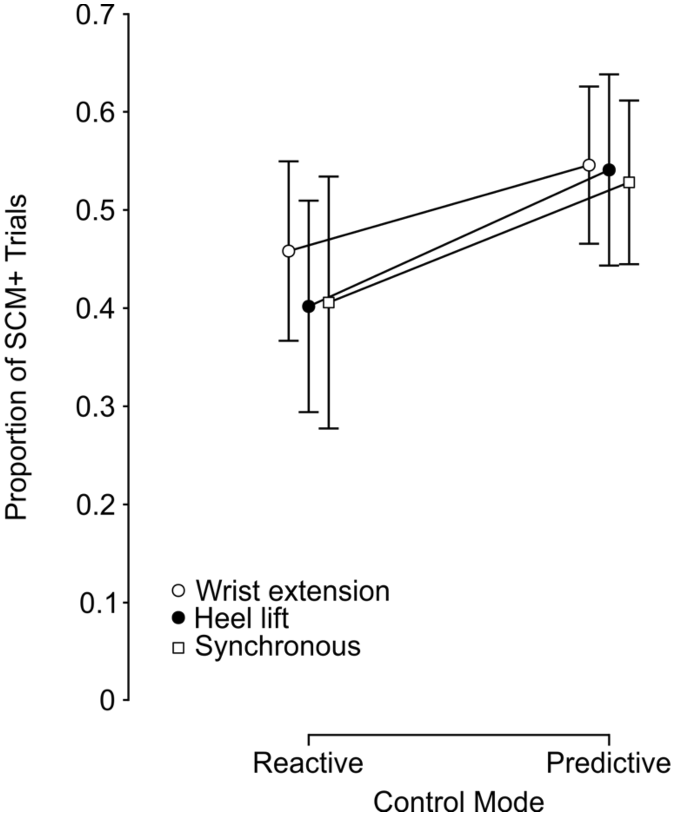

Figure 3. Mean proportion (error bars: 95% CI) of startle trials where a burst of EMG activity was seen in the sternocleidomastoid (SCM) muscle as a function of control mode and task (wrist extension, white circles; heel lift, black circles; synchronous, white squares).

3.2 EMG Onset Asynchrony

EMG onset asynchrony as a function of trial type and control mode is shown in Figure 4. Linear Mixed Effects (LME) analysis revealed significant main effects for Trial Type (F(2,1870.9) = 10.697, $p < 0.001$) and Control Mode (F(1,1865.9) = 267.598, $p < 0.001$). These main effects were superseded by a significant interaction between Trial Type and Control Mode (F(2,1866.8) = 13.463, $p < 0.001$). Post-hoc tests showed that there were no differences in EMG onset asynchrony under reactive control across all trial types (all p values > 0.190). However, under predictive control, EMG onset asynchrony was significantly smaller in SCM+ trials (-4.5 ms, 95% CI [-10.4, 1.4]) compared to both SCM- trials (-12.7 ms, 95% CI [-18.9, -6.6]; p = 0.012) and control trials (-16.6 ms, 95% CI [-21.9, -11.3]; p < 0.001), but there was no difference in EMG onset asynchrony between SCM- and control trials (p = 0.352). Finally, EMG onset asynchrony was significantly different between predictive and reactive control modes for each trial type (all p values < 0.001).

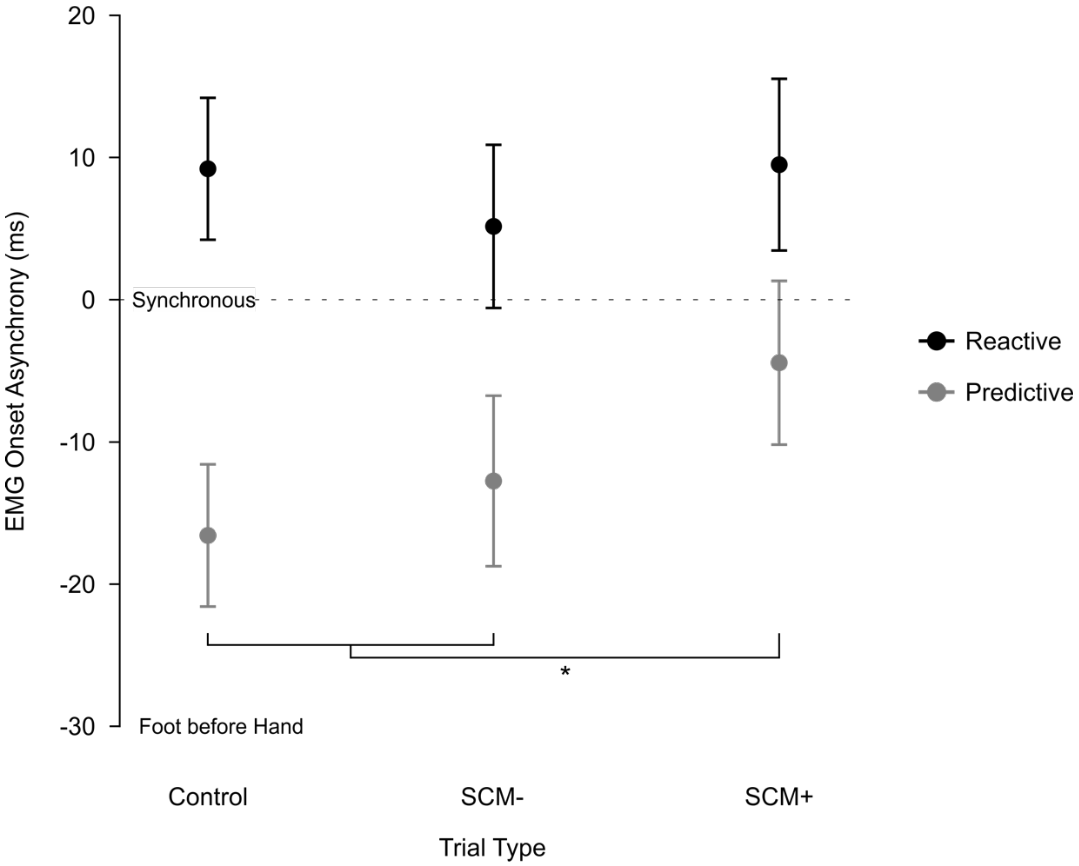

Figure 4. EMG onset asynchrony (error bars: 95% CI) as a function of trial type (control, SCM-, SCM+) and control mode (reactive control: black; predictive control: grey). Zero-point represents synchronous EMG onset. Negative asynchrony values indicate that the EMG onset of the foot preceded that of the hand. Asterisks (*) represent significant differences (p < 0.05) between the SCM+ trials and both the control and SCM- trials in the predictive condition.

3.3 Displacement Onset Asynchrony

Displacement onset asynchrony as a function of trial type and control mode is shown in Figure 5. LME analysis revealed a significant main effect of Trial Type (F(2,1867.7) = 10.759, $p < 0.001$), and a significant main effect of Control Mode (F(1,1865.3) = 361.651, $p < 0.001$). These main effects were superseded by a significant interaction between the factors (F(2,1865.7) = 16.426, $p < 0.001$). Post-hoc tests indicated that in the reactive control mode there was no difference in displacement onset asynchrony between the SCM+ trials and both the control trials ($p = 0.156$), and SCM- trials ($p = 0.252$); however, displacement onset asynchrony was significantly smaller in SCM- trials (21.0 ms, 95% CI [12.6, 29.3]) compared to control trials (30.7 ms, 95% CI [22.7, 38.7]; $p < 0.001$). Under predictive control, displacement onset asynchrony was significantly larger in SCM+ trials (10.2 ms, 95% CI [1.9, 18.6]) compared to both SCM- trials (1.1 ms, 95% CI [-7.4, 9.6]; $p = 0.002$) and control trials (2.3 ms, 95% CI [-5.7, 10.3]; $p < 0.001$). However, there was no difference in displacement onset asynchrony between predictive control trials and predictive SCM- trials ($p = 0.990$). There was also a significant difference in displacement onset asynchrony between the predictive and reactive control modes for each trial type (all p values < 0.001).

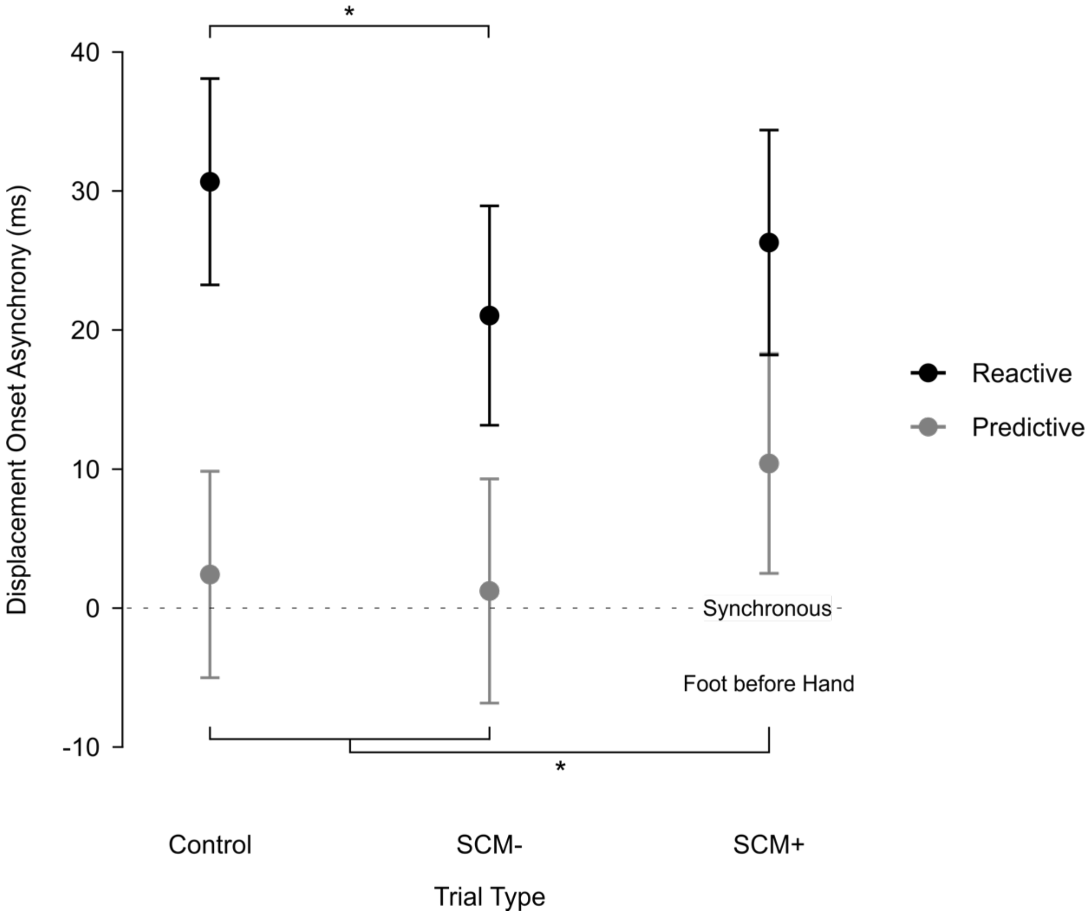

Figure 5. Displacement onset asynchrony (error bars: 95% CI) as a function of trial type (control, SCM-, SCM+) and control mode (reactive control: black; predictive control: grey). Zero-point represents synchronous displacement onset. Negative asynchrony values indicate that the foot movement preceded the hand movement. Asterisks (*) represent significant differences (p < 0.05) between the control trials and the SCM- trials in the reactive condition or between the SCM+ trials and both the control and SCM- trials in the predictive condition.

3.4 EMG Onset Time for the Wrist Extension Movement (Reactive)

Figure 6 shows EMG onset time for the wrist extension movement in the reactive condition as a function of trial type and task. LME analysis revealed a significant main effect of Trial Type (F(2,1446.5) = 397.388, $p < 0.001$), but the main effect of Task was not significant (F(1,1439.7) = 0.0174, $p = 0.895$). There was, however, a significant interaction between Trial Type and Task (F(2,1440.7) = 5.659, $p = 0.004$). Post-hoc tests for comparisons of interest indicated that there were significant differences in EMG onset time between all trial types for both the isolated and synchronous task conditions (all p values < 0.001). While there were no differences in EMG onset time between tasks in SCM- trials (p = 0.147), or in SCM+ trials (p = 0.954), there was a trend towards EMG onset time on control trials occurring earlier for the isolated task (212.0 ms, 95% CI [201.0, 224.0]) than the synchronous task (221.0 ms, 95% CI [210.0, 232.0]); however, it did not reach the threshold for significance (p = 0.055).

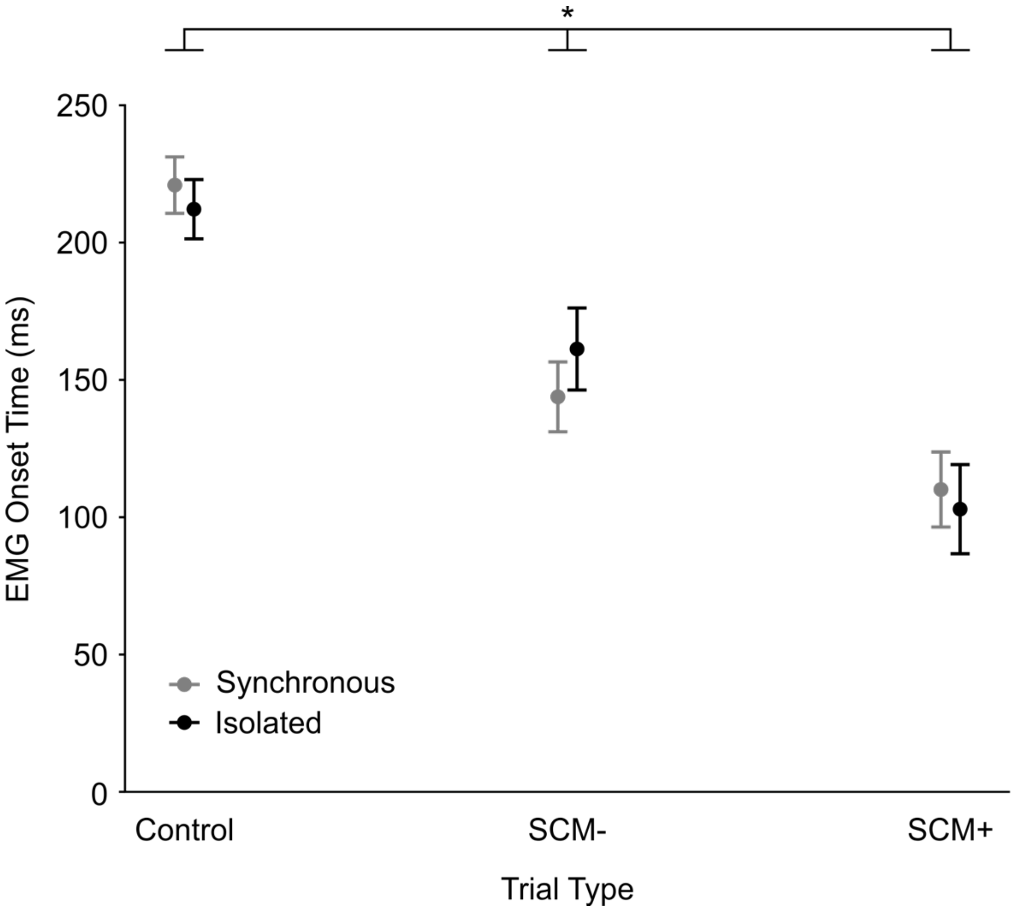

Figure 6. Estimated marginal means for EMG onset time (error bars: 95% CI) for the wrist extension movement under reactive control as a function of trial type (control, SCM-, SCM+) and task (isolated: black; synchronous: grey). Asterisks (*) represent significant differences (p < 0.05) between trial types for both the isolated and the synchronous tasks.

3.5 EMG Onset Time for the Wrist Extension Movement (Predictive)

EMG onset time for the wrist extension movement in the predictive condition is shown as a function of trial type and task in Figure 7. LME analysis revealed a significant main effect of Trial Type (F(2,1424.8) = 70.896, $p < 0.001$), where EMG onset occurred earliest on SCM+ trials (-67.4 ms, 95% CI [-80.9, -53.8]), and EMG onset on SCM- trials occurred both significantly later than SCM+ trials (-44.4 ms, 95% CI [-58.2, -30.7]), and significantly earlier than control trials (-27.0 ms, 95% CI [-39.3, -14.6]) (all p values < 0.001). There was no significant main effect of Task (F(1,1417.2) = 0.0002, p = 0.989), and no significant interaction between the factors (F(2,1417.2) = 0.308, p = 0.735).

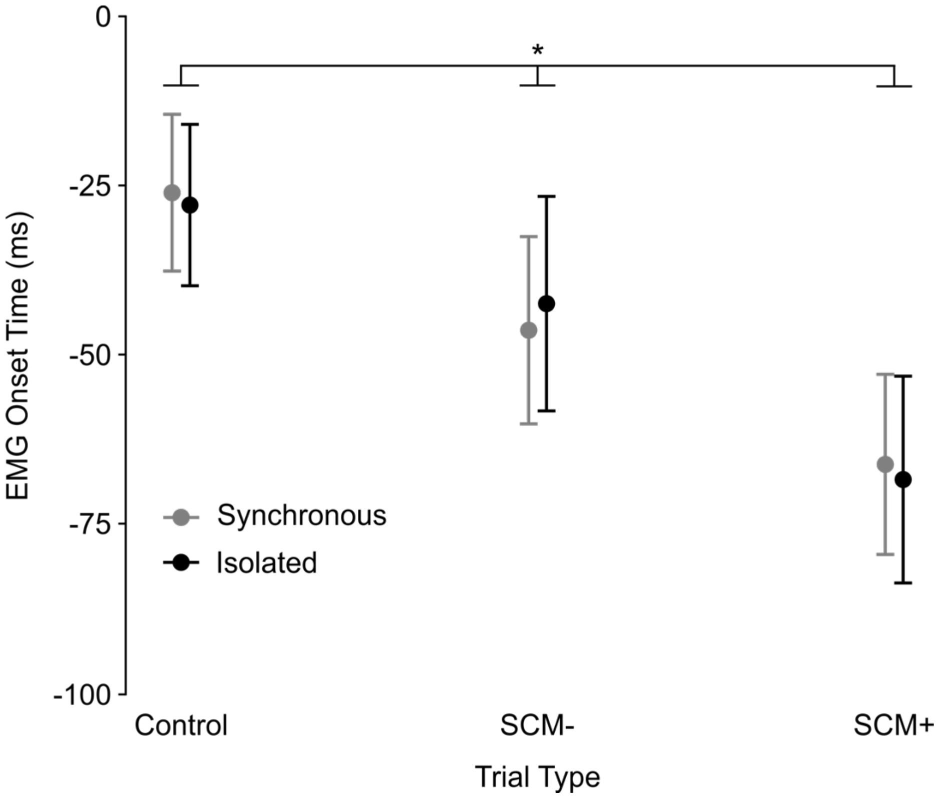

Figure 7. Estimated marginal means for EMG onset time (error bars: 95% CI) for the wrist extension movement under predictive control as a function of trial type (control, SCM-, SCM+) and task (isolated: black; synchronous: grey). Negative EMG onset time values indicate that the movement was initiated prior to the target. Asterisks (*) represent significant differences ($p < 0.05$) between trial types for both the isolated and the synchronous tasks.

3.6 Post-SAS EMG Onset for the Wrist Extension Movement

Post-SAS EMG onset for the wrist extension movement as a function of SCM response (+/-) and control mode can be seen in Figure 8. LME analysis revealed significant main effects of SCM Response (F(1,701.8) = 71.501, $p < 0.001$), and Control Mode (F(1,711.91) = 100.451, $p < 0.001$), but no main effect of Task (F(1,711.01) = 0.259, p = 0.611). LME analysis also revealed a significant interaction between SCM Response and Control Mode (F(1,717.73) = 38.123, $p < 0.001$), with post-hoc tests indicating that in the reactive control mode post-SAS EMG onset occurred at a significantly shorter latency on SCM+ trials (99.8 ms, 95% CI [85.6, 114.0]) compared to SCM- trials (158.3 ms, 95% CI [144.6, 172.0]; $p < 0.001$). In contrast, under predictive control, there was no difference in post-SAS EMG onset latency between the SCM+ trials (87.0 ms, 95% CI [73.1, 101.0]) and the SCM- trials (101.3 ms, 95% CI [87.1, 116.0]; p = 0.068). Additionally, post-SAS EMG onset occurred at a significantly shorter latency on SCM- trials in the predictive condition as compared to the reactive condition ($p < 0.001$), and while there was a trend towards post-SAS EMG onset occurring earlier on SCM+ trials in the predictive condition than in the reactive condition, it did not reach the threshold for significance (p = 0.053). LME analysis found no significant interactions between SCM Response and Task (F(1,712.39) = 1.782, p = 0.182), Control Mode and Task (F(1,710.43) = 0.438, p = 0.509), and no three-way interaction between SCM Response, Control Mode, and Task (F(1,711.85) = 1.636, p = 0.201).

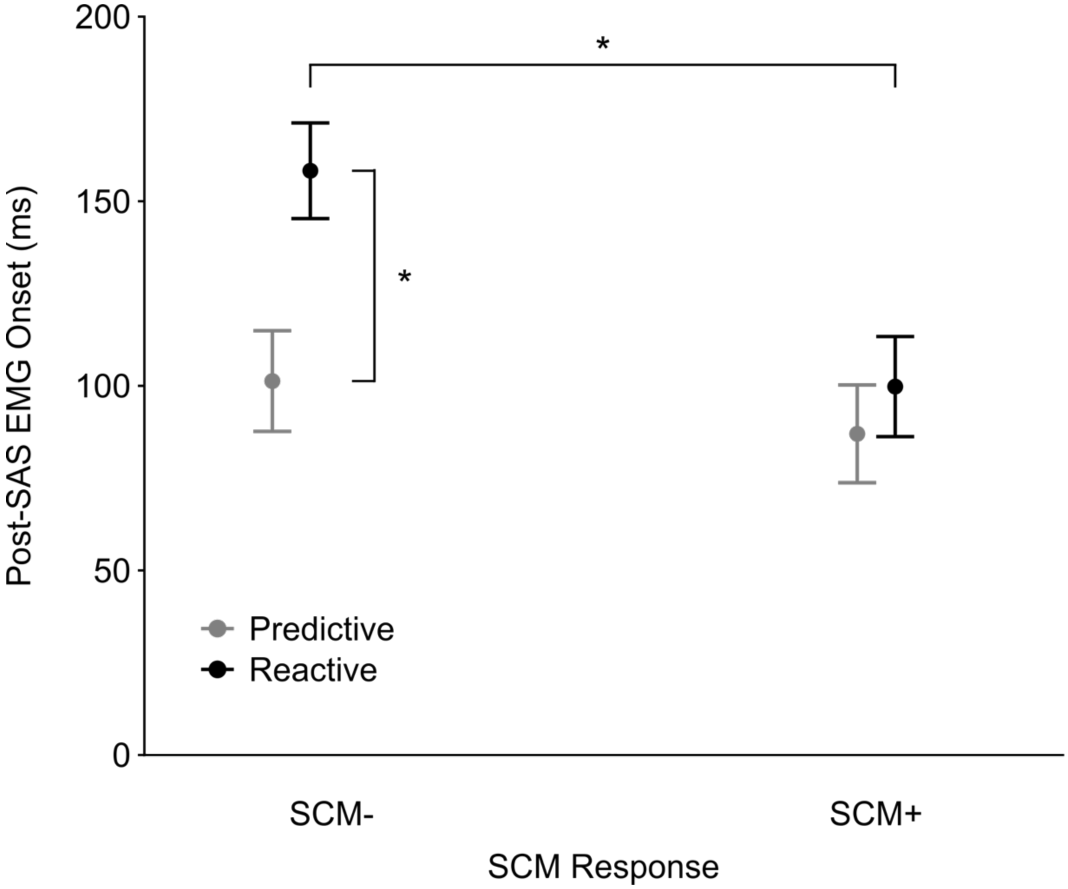

Figure 8. Estimated marginal means for post-SAS EMG onset (error bars: 95% CI) for the wrist extension movement (collapsed across tasks) as a function of SCM response (+/-) and control mode (reactive control: black; predictive control: grey). Asterisks (*) represent significant differences ($p < 0.05$) between reactive and predictive control on SCM- trials or between SCM- trials and SCM+ trials in the reactive condition.

3.7 EMG Onset Time for the Heel Lift Movement (Reactive)

Figure 9 shows EMG onset time for the heel lift movement in the reactive condition as a function of trial type and task. LME analysis revealed a significant main effect of Trial Type ($F(2,1428.2) = 566.829$, $p < 0.001$), indicating that EMG onset time occurred earliest on SCM+ trials (120.0 ms, 95% CI [108.0, 132.0]), with EMG onset time for SCM- trials occurring both significantly later than SCM+ trials (147.0 ms, 95% CI [135.0, 159.0]), and significantly earlier than control trials (229.0 ms, 95% CI [219.0, 240.0]) (all p values <

0.001). There was no main effect of Task (F(1,1419.5) = 0.009, p = 0.923), and no significant interaction between Trial Type and Task (F(2,1421.2) = 0.888, p = 0.412).

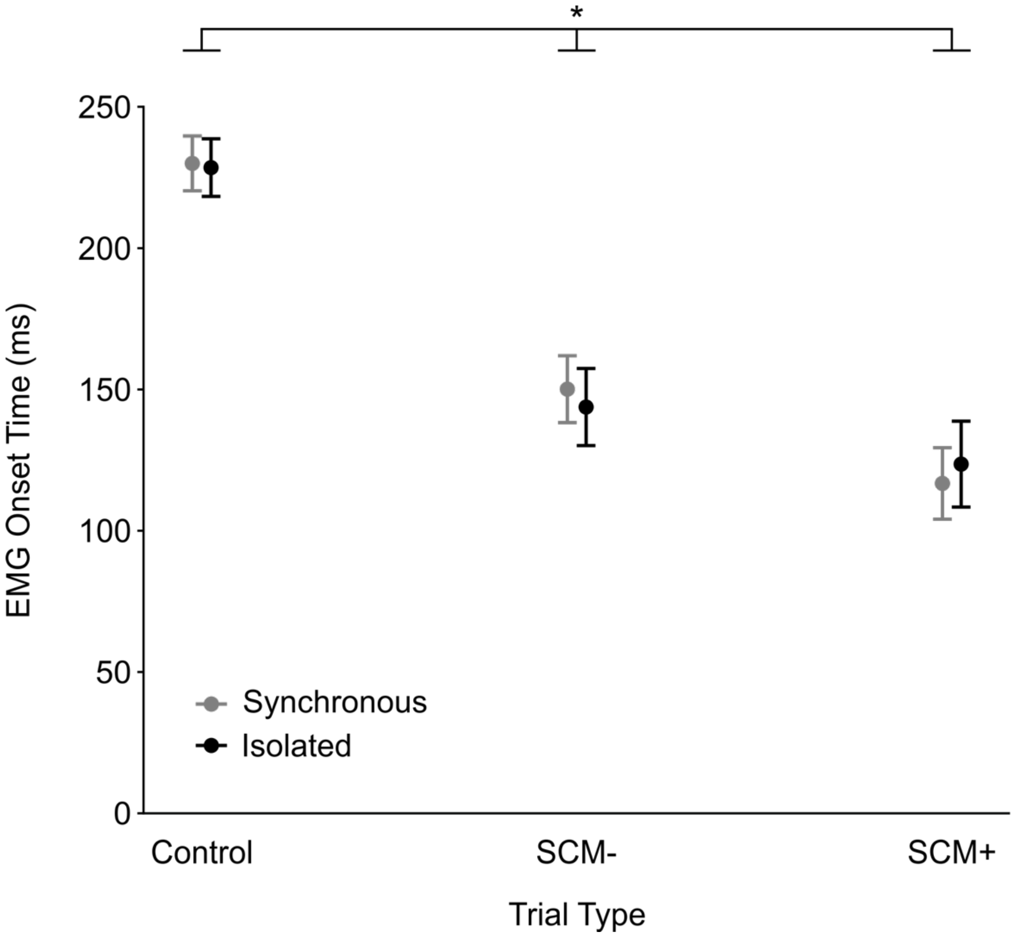

Figure 9. Estimated marginal means for EMG onset time (error bars: 95% CI) for the heel lift movement under reactive control as a function of trial type (control, SCM-, SCM+) and task (isolated: black; synchronous: grey). Asterisks (*) represent significant differences (p < 0.05) between trial types for both the isolated and synchronous tasks.

3.8 EMG Onset Time for the Heel Lift Movement (Predictive)

EMG onset time for the heel lift movement in the predictive condition is shown as a function of trial type and task in Figure 10. LME analysis revealed a significant main effect of Trial Type (F(2,1445.4) = 29.678, p < 0.001), where EMG onset occurred significantly later on control trials (-43.1 ms, 95% CI [-55.0, -31.1]) compared to both SCM- trials (-58.1

ms, 95% CI [-71.8, -44.5]; p = 0.001) and SCM+ trials (-70.7 ms, 95% CI [-84.1, -57.3]; p < 0.001), and there was a trend towards EMG onset occurring earlier on SCM+ trials than SCM- trials (p = 0.058). There was no main effect of Task (F(1,1437.9) = 0.029, p = 0.865), and no significant interaction between Trial Type and Task (F(2,1437.5) = 0.204, p = 0.815).

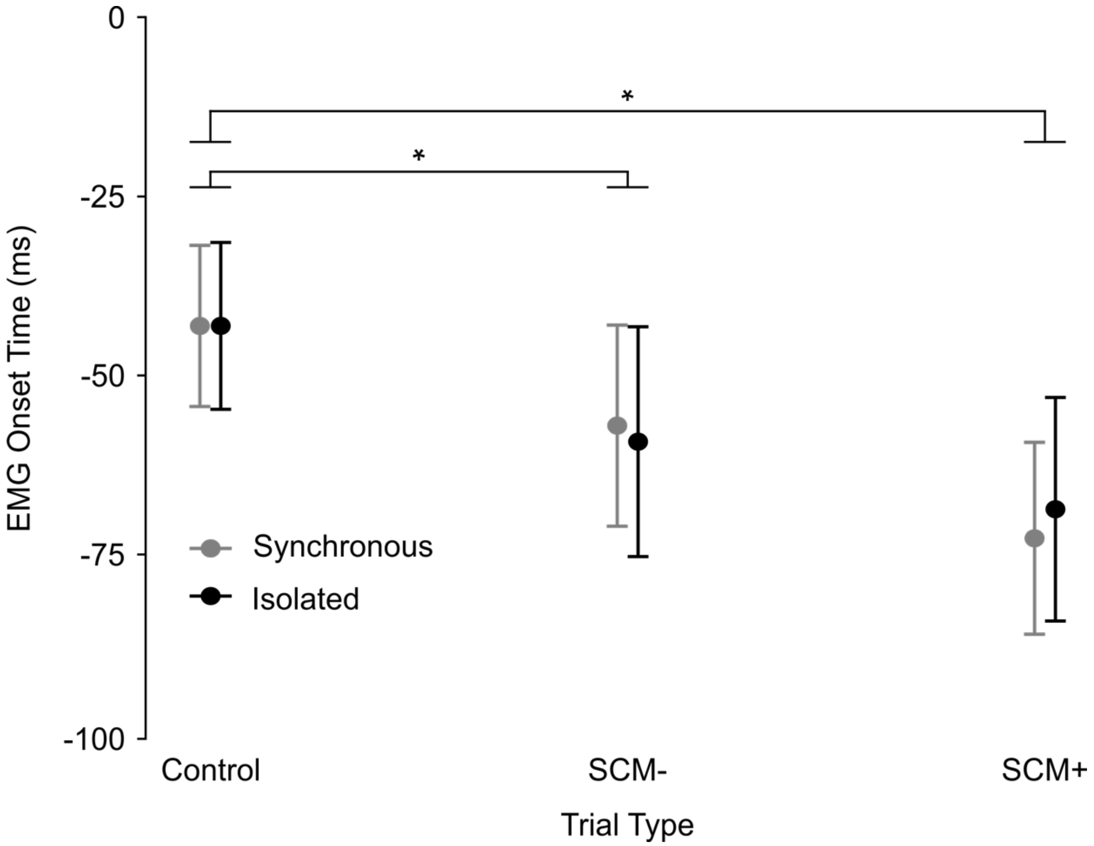

Figure 10. Estimated marginal means for EMG onset time (error bars: 95% CI) for the heel lift under predictive control as a function of trial type (control, SCM-, SCM+) and task (isolated: black; synchronous: grey). Negative EMG onset time values indicate that the movement was initiated prior to the target. Asterisks (*) represent significant differences (p < 0.05) between control trials and SCM- trials or control trials and SCM+ trials for both the isolated and synchronous tasks.

3.9 Post-SAS EMG Onset for the Heel Lift Movement

Post-SAS EMG onset for the heel lift as a function of SCM response (+/-) and control mode can be seen in Figure 11. LME analysis revealed significant main effects of SCM Response (F(1,564.90) = 33.087, $p < 0.001$) and Control Mode (F(1,723.33) = 225.632, $p < 0.001$), but no main effect of Task (F(1,719.69) = 0.021, $p = 0.884$). There was also a significant interaction between SCM Response and Control Mode (F(1,730.81) = 33.943, $p < 0.001$), with post-hoc tests indicating that post-SAS EMG onset occurred at a significantly shorter latency on reactive SCM+ trials (112.5 ms, 95% CI [102.4, 122.7]) compared to reactive SCM- trials (153.4 ms, 95% CI [144.1, 162.7]; $p < 0.001$). In contrast, under predictive control, there was no difference in post-SAS EMG onset latency between the SCM+ trials (84.1 ms, 95% CI [74.6, 93.6]) and the SCM- trials (87.4 ms, 95% CI [77.5, 97.2]; $p = 0.916$). Additionally, for both SCM- and SCM+ trials, post-SAS EMG onset occurred at a significantly shorter latency under predictive control than under reactive control (both p values < 0.001). There were no significant interactions between SCM Response and Task (F(1,724.13) = 2.384, $p = 0.123$), Control Mode and Task (F(1,719.07) = 0.066, $p = 0.798$), and there was no significant three-way interaction between SCM Response, Control Mode, and Task (F(1,725.53) = 0.002, $p = 0.966$).

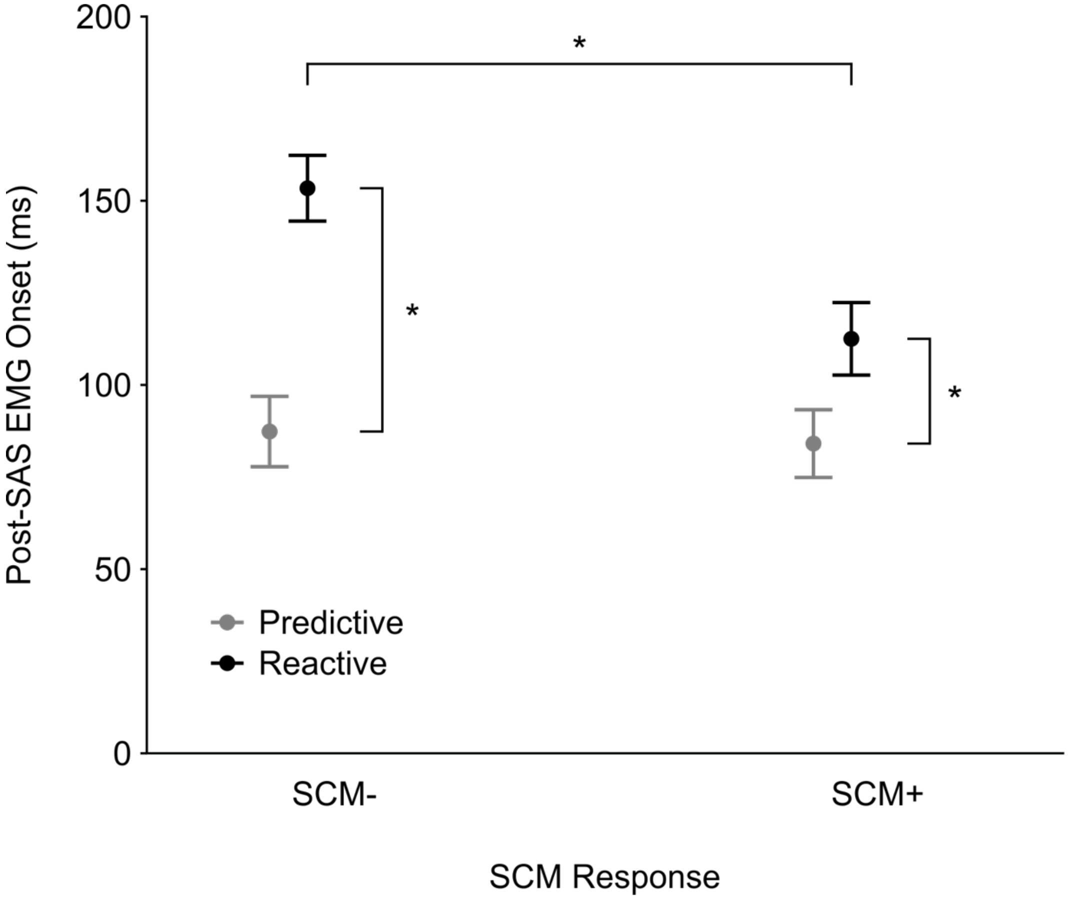

Figure 11. Estimated marginal means for post-SAS EMG onset (error bars: 95% CI) for the heel lift (collapsed across tasks) as a function of SCM response (+/-) and control mode (reactive control: black; predictive control: grey). Asterisks (*) represent significant differences ($p < 0.05$) between reactive and predictive control modes or between SCM- trials and SCM+ trials in the reactive condition.

4. Discussion

The purpose of the present experiment was to determine if synchronous hand and foot movements are planned differently under reactive versus predictive modes of control. Specifically, the experiment investigated whether the two movements are prepared as a single “package” that is initiated with a timing structure that depends on the mode of control, or whether the movements are prepared as individual components and triggered separately. In order to determine what is being prepared in advance, a SAS (114 dB) was presented 150 ms prior to the imperative stimulus on a subset of trials. Replicating previous results, greater EMG onset asynchrony was observed on the predictive control trials, whereas there was close to co-activation of the ECR and gastrocnemius muscles on the reactive control trials (Figure 4). The opposite pattern was observed for displacement onset asynchrony where the hand movement preceded that of the foot in the reactive control trials, while the movements were essentially synchronized in the predictive control trials (Figure 5). Additionally, the results of the present experiment revealed that the differential timing structures between the responses was mostly maintained under both reactive and predictive modes of control when involuntarily triggered by the SAS. However, the EMG onset asynchrony was significantly smaller on predictive SCM+ trials (Figure 4). When examining the effect of a SAS on EMG onset time in each limb, the results showed that while the SAS led to significantly earlier EMG onsets under both modes of control, there was no significant difference between either isolated task and the synchronous task. Overall, these results indicate that in both cases of the synchronous task, the individual responses are prepared and triggered as a single "package" and that the timing component, which differs between the control modes, is pre-programmed as part of that package.

Previous studies examining synchronous hand and foot movements have shown that when the synchronous movement is externally triggered, the EMG responses are synchronized in order to perform the task, but differences in the length of the efferent pathways and the muscular activity required to overcome the limb inertia results in the hand movement preceding the foot movement (Bard et al., 1992; Blouin et al., 2004). The results of the present experiment showed that the ECR muscle was activated only slightly earlier than the gastrocnemius muscle on control trials in the reactive condition, resulting in the wrist displacement preceding the heel displacement by 31 ms (Figures 4 and 5). These results support the idea that when synchronous hand and foot movements are externally triggered, the motor commands are simultaneously released through a common triggering signal to both effectors (Bard et al., 1991). With respect to the predictive condition, the results from this study revealed that the gastrocnemius muscle was activated approximately 17 ms earlier than the ECR muscle on control trials, which is consistent with previous research, and is thought to occur as the motor commands are planned and released based on the anticipated sensory consequences of the movement (Bard et al., 1991). Although previous research has shown that the foot displacement slightly precedes that of the hand on control trials in the predictive condition (Bard et al., 1991), the results from this study revealed that the predictive condition produced a less positive asynchrony compared to the reactive condition, but that the wrist extension movement still preceded the heel raising movement on control trials (Figure 5). This finding is similar to results reported by LaRue (2007) when an anticipation-timing task was used instead of a self-paced task. The author suggested that the smaller magnitude of change in terms of the asynchrony may be due to either increased variability in the anticipated perception of the alignment between the sweeping clock hand and the target, or due to the perceptual-motor processes competing with the processes involved in adjusting the release of the motor commands (LaRue, 2007).

To examine response preparation and determine what aspects of a movement are pre-programmed, researchers have used a SAS in conjunction with, or in place of the imperative stimulus to involuntarily trigger the prepared response. When a startle reflex is observed, the prepared response is thought to occur at a similar latency to the startle reflex response due to either the startle reflex pathway mediating the release of the subcortically stored response, or due to startle-related activation of initiation pathways (Carlsen & Maslovat, 2019). In the current experiment, the differential timing structures between the responses was mostly maintained under both modes of control when involuntarily triggered by the SAS. However, the EMG onset asynchrony observed on predictive SCM+ trials was significantly smaller than those on predictive control trials (-4.52 ms vs. -16.61 ms). The fact that the asynchrony is maintained suggests that the timing component is pre-programmed as part of the package. Furthermore, the smaller EMG onset asynchrony observed on predictive SCM+ trials could potentially be explained by an increase in the pacemaker rate of an internal clock (Maslovat et al., 2009). It has been suggested that when a multi-limb task includes a between-limb timing requirement, participants adopt a timing mechanism in order to perform the task (Maslovat et al., 2009). A pulse-accumulator model, put forward by Block and Zakay (1996), proposed that time duration estimation is driven by pulses produced by a neural pacemaker that accumulate until a threshold level is achieved. The authors also proposed that the rate of the pacemaker pulses is influenced by the participant's arousal level (Block & Zakay, 1996). Additionally, previous studies have shown that participants tend to underestimate time intervals when arousal levels increase due to an accelerated pacemaker (Gruber & Block, 2005; Penton-Voak et al., 1996). Based on this, Maslovat and colleagues (2009) suggested that the use of a SAS may have increased the participant's arousal level, which then sped up the pacemaker rate resulting in the shorter between-limb timing delay.

In both limbs and under both modes of control, the presentation of a SAS resulted in significant reductions in EMG onset time. More specifically, in the reactive condition, EMG onset occurred significantly earlier on SCM+ trials than on SCM- trials for both the wrist extension and heel lift movements (Figures 6 and 9). This finding is consistent with previous studies that have shown that there is a greater decrease in EMG onset time when a startle reflex is elicited compared to when it is not, providing evidence that the StartReact effect is due to activation of the startle reflex pathway and not the stimulus intensity effect (Carlsen et al., 2007; Carlsen & Maslovat, 2019). In the predictive condition, EMG onset occurred at a significantly shorter latency on SCM+ trials compared to SCM- trials for the wrist extension movement; however, there was no difference between the SCM+ and SCM- trials for the heel lift movement (Figures 7 and 10), which may have been due to a lack of power or the nature of the task. In order to initiate the heel lift movement coincidently with the clock hand reaching the target, EMG onset occurred approximately 43 ms prior to the target on control trials. Based on this timing, the window for EMG onset time modulation between SCM+ and SCM- trials was relatively small. Additionally, the results from the present experiment showed that for both control modes, there was no difference between the isolated and synchronous tasks for both the wrist extension movement and the heel lift movement. This suggests that the level of preparation was similar regardless of whether the movement was being performed in isolation or synchronously.

In conclusion, the present results suggest that when performing synchronous hand and foot movements under either reactive or predictive modes of control, the individual responses are prepared and initiated as a single “package” with a built-in timing component that depends on the control mode. Additionally, when the predictive synchronous movement is triggered by a SAS, the subsequent increase in cortical activation appears to modulate the timing resulting in a decreased between-limb delay.

Chapter 3: General Discussion

Synchronous movements of the hand and foot have previously been investigated under both reactive and predictive modes of control. It has been shown that under reactive control, the EMG responses are synchronized, resulting in the hand displacement preceding that of the foot. However, under predictive control, the motor commands are organized such that the displacement onset occurs relatively synchronously (Bard et al., 1991). The purpose of the current experiment was to investigate whether these distinct reactive and predictive EMG responses are due to differences in the pre-programmed timing initiation structure of the responses. In order to probe advance preparation, a StartReact paradigm was used as it has previously been shown that a SAS can involuntarily trigger a prepared response in association with a startle reflex (Carlsen et al., 2012). Consistent with previous literature, results from the control trials showed that under reactive control, the EMG responses were nearly co-activated, resulting in the hand displacement preceding that of the foot, whereas under predictive control, the motor commands were organized such that the displacement onset was nearly synchronized, rather than the EMG responses. Results from the startle trials revealed that the differential timing structures between the EMG responses was mostly maintained under both reactive and predictive modes of control, which suggests that the hand and foot movements are prepared and initiated as a single “package” with a pre-programmed timing delay. Additionally, the results indicate that in both limbs and under both control modes, there was no difference in EMG onset time between the isolated and synchronous tasks when a SAS was presented, suggesting that the level of preparation was similar regardless of whether the movement was performed in isolation or as part of a multi-limb synchronous movement.

Many previous studies have provided behavioural and neurophysiological evidence for advance motor preparation. For example, Leuthold and colleagues (1996) demonstrated that in a pre-cueing paradigm, when certain aspects of the upcoming movement were pre-cued, the onset of the LRP prior to the go-signal was indicative of advance response preparation. In terms of behavioural evidence, the StartReact paradigm has been shown to be an effective tool to examine motor preparation in various voluntary movements. For example, Maslovat and colleagues (2009) used a SAS to probe for advance preparation in an asynchronous bimanual movement and found that although the SAS triggered the intended movement, the increase in neural activation via the SAS significantly shortened the between-arm delay and within-arm EMG pattern as compared to the control trials. Similarly, in the current experiment, the differential timing structures between the hand and foot responses observed under both reactive and predictive modes of control was mostly maintained when involuntarily triggered by the SAS; however, the EMG asynchrony was significantly smaller on predictive SCM+ trials. These results add to our understanding of the preparation of synchronous hand and foot movements under both modes of control as it suggests that the differential timing structures of the reactive and predictive responses is pre-programmed along with the movements. Moreover, the results support the notion that the use of a SAS can significantly shorten the between-limb delay via an accelerated pacemaker as proposed by Maslovat and colleagues (2009).

1. Limitations and Future Directions

A limitation of the present experiment was the use of an anticipation-timing task in the predictive condition. Although many previous studies examining synchronous hand and foot movements have used a self-paced task in the predictive condition, using a self-paced task with the current experimental design would require participants to self-initiate the movements within a time frame and a large number of additional trials to try to deliver the SAS at a specific time point relative to the unknown initiation time in a self-paced task. Thus, in order to use a SAS to probe for advance motor preparation, an anticipation-timing task had to be used in the predictive condition. However, due to the nature of the RT and anticipation-timing tasks, EMG onset time could not be directly compared in the same manner. Future studies should look to determine if the presentation of a SAS can be consistently timed in a self-paced task to ultimately replicate the experiment by Bard and colleagues in 1991 with the StartReact paradigm. Another limitation was the time at which the SAS was delivered, as it is possible that the SAS was delivered too late to allow for EMG onset time differences between the SCM+ and SCM- trials for the heel lift movement in the anticipation-timing task. A future direction could be to repeat this experiment and deliver the SAS at time points slightly earlier than 150 ms prior to the imperative stimulus to increase the window for EMG onset time modulation in the anticipation-timing task. Lastly, the results of the present experiment indicate that the delay between the initiation of the hand and foot responses is pre-programmed under predictive control. However, it is unclear whether this initiation delay is innate, or whether it is learned with practice. Given that the current experiment used well practiced movements, an interesting addition to this study would be to use novel or uncommon movements in order to determine if the timing delay is learned.

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Appendix A

Edinburgh Handedness Inventory (Oldfield, 1971)

Your participant ID:____________

Please indicate with a one (1) your preference in using your left or right hand in the following tasks.

Where the preference is so strong you would never use the other hand, unless absolutely forced to, put a two (2).

If you are indifferent, put a one in each column (1 | 1).

Some of the activities require both hands. In these cases, the part of the task or object for which hand preference is wanted is indicated in parentheses.

Task / Object	Left Hand	Right Hand
1. Writing		
2. Drawing		
3. Throwing		
4. Scissors		
5. Toothbrush		
6. Knife (without fork)		
7. Spoon		
8. Broom (upper hand)		
9. Striking a Match (match)		
10. Opening a Box (lid)		
Total checks:	LH =	RH =
Cumulative Total	CT = LH + RH =	
Difference	D = RH – LH =	
Result	R = (D / CT) × 100 =	
Interpretation: (Left Handed: R < -40) (Ambidextrous: -40 ≤ R ≤ +40) (Right Handed: R > +40)		

Please stop