

Investigating reticulospinal contributions to tasks with postural demands

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Statement of Contributors

I, Cassandra Santangelo, declare that I have written the following thesis document in collaboration with my thesis supervisor, Dr. Anthony Carlsen, and the support of my thesis advisory committee, Dr. Dana Maslovat and Dr. Yves Lajoie.

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Abstract

Although early research of the reticulospinal tract suggested that its involvement in motor control was only in unconscious movements, recent studies using startle have provided evidence that it also contributes to voluntary movements. Furthermore, the anatomical and functional requirements of a task, such as the involvement of more proximal musculature and bilateral actions, may modulate the amount of reticulospinal contribution to voluntary movements. Specifically, the magnitude of the reaction time difference seen when a startle reflex is elicited (i.e., StartReact effect) can provide insight into the degree to which reticular structures are involved. It remains unknown whether the addition of a postural demand to a task increases reticulospinal drive relative to the same task without the postural demand. The present study used simple reaction time (RT) tasks to examine the effect of postural demand on the shortening of RT following a startling acoustic stimulus (SAS). In the lower limb task, participants executed two ankle plantar flexion tasks, one while seated and one while standing. In the standing task, participants needed to maintain whole-body balance following the voluntary movement whereas no postural demand of the lower limbs is present when participants are seated. In the upper limb task, participants executed two grip-release tasks, one with the forearm resting on a table, and one without forearm support. In the task without the support, participants needed to maintain the posture of the upper limb following grip-release. Auditory warning and “go” signals were used for all tasks. On 20% of trials the control “go” signal was replaced by a startling acoustic stimulus (SAS; 115 dB). The primary dependent measure, premotor RT, which was used to examine the StartReact effect, was measured using electromyography and analyzed using a linear mixed effects model. Given that the reticular system is thought to be a contributor to postural maintenance, it was hypothesized that voluntary movements with a postural demand would

exhibit a larger StartReact effect than similar movements without a postural requirement. The results showed that postural demand did not result in a significant difference in RT when a startle reflex was elicited by the SAS in either the calf raise nor the grip release task. Thus, it is proposed that response complexity may have confounded postural demand in that tasks with greater postural demand are also more complex. Response complexity has previously been shown to decrease one's ability to prepare motor responses, which in turn reduces susceptibility to startle. In conclusion, postural demand did not increase reticulospinal drive, instead it is proposed that the increased response complexity led to a decreased effect of startle.

List of Abbreviations

APA: Anticipatory postural adjustment

BB: Biceps brachii

CPA: Compensatory postural adjustment

EDC: Extensor digitorum communis

EMG: Electromyography

LME: Linear mixed effects

MG: Medial gastrocnemius

RT: Reaction time

SAS: Starting acoustic stimulus

SCM: Sternocleidomastoid muscle

SCM-: Trials on which a SAS was presented, and no startle reflex was observed in the SCM

SCM+: Trials on which a SAS was presented, and a startle reflex was observed in the SCM

TA: Tibialis anterior

TB: Triceps brachii

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Chapter 1: Literature Review

1. Response Programming

1.1 Information Processing Model

A dominant model of human information processing considers the human to process sensory input in a predominantly serial order such to produce an output (or response). In terms of motor control, a stimulus may be the presentation of a light or auditory tone and the response may be a movement. For example, at the start of a race, a track athlete hears the gun and responds by pushing off the starting block. In this model the cortical processes that occur between the stimulus and response are difficult to measure, but so long as the experimental design keeps most variables unchanged, response characteristics can provide insight to the processes within the “black box”. A chronometric approach uses differences in reaction time (RT), the time between the presentation of an unanticipated stimulus and response initiation, to infer changes in cortical processes.

Donders (1969) employed a “subtractive method” to try to measure the durations of various stages of human information processing using three distinct reaction time tasks. Donders suggested the presence of many possible cortical processes, including perception of a stimulus, complete conception or recognition of a stimulus, discrimination of a stimulus from other possible stimuli, and expression of will, differed between these tasks. A modern conceptualization uses terms such as stimulus identification, stimulus discrimination, response selection, and response programming to describe the processes. Donders’ first task was a simple RT task where a single stimulus was presented requiring the execution of a known movement. This task is believed to require only two stages of information processing: stimulus identification and response programming. The second task, known as a choice RT task, presented one of two

possible stimuli, each having a unique motor response, and requiring the execution of the correct response given the stimulus presented. This task requires four stages of information processing: stimulus identification, stimulus discrimination, response selection, and response programming. The last task, known as a discrimination task, also presented one of two possible stimuli, however, only one stimulus required the execution of a singular motor response. Three stages of information processing are required for this task: stimulus identification, stimulus discrimination, and response programming. Donders found that RTs were shorter within a simple RT paradigm compared to discrimination and choice paradigms and that RTs were shorter within a discrimination paradigm compared to a choice paradigm. By subtracting the RT measured in the simple task from that measured in the discrimination task the time required for the stimulus identification stage can be determined. The time required for the response selection stage can similarly be determined by subtracting the RT measured in the discrimination task from that measured in the choice RT task.

When task parameters are known, some cortical processes may occur prior to the imperative stimulus. For example, in a simple RT paradigm the motor response is known in advance, allowing for the response to be selected and prepared prior to the imperative stimulus. Since these processes no longer occur after the imperative stimulus, RT shortens. This is one explanation for the length of RTs that are observed across RT tasks; choice RT requires the most processes to occur after the imperative stimulus, therefore choice RT has the longest RTs.

1.2 Motor Program Theory

Evidence that rapidly executed movements could be completed without sensory feedback (i.e., open-loop) gave rise to research investigating advance motor programming. For example, many targeted ballistic limb movements involve a triphasic electromyography (EMG) pattern.

The pattern consists of a first burst of the agonist muscle, a second burst of the antagonist muscle, and a third, smaller, burst of the agonist muscle. Wadman et al. (1979) found that following mechanical blocking of the arm during elbow extension, the triphasic muscle activation pattern was unaffected for up to 100 ms following EMG onset. Thus blocking paradigms have previously shown that even when voluntary movement is interrupted, the triphasic EMG pattern is preserved, suggesting that the pattern is “programed” as one command and not three separate commands (Wadman et al., 1979). The idea of a “motor program” stored in memory and recalled for movement execution was first suggested by Keele (1968), who defined a motor program “as a set of muscle commands that are structured before a movement sequence begins and that allows the entire sequence to be carried out by peripheral feedback” (p.387).

Keele’s theory for motor programming suggested that movement details are specified within high level processes. However, other researchers pointed out that requiring the cortex to retrieve a specific motor program from memory for execution would be cumbersome. Hughes & Abbs (1976) presented the consideration of “motor equivalence” which represents a class of movements with varying task demands. This “context-conditioned variability” (Turvey et al., 1982) would require infinite similar motor programs under Keele’s definition of a motor program. The problem of motor novelty poses similar issues as due to the many degrees of freedom of the human, there are small differences when reproducing the same movement, each trial is slightly unique (Morris et al., 1994).

Schmidt (1975) proposed that a “generalized motor program” (GMP) may solve many of these issues. Some evidence for these GMPs came from handwriting studies by Raibert (1997) who found a pattern when participants signed their name with different effectors (dominant hand,

non-dominant hand, and foot). They suggested an action within a class (e.g., signing one's name) has consistent characteristics irrespective of task parameters (e.g., effector). GMPs are conceptualized as a general plan that can be used for a variety of similar movements, and allow for task specific parameters (such as effector) to be controlled by lower-level processing (such as the brainstem and spinal cord) (Morris et al., 1994). In this way, GMPs addressed the storage, movement variability, and movement novelty problems, and as a result, Keele later updated his definition of a motor program to be "an abstract representation of a given movement" (Keele et al., 1990).

Early versions of GMP theory stated that the relative timing of and between events of a motor task were controlled by higher-level programming as previous studies had suggested that the parameters of a movement were specified prior to motor initiation (Pew, 1974). Therefore, these relative timings would be invariant when the same motor task is executed by different effectors. However, Zelaznik et al. (1986) found that acceleration patterns were not invariant, as GPM theory suggested. Furthermore, GMP theory also did not explain the control of "free" movements which Easton (1972) suggested do not require specification from higher-level processes, as they result from gravity, momentum, and the elastic properties of soft tissue. These criticisms gave rise to the dynamical systems approach to motor control which suggested that instead of central programs specifying movement, the interaction between the motor system and the environment dictate the motor outcome. However, this approach also had its limitations as it did not explain cases in which muscle activation occurs, but no movement is produced (for examples see Latash & Gottlieb, 1991 and Wadman et al., 1979).

Motor program and dynamical system theories are not inherently mutually exclusive. Researchers have considered the possibility that both cognitive and biomechanical constraints to

motor behaviour exist. Although traditional hierarchical theories of motor control stated that stages of information processing, such as coding, motor programming, and motor initiation, occurred serially in specific regions of the cortex and descending pathways, recent suggestions of greater interconnectivity and parallel pathways provide an alternative to serial processing. Therefore, it is possible that motor programming occurs across multiple levels, with abstract motor representation components which are specified at both higher and lower levels. This would also require less processing to occur within the cortex and alleviates the need to store infinite motor programs within the cortex.

1.3 Motor Cortical Cell Assemblies

Although "motor programs" are generally considered to be an abstract representation or metaphor for how motor actions are constructed, several researchers have posited neural structures and mechanisms that may underpin their existence. Cell assembly theory suggests that motor actions are prepared by increasing the strength of synaptic connections between cortical motor neurons prior to motor output (Hebb, 1949). This neural network then acts as a functional unit (i.e., a cell assembly). During preparation for motor output, the activation of the cell assembly (a network of motor cortical cells with increased synaptic strength) increases, remaining below a threshold referred to as the "ignition point" such that only a small amount of additional activity is needed to "ignite" the assembly (Wickens et al., 1994). The neural signal to initiate the motor task is not sent forth so long as activation remains below this threshold, however, once the threshold is crossed, the activation is sufficient to release the signal for motor output to the spinal cord.

2. Descending Pathways

Once a motor command is initiated by the cortex, it is relayed via several descending pathways. Studies investigating the role of the corticospinal and the reticulospinal pathways arose from anatomical findings suggesting cortical and subcortical pathways had different termination sites (Kuypers, 1960; Kuypers et al., 1962). This led to foundational studies by Lawrence & Kuypers (1968a, 1968b) in which the descending pathways of macaque monkeys were lesioned and movement impairments were reported following each lesion. Upon first lesioning the corticospinal tract, monkeys were able to regain gross movements and movements related to gait and posture. Although the digits were still able to be used for less complex movements such as gasping and climbing, fine movements of individual digits of the hand were permanently impaired following this lesion. The researchers then lesioned the reticulospinal tract and found that gross movements of proximal muscles were impaired. This lesion also caused impairments of postural control and gait. These findings gave rise to the interest of investigating the role of the reticulospinal pathway in voluntary movement as many such movements remained intact following lesion to the corticospinal pathway. These studies also emphasized the importance of the reticulospinal pathways in contributions to postural control.

A variety of protocols exist to measure contributions of descending pathways to control of voluntary movement. Invasive procedures, such as single-neuron recordings can be used in animal studies with non-human primates and cats, require surgical interventions and the termination of the subject for dissection of the cerebral cortex (see Prentice & Drew, 2001; Riddle et al., 2009; Tapia et al., 2022 for examples). In human studies, electroencephalography recordings offer good temporal recordings, however, unspecific spatial recordings as electrodes placed on the scalp are unable to identify the depth of the activated neurons within the cortex

(Babiloni et al., 1995). On the other hand, magnetic resonance imaging provides good spatial recordings, but poor temporal recordings as time is required for blood flow to change within the cortex (Sturzbecher & de Araujo, 2012). The aforementioned methods can be expensive and time consuming; however, as an alternative, some recent studies have employed a startle reflex to examine contributions of the reticulospinal tract to voluntary movements.

3. The Startle Reflex

The startle reflex is a neurophysiological response to a startling stimulus (Landis & Hunt, 1939). Although the response may be observed following a variety of stimulus modalities including tactile, vestibular, and visual, the response is most reliable following a startling acoustic stimulus (SAS) (Yeomans & Frankland, 1996). The behavioural response was characterized by Landis & Hunt (1939) as hunching of the shoulders and flexion of the neck muscles, thereby acting as an adaptive protective response of the neck to unexpected attacks from behind. Although an eyeblink is typically considered to be part of the startle response, studies have suggested that the blink reflex may in some cases be independent of the startle reflex (Brown et al., 1991). Thus, an alternative primary indicator of the startle response is a short latency burst of EMG activity in sternocleidomastoid (SCM). This muscle has been shown to be the most consistently activated and to have the shortest latency of alternative indicators (latency: 40.4 ms – 136.0 ms; mean = 58.3 ms; Brown et al., 1991).

The conduction pathway of the human startle reflex has been proposed to originate in the cochlear nuclei which then activates the caudal reticular formation of the brainstem. The giant neurons of the nucleus reticularis pontis caudalis then relays the signal to motoneurons of the spinal cord and brainstem along the reticulospinal tract (Yeomans & Frankland, 1996).

4. The StartReact Effect

Recent studies that have used a startling acoustic stimulus (SAS) within a simple RT paradigm to investigate motor preparation have shown that when a SAS elicits a startle reflex the prepared response is involuntarily triggered at short latency. This phenomenon, known as the StartReact effect, can be used to investigate preparation of a voluntary movement. Interestingly, Valls-Solé et al. (1999), used wrist flexion and extension movements within a StartReact paradigm, and found that when a SAS was presented response latency was shorter than what could be explained using the typical cortical pathways. Moreover, because the relative timing of the triphasic muscle bursts associated with the movements was preserved, it was suggested that details of EMG pattern were stored as a single motor plan whose release was triggered by the SAS.

4.1 Mechanisms of the StartReact Effect

Valls-Solé et al. (1999) found that when a SAS is presented prior to an imperative stimulus, premotor RT is shorter than the normal calculated time required for a movement to be conducted by way of the corticospinal tract. Thus, these researchers hypothesized the reticulospinal tract as an alternative pathway that may conduct the motor plan. Specifically, the authors proposed a subcortical storage hypothesis in which details of the motor plan are stored in the reticular formation of the brainstem and when a SAS is presented prior to or in place of a control stimulus, it elicits the startle reflex which activates these same subcortical structures, triggering the release of the motor plan without the usual command from the cortex (Valls-Solé et al., 1999). The involuntary release of a pre-planned motor response following a SAS has been replicated for various movements (for examples see Carlsen et al., 2004a; Castellote et al., 2007; MacKinnon et al., 2007).

Another proposed explanation for this phenomenon was that the SAS increased general neural excitability, resulting in the shorter latencies observed (Valls-Solé et al., 1995). This hypothesis was investigated by Carlsen et al. (2004a) using simple and choice RT tasks. Since participants would know the required response before stimulus presentation in a simple RT paradigm, they could presumably prepare their movement in advance. However, the required response in a choice RT task is not known in advance, thus participants are only able to prepare their movement once the imperative stimulus is presented. If the StartReact effect was the result of increased general neural excitability, no difference in the amount of RT shortening (i.e., decrease in premotor reaction time) would be observed between RT tasks. However, what the researchers found is that the SAS only decreased RT for the simple RT task and not the choice RT task. This finding was thought to provide further evidence in support of the subcortical storage hypothesis as only the task allowing for a motor response to be pre-programmed was facilitated by startle. Additional evidence for a stored motor plan came from Carlsen et al. (2004b) where participants completed 20, 40, and 60 degree wrist extension tasks within a simple RT paradigm. When compared to a control stimulus, responses triggered by the SAS maintained EMG phasic patterns and movement characteristics. Therefore, the executed movements were indeed task-specific motor plans.

Further evidence for the involvement of subcortical structures in the StartReact effect comes from research involving patient populations. Reaction times of patients with hereditary spastic paraplegia, which causes degeneration of the axons of the corticospinal tract, were not different to those of control participants following a SAS (Nonnekes, Oude Nijhuis, et al., 2014). Similar results have been reported in chronic stroke (Coppens et al., 2018; Honeycutt & Perreault, 2012) and Parkinson's disease populations (Carlsen et al., 2013; Nonnekes, Geurts, et

al., 2014). These findings suggest that an alternative pathway may indeed be involved as these patients have damage to their corticospinal pathway, however, no deficit in RT is observed following the SAS.

Although the evidence in support of the subcortical storage hypothesis is compelling, studies have also shown the importance of cortical contributions to the StartReact effect. Alibiglou & MacKinnon (2012) used transcranial magnetic stimulation to induce a silent period within the cortex and found that reaction time following the presentation of a SAS was significantly longer than presenting SAS without the silent period. This critical finding suggests some involvement of the cortex in the StartReact effect. This led researchers to hypothesize that the SAS, which activates the startle reflex pathway, also increases the activation of initiation processes within the cortex by way of nearby subcortical structures. As previously discussed, cell assembly theory suggests that during motor preparation the activation of specific cortical motor neurons is increased, requiring only a small amount of additional activity to release the motor response. It has been suggested that the SAS may provide this additional activity during a StartReact paradigm, thereby triggering the release of the “motor program” which is stored in the cortex (Carlsen et al., 2012).

The effect of stimulus intensity has been considered to have a confounding impact on StartReact studies as it is well known that RT is shorter when louder auditory stimuli are presented (Woodworth, 1938). However, Carlsen et al. (2007) provided evidence that the StartReact effect is distinct from stimulus intensity effects by presenting stimuli between 82 dB – 124 dB during a simple RT task. They found that RT is significantly shorter when a startle reflex is confirmed (SCM+) compared to when it is not (SCM-), irrespective of which stimulus intensity was presented. Therefore, many studies have followed recommendations of using short

latency EMG activation in SCM to confirm the startle reflex (Carlsen et al., 2011), and thus the activation of the reticular formation, following the presentation of a SAS – although some continue to argue that this is not necessary (see Carlsen & Maslovat, 2019).

A recent review regarding the mechanisms of the StartReact effect by Carlsen & Maslovat (2019) proposed a hybrid mechanism which considers both cortical and subcortical contributions to the StartReact effect. They suggest motor preparation occurs at various levels of the central nervous system including the cortex, subcortical structures, and the spinal cord, and that these contributions to response programming may be dependent on specifics of the task. Specifically, they argued that the relative contribution of the reticulospinal tract to a movement may be modulated by task parameters as the reticulospinal system is thought to contribute more to particular actions such as those involving flexion, proximal movements, and posture. For example, a recent study by Maslovat et al. (2023) used the StartReact effect to investigate relative reticulospinal contribution to proximal (upper arm) and distal (finger) bilateral abduction movements. They reported a greater StartReact effect, and therefore greater reticulospinal drive, for the proximal task when compared to the distal task. Similarly, when a finger pinch task is performed alone no StartReact effect was observed, whereas when an elbow flexion task was combined with a finger pinching task a StartReact effect was observed, thus demonstrating that the addition of more proximal task elements may also increase reticulospinal drive (Castellote & Kofler, 2018). Moreover, Smith et al. (2019) found that a wrist flexion task involved greater relative drive from the reticulospinal tract than a wrist extension task, and by (Maslovat et al., 2020) who found that a bilateral finger abduction task has greater contribution from the reticulospinal tract than does a unilateral finger abduction task. The reticulospinal system is also

thought to play a greater role in postural control, which tends to be more unconsciously mediated.

5. Anticipatory Postural Adjustments (APAs)

Voluntary movements, especially those involving the movement of a body segment, may displace whole-body centre of pressure (CoP). These focal movements can be thought of as “self-initiated perturbations” (Aruin, 2002) as they may displace CoP outside of the base of support, thus disturbing the balance equilibrium. To maintain whole-body balance in these situations, the body makes what are called “postural adjustments”. Postural adjustments which occur prior to the onset of the focal movement are known as anticipatory postural adjustments (APAs). Alternatively, postural adjustments which occur after the onset of the focal movement are called compensatory postural adjustments (CPAs). APAs are thought to reduce the impact of the perturbations caused by the voluntary movement (Bouisset & Zattara, 1987; Massion, 1992), whereas CPAs aim to restore equilibrium following the focal movement (S. M. Henry et al., 1998). Motor responses may include either APAs or CPAs or both depending on the task at hand (Bouisset & Zattara, 1987).

Two models have been proposed to explain the preparation of APAs. A first model suggests that APAs are prepared as a component of the focal movement they accompany, rather than as an additional command (Aruin & Latash, 1995). Findings from bimanual load-lifting tasks support this model as they suggest that the relative timing between the onset of the APA and the focal movement is preserved (Massion, 1994; Paulignan et al., 1989). Moreover, it was found that the timing between the APA and voluntary movement is preserved following the presentation of a startle acoustic stimulus during a standing rise to toe-tips task (Valls-Solé et al., 1999). An alternative model suggests that APAs are prepared independently and in parallel to the

focal movement they accompany (Massion, 1992). In support of this model, it was found that the relative onset timing of an APA and a focal movement is dependent on the mode of control (Lee et al., 1987). During a RT paradigm onset of the APA and the focal movement were simultaneous, whereas during a self-paced paradigm onset of the APA proceeded onset of the focal movement. Furthermore, it was found that a startling acoustic stimulus elicits the release of APAs for both imagined and executed grip release tasks, but focal responses were only involuntarily released for executed and not imagined tasks (Eagles et al., 2015).

Where APAs are thought to be preplanned based on predicted movement outcomes, CPAs are thought to be the result of sensory feedback mechanisms (Alexandrov et al., 2005). However, both postural responses are dependent on characteristics of the voluntary movement such as the magnitude and direction of the focal movement (Aruin & Latash, 1995, 1996; Dimitrova et al., 2004) as well as whole-body stability prior to the movement (Aruin et al., 1998; S. M. Henry et al., 2001). Interestingly, in an environment of little stability an APA may be viewed as an additional perturbation to the perturbation caused by the focal movement. In turn, the body may be unwilling to generate APAs and may instead chose to rely on CPAs (Aruin et al., 1998). Therefore, for APAs to be measurable, the magnitude of the perturbation caused by the voluntary movement must be large enough to require a preplanned postural adjustment and the body must not be in a state of postural instability prior to movement onset.

6. General Introduction

The role of the reticulospinal tract in postural control has been well-documented, however, it remains unknown whether the postural demand of a task is a parameter which modulates reticulospinal drive. Axial muscles typically have a greater role in maintenance of posture and balance than do muscles of the appendicular skeleton, however, these more distal

muscles can be involved in postural control both for maintenance of balance and for maintaining within-limb postures. When standing, the gastrocnemius contributes to whole-body posture, and the triceps brachii can contribute to maintenance of upper limb postures. For example, when a person removes a drink off a tray being held by a waiter, the weight of the tray changes but the waiter must maintain the same upper limb posture as to not drop the remaining drinks. This, presumably, requires an anticipatory postural adjustment in the upper limb.

The current research aimed to investigate potential contributions of the reticulospinal system to tasks with different postural contexts (high and low). Although evidence suggests the reticulospinal system is involved in voluntary movements, it likely plays a greater role when postural control is involved in the task. The present study explored reticulospinal contributions of the upper and lower limbs independently. The unilateral upper limb tasks compared premotor RTs in the extensor digitorum communis during two grip release tasks, one of which requiring the maintenance of upper limb posture. The bilateral lower limb tasks compared premotor RTs of the medial gastrocnemii during standing and seated rise to tip-toes tasks. The present study proposed the use of these tasks, which are similar to those used by Valls-Solé et al. (1999) (calf raise task) and Eagles et al. (2015) (grip release task), as these authors report the observation of APAs with these tasks. If movements with greater postural demands involve greater involvement of the reticulospinal system than it was expected that the magnitude of the RT shortening effect of startle will be larger. Specifically, it is hypothesized that the tasks with greater postural demand will demonstrate a larger StartReact effect, characterized by a greater RT difference between trials in which a startle reflex is observed (SCM+) and not observed (SCM- trials), than their focal counterpart (i.e., similar tasks without postural demands).

Chapter 2: Research Article

1. Introduction

The preparation of voluntary movements can be examined using the “StartReact” effect wherein a startling acoustic stimulus (SAS) that can elicit a startle reflex is presented in place of the typical “go” signal during a simple reaction time task, and triggers the involuntary release of a planned movement. Using a SAS during simple reaction time (RT) tasks, Valls-Solé et al. (1999), confirmed activation of the reticulospinal pathway on SAS trials using EMG on the SCM and found that onset latency was shorter when the SAS was presented compared to the control stimulus, yet timing and duration of muscle bursts were conserved. These results suggest that the StartReact effect may provide specific insight into reticulospinal contributions to planned actions.

More recently, it has been suggested that task parameters may modulate reticulospinal drive, and that this, in turn, might have an influence on the StartReact effect. For example, Smith et al. (2019) applied high intensity transcranial magnetic stimulation (TMS) to induce a RT delay during a StartReact paradigm where participants executed targeted wrist flexion or extension movements. The researchers proposed that tasks which rely more heavily on corticospinal contributions would have a greater RT delay induced by TMS, whereas tasks which have greater reticulospinal drive would have a smaller RT delay. Their results showed that a larger RT delay was observed for the extension task compared to the flexion task, suggesting that the flexion task likely received greater reticulospinal drive than the extension task. Similarly, Maslovat et al. (2020) examined relative reticulospinal contributions to bimanual and unimanual finger abduction tasks using a StartReact paradigm. They compared RTs on trials where a SAS was presented and a startle reflex in sternocleidomastoid (SCM) was observed (SCM+) and where the

same SAS was presented but no startle reflex was observed (SCM-). Since the startle reflex is indicative of the activation of the reticular formation, the authors reasoned that if a task had greater reticulospinal drive, then a larger degree of RT shortening would be observed on SCM+ trials. They found that RT was only significantly shortened on SCM+ as compared to SCM- trials for bimanual movements, but not for a unimanual task, suggesting that the bimanual task has greater reticulospinal drive. Finally, Maslovat et al. (2023) used a similar StartReact paradigm to examine relative reticulospinal contributions of proximal and distal effectors. It was expected that proximal effectors would receive a larger amount of reticular drive (Prentice & Drew, 2001), which may be seen in the size of the StartReact effect. Similar to the results seen for unimanual versus bimanual actions, the magnitude of the RT shortening on SCM+ trials (as compared to SCM- trials) was greater for the proximal task, supporting the hypothesis.

It remains unknown whether other task parameters, such as increased postural demand, also modulate reticulospinal drive. The present study aimed to determine whether the magnitude of the StartReact effect is significantly larger for a task with a postural requirement compared to the same task without postural demand. It was hypothesized that a task with greater postural demand would have a larger magnitude of the StartReact effect because the reticulospinal tract is involved in maintenance of posture.

2. Methodology

2.1 Participants

Thirty healthy young adults (20 female; Mean_{age} = 21.6 years) with normal or corrected to normal vision, who self-reported being right-handed or ambidextrous, and having no history of neuromuscular disease were recruited to participate in the present study. This sample size was determined using an a priori sample size calculation completed in G*Power (Faul et al., 2009)

based on the results of Maslovat et al., 2023, from which the effect size of distal and proximal tasks on simple reaction time was calculated (Cohen's $d = 0.563$). Another study which examined simple reaction time of bimanual and unimanual tasks used a sample size of 19 participants and found an effect size of 0.612. The present study used linear mixed effects models for analyses; however, the G*Power program does not allow for sample size calculations for this type of test, therefore the power analysis was completed for a two-way repeated measures analysis of variance. This analysis determined a sample size of 10 participants would be required to reveal effects of task context on simple reaction time. However, the study used to estimate effect size included a sample size of 25 participants, and thus the present study used a sample size of 30 participants to ensure sufficient power to detect potential differences.

Participants were recruited using postings placed around the University of Ottawa, and through the Integrated System of Participation in Research (ISPR) Student Pool at the University of Ottawa. Written consent was obtained from all participants prior to their participation in the study. The study was conducted in accordance with ethical guidelines approved by the University of Ottawa's Research Ethics Board and conformed to the guidelines of the Declaration of Helsinki.

2.2 Task & Apparatus

Participants performed simple reaction time (RT) tasks using the upper and lower limbs within high and low postural demand contexts. The lower limb high postural demand task required the maintenance of whole-body posture while the upper limb high postural demand task required the maintenance of within-limb posture. In contrast, the upper and lower limb low postural demand tasks did not include an explicit postural element. Participants were presented with an auditory tone (80 dB, 200 Hz, 100 ms) which acted as a warning to prepare the required

movement. This was followed by a variable foreperiod (1500-2500 ms) prior to an auditory go-signal (Control = 82 dB; 1000 Hz, 40 ms). The Control imperative stimulus was replaced on 20% of trials by a startling acoustic stimulus (SAS = 115 dB; white noise, 25 ms). Participants were instructed to execute their response as fast as possible following the presentation of the imperative stimulus.

The SAS of 115 dB was chosen as it has been shown to result in an approximately equivalent number of trials in which a startle reflex is observed (SCM+) and not observed (SCM-) (Carlsen, 2015). Analog signals were generated using digital to analog hardware (PCIe-6321, National Instruments Inc., Austin, TX) and were amplified and presented using a loudspeaker (M54-H, MG Electronics, Inc., Hauppauge, NY) placed 30 cm behind the participant's head. The intensities of the auditory stimuli were confirmed using a precision sound level meter (Cirrus Research Optimus, CR:162C; A-weighted, impulse setting) placed at the position of the participant's left ear.

In the lower limb simple RT tasks, participants performed a calf raise while standing (high postural demand context) and while seated (low postural demand context). In the standing calf raise task participants stood with feet together (i.e., medial malleoli touching) on a force platform and performed their calf raise with their arms by their side, looking straight ahead. Participants were barefoot as footwear has been shown to modify postural responses via somatosensory information (Maejima et al., 2000). They were instructed to pause while on their toe-tips before returning to the starting position. In the seated calf raise task, the height of the chair was adjusted such that the participant's feet rested on the ground and their knees were flexed at 90 degrees. Galvanic vestibular stimulation has shown that when a participant is seated, as opposed to standing, no vestibular-evoked response is observed in the medial gastrocnemius

nor the tibialis anterior, suggesting these muscles are not contributing to the seated posture (Britton et al., 1993).

In the upper limb simple RT tasks, participants performed speeded grip releases while seated. One grip release task was performed without a place to rest the arm (i.e., unsupported; high postural demand context). Here, participants held a plunger with a 2.5-lbs weight on its distal end in their right hand with their upper arm in parallel with their torso, their elbow flexed at 90-degrees, and their wrist in a neutral position. Participants were tasked with releasing their grip on the plunger as quickly as possible in response to the imperative stimulus while also maintaining the 90-degree posture of the limb. Participants were cued to maintain a relaxed posture of the arm in order to minimize co-contraction of the arm muscles. Participants also performed the same grip release task as previously described with their forearm resting on a table (i.e., supported; low postural demand context), which minimized the postural requirement.

Participants completed 10 practice trials of each task prior to testing trials. The SAS was not presented on practice trials. Participants then completed 40 testing trials of each task (32 control and 8 SAS). Visual feedback informing participants of their reaction time was provided following each trial. Visual feedback of elbow flexion angle was provided prior to the warning stimulus and remained until the trial was completed (upper limb tasks only). A variable foreperiod of 1500-2500 ms was used in order to reduce the participant's ability to anticipate the go-signal. Participants were given the option to rest following a block of 20 trials to minimize fatigue. The SAS was not presented on the first or second trial of a block, nor immediately following another SAS trial. Task order was counterbalanced across participants. Testing sessions lasted approximately 90 minutes.

2.3 Recording Equipment

Surface electromyography (EMG) was collected using bipolar preamplified surface electrodes (Delsys Bagnoli DE-3.1; Delsys Inc., Natick, MA) connected to an external amplifier system (Delsys Bagnoli-8) via shielded cabling. Electrodes were placed on the left and right sternocleidomastoid (SCM) muscles for all tasks to confirm the presence of the startle reflex. For the lower limb tasks, EMG was placed on the muscle bellies of the right medial gastrocnemius (MG) and right tibialis anterior (TA) muscles. For the upper limb tasks, EMG was placed on the right upper limb only, on the lateral head of the triceps brachii (TB), the long head of the biceps brachii (BB), the right extensor digitorum communis (EDC). The location of EMG electrodes was determined by palpation. The skin was cleaned using an abrasive gel (Nuprep) and an alcohol swab. EMG electrodes were placed in parallel to muscle fiber orientation using two-sided adhesive tape.

An electrogoniometer (Biometrics 1707, Gwent, UK) was placed on the right arm spanning the elbow using double sided tape such that one part was secured to the lateral aspect of the upper arm and the other part to the posterior part of the forearm. A data acquisition unit (DataLink DLK900, Biometrics Ltd., Gwent, UK) with real-time analog output was connected to the goniometer. Participants were provided with real-time feedback regarding their elbow angle for the entirety of each trial.

For the lower limb tasks participants stood on or sat in front of a force platform (Kistler 9286BA) connected to an amplifier (Kistler 9865 Charge Amplifier) such that their feet were placed in the centre of the force platform. Ground reaction forces (GRFs) were collected such that the time to peak positive and negative forces in the anterior-posterior (A-P) direction could be derived. Band-pass filtered (20-450 Hz) EMG and raw GRF signals were digitally sampled at

1000 Hz (PCIe-6321, National Instruments Inc.) for 3 s starting 1 s prior to the imperative stimulus on each trial.

2.4 Data Reduction

EMG characteristics were determined from the raw data using a custom LabVIEW analysis program. EMG data for each trial was full-wave rectified, and dual-pass filtered using a 25 Hz low-pass second-order elliptic filter. EMG onset was initially determined as the first point where the rectified and filtered EMG reached a value greater than 2 standard deviations above the baseline noise and remained above this threshold for at least 20 ms. EMG offset was initially determined as the first point after peak EMG where EMG decreased below 20% of the peak value of the burst. These data were visually inspected and manually adjusted where necessary.

Time to peak A-P force was determined from the GRF raw data using a custom LabVIEW analysis program. Force data for each trial were dual-pass filtered using a 10 Hz low-pass fourth-order Butterworth filter. Peak anterior and posterior force was initially determined as the maximum and minimum force in the A-P direction, respectively. These data were visually inspected and manually adjusted where necessary.

The primary dependant variable of premotor reaction time (RT) was defined as the time from the presentation of the imperative stimulus (either Control or SAS) to the time of EMG onset in the agonist muscle. Task-related EMG measures were also examined, such as peak agonist amplitude, calculated from rectified and filtered EMG as the largest EMG amplitude in the 100 ms following EMG onset, and agonist Q_{30} , calculated as a numeric integration of the 30 ms of rectified raw EMG following EMG onset. These measures for each trial were normalized as a proportion of the participant's grand mean amplitude of that muscle in control trials.

Previous studies have shown that although the timing of EMG burst patterns remain unaffected

by a SAS stimulus, the amplitude of the agonist burst is often larger due to greater overall activity in the motor system (Carlsen & Maslovat, 2019). Startle-related EMG characteristics were also analyzed. If a startle reflex was observed in the SCM within 20-120 ms following the SAS, the trial was categorized as a SCM+ trial, whereas if a startle reflex was not observed, the trial was categorized as a SCM- trial. The incidence of the startle reflex was defined as the proportion of trials in which the SAS was presented that a startle reflex was observed (i.e., number of SCM+ trials divided by total number of SAS trials). For trials on which a startle reflex was observed (i.e., SCM+ trials), SCM onset latency, peak SCM amplitude, and SCM Q30 were determined. These measures were calculated because if greater baseline activity was present in reticular structures as a result of preparation of a task with a higher postural demand, this may result in facilitation of the startle reflex. Onset of postural adjustments was defined as the time at which EMG activity either increased or decreased 2 standard deviations above or below baseline activity for both grip release and calf raise tasks. In the grip release task postural adjustments were categorized as either a) an anticipatory postural adjustment (APA): where suppression in the BB was observed prior to voluntary movement onset, or b) a compensatory postural adjustment (CPA,) where increased activation in the TB was observed following voluntary movement onset. The incidence of APAs was defined as the proportion of trials in which an APA was observed for a given postural context. Similarly, the incidence of CPAs was defined as the proportion of trials in which a CPA was observed for a given postural context.

Practice trials were not included in analyses. Trials with the following errors were also excluded from analyses: Anticipation trials were defined as having a premotor RT faster than 50 ms (33 trials removed). Slow RT trials were defined as having a premotor RT greater than 2 standard deviations greater than the task mean (mean of all participants for each task; 118 trials

removed). Movement errors were also identified (e.g., failure to release the plunger; 29 trials removed). This resulted in a retention rate of 96.25% (4620 retained of 4800 collected).

2.5 Statistical Analyses

All variables were analyzed from the right side only. The dependent variables of premotor RT and task-related EMG amplitude measures (peak agonist amplitude and agonist Q₃₀) were analyzed for each task (upper / lower limb) separately using linear mixed effects (LME) models with interacting fixed factors of postural demand (2 levels: high and low) and stimulus type / startle reflex presence (3 levels: Control, SCM+, SCM-), with intercepts for participants specified as a random effect (e.g., [model = premotor RT ~ Context*Stimulus + (1| Participant)]). The incidence of the startle reflex between postural demand (high and low) was analyzed for the upper and lower limb tasks separately using paired samples t-tests. For SCM+ trials only, EMG characteristics of the startle reflex (SCM onset, SCM Q₃₀, and peak SCM amplitude) were analyzed using LME models with a fixed factor of postural demand (2 levels: high and low) and intercepts for subjects were specified as a random effect. Time to peak A-P forces were analyzed for the lower limb task using LME models with interacting fixed factors of postural demand (2 levels: high and low) and stimulus type / startle reflex presence (3 levels: Control, SCM+, SCM-), and intercepts for participants were specified as a random effect.

An alpha of .05 was used for all analyses. Data were screened for homoscedasticity and approximate normal distribution of residuals. All analyses were performed using the statistical software package R (4.2.1) (R Core Team, 2019). The lmerTest (Bates et al., 2015) and lme4 (Kuznetsova et al., 2017) packages were used to provide p-values for linear mixed effects analyses. The emmeans package (Lenth, 2016) was used for planned pairwise contrasts with Tukey's HSD Post-hoc correction for multiple comparisons. Therefore, data are reported as

estimated marginal means with 95% confidence intervals. For t-tests, Cohen's d values were provided as a measure of effect size using the effectsize package (Steiger, 2004). The flexplot package (Fife, 2022) was used to graph the data.

3. Results

3.1 Premotor RT

Premotor RT was compared between stimulus condition and postural contexts for the grip release (Fig. 1A) and calf raise tasks (Fig. 1B). Analysis of premotor RT in the grip release task found significant main effects of Condition ($F(2, 2273.9) = 339.78, p < .001$) and Context ($F(1, 2266.4) = 16.77, p < .001$). No interaction between the factors was observed ($p = .903$). Post-hoc analyses revealed a difference in premotor RT between SCM+ and SCM- condition (i.e. a StartReact effect) for both the supported (SCM+ mean = 98 ms, 95% CI [85.1, 101], SCM- mean = 121 ms, 95% CI [107, 133]; $p = .003$) and unsupported (SCM+ mean = 108 ms, 95% CI [93, 122], SCM- mean = 134 ms, 95% CI [122, 146]; $p < .001$) tasks.

Analysis of premotor RT in the calf raise tasks found significant main effects of Condition ($F(2, 2289.3) = 241.71, p < .001$) and Context ($F(1, 2284.1) = 1124.66, p < .001$). These effects were superseded by a significant interaction effect between the factors ($F(2, 2285.5) = 119.66, p < .001$). Post-hoc analyses revealed that in the seated task, the SCM+ (mean = 124 ms, 95% CI [107, 140]) and SCM- conditions (mean = 122 ms, 95% CI [106, 138]) were not significantly different ($p = 1$). A significant SCM+/- difference in premotor RT was observed for the standing task (SCM+ mean = 213 ms, 95% CI [196, 230], SCM- mean = 251 ms, 95% CI [235, 267]; $p < .001$).

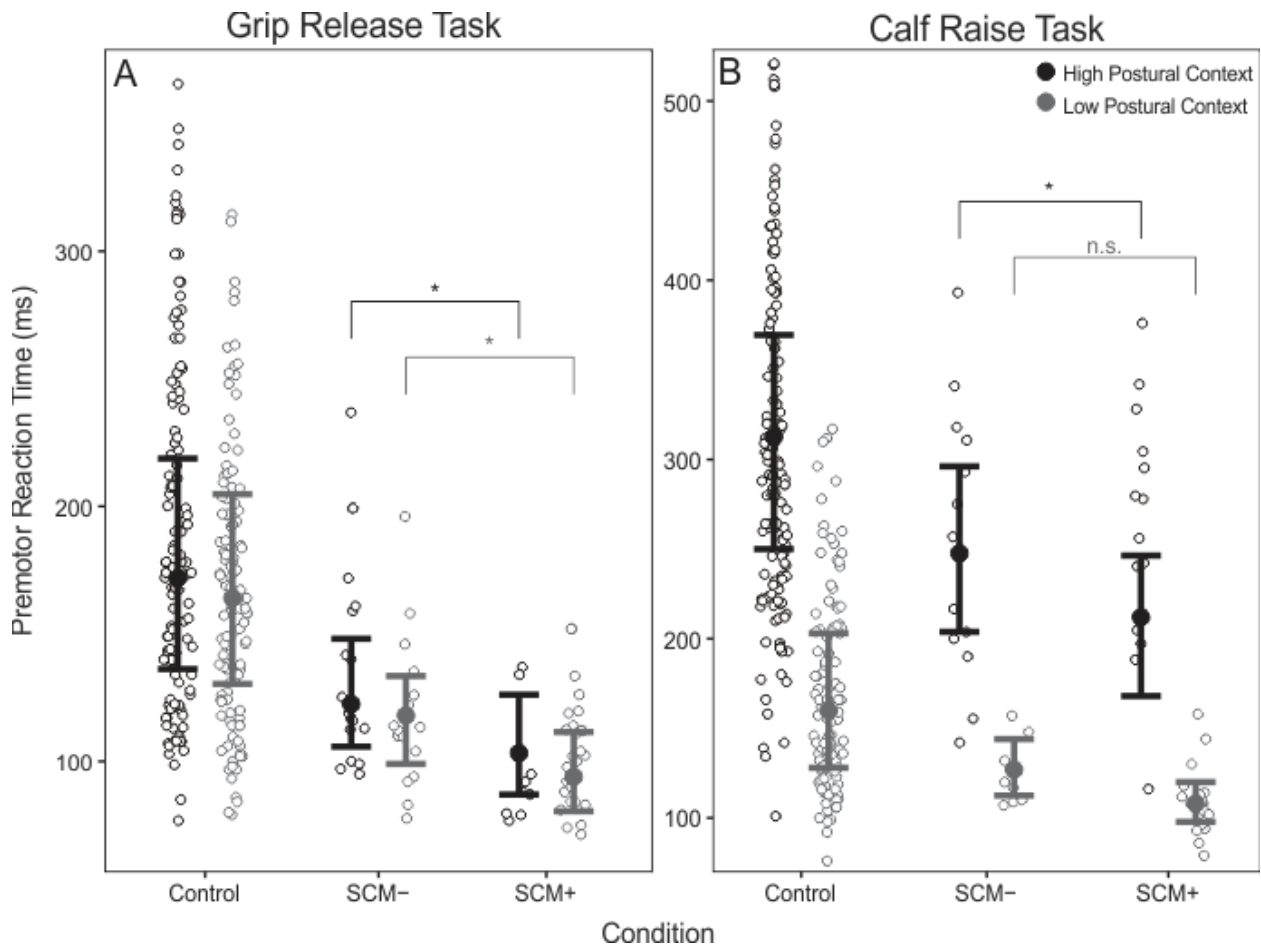


Figure 1: Premotor Reaction Time (ms) showed for Control and SAS stimulus conditions. The SAS stimulus condition is divided into responses with a startle reflex (SCM+) and ones without (SCM-). Panel (A) shows results for the grip release task and panel (B) shows results for the calf raise task. Significant differences between SCM + and SCM- conditions are indicated with an asterisk (*). Circle markers represent data points from a sample of 200 individual trials. Error bars represent quartiles.

3.2 Task-related EMG Characteristics

Task-related EMG characteristics were compared between stimulus conditions and postural context for grip release (Fig. 2A-B) and calf raise tasks (Fig. 2C-D). Analysis of peak agonist amplitude in the grip release task found significant main effects of Context ($F(1, 2266.1) = 31.92, p < .001$) and Condition ($F(2, 2267.4) = 120.52, p < .001$), however, these main effects were superseded by a significant interaction effect between the factors ($F(2, 2266.2) = 11.35, p < .001$). Post-hoc analysis revealed an SCM+/- difference in peak agonist amplitude for

unsupported grip release task (SCM+ mean = 0.342, 95% CI [0.290, 0.394]; SCM- mean = 0.287, 95% CI [0.237, 0.338]), but not for the supported grip release task (SCM+ mean = 0.330 mV, 95% CI [0.279, 0.381]; SCM- mean = 0.348 mV, 95% CI [0.297, 0.399]; Fig. 2A). Analysis of agonist Q30 in the grip release task found significant main effects of Context ($F(1, 2266.1) = 25.84, p < .001$) and Condition ($F(2, 2268.5) = 71.98, p < .001$). No interaction between the factors was observed ($p = .109$). Agonist Q30 was significantly larger for the supported (0.00444 mV*ms, 95% CI [0.00375, 0.00513]) compared to the unsupported (0.00391 mV*ms, 95% CI [0.00321, 0.00460]) grip release task ($t(2266) = -5.08, p < .001$; Fig. 2B). Post-hoc analysis revealed that agonist Q30 was significantly larger for SCM+ (0.00481 mV*ms, 95%CI [0.00409, 0.00552]) compared to SCM- (0.00421 mV*ms, 95% CI [0.00351, 0.00492]; $t(2271) = -3.71, p < .001$; Fig. 2B) conditions.

Analysis of peak agonist amplitude in the calf raise task found significant main effects of Context ($F(1, 2284.0) = 1004.56, p < .001$) and Condition ($F(2, 2286.4) = 53.84, p < .001$). No interaction effect between these factors was observed ($F(2, 2284.6) = 0.83, p = .437$). Peak agonist amplitude was significantly larger for the standing (0.334 mV, 95% CI [0.296, 0.373]) compared to the seated (0.129 mV, 95% CI [0.091, 0.167]) calf raise task ($t(2284) = 31.70, p < .001$; Fig. 2C). Post-hoc analysis revealed that peak agonist amplitude was significantly larger for SCM+ (0.270 mV, 95% CI [0.230, 0.310]) compared to SCM- (0.228 mV, 95% CI [0.189, 0.267]; $t(2289) = -4.29, p < .001$; Fig. 2C) conditions. Analysis of agonist Q30 in the calf raise task (Fig. 2D) found significant main effects of Context (lower: $F(1, 2284.1) = 617.33, p < .001$) and Condition (lower: $F(2, 2287.8) = 128.58, p < .001$); however these main effects were superseded by a significant interaction effect between the factors ($F(2, 2285.1) = 3.35, p = .035$). Post-hoc analysis revealed that in both contexts of the calf raise task, agonist Q30 was

significantly larger for the SCM+ condition compared to the SCM- condition (seated SCM+ mean = 0.002173, 95% CI [0.001742, 0.00260]; seated SCM- mean = 0.001486, 95% CI [0.001065, 0.00191]; standing SCM+ mean = 0.004207, 95% CI [0.003772, 0.00464]; standing SCM- mean = 0.003680, 95% CI [0.003262, 0.00410]).

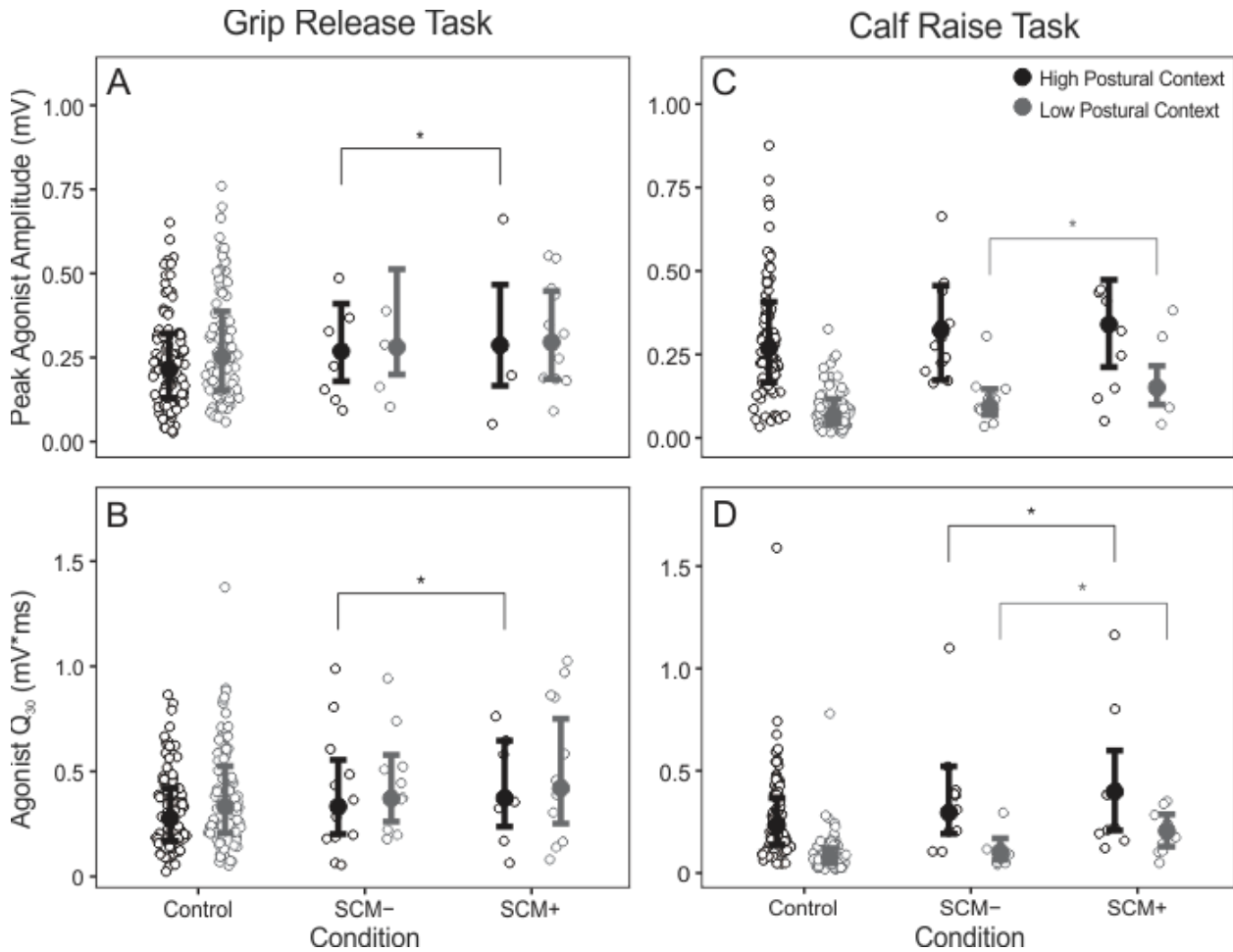


Figure 2: Task-related EMG characteristics showed for Control and SAS stimulus conditions. The SAS stimulus condition is divided into responses with a startle reflex (SCM+) and ones without (SCM-). Panels in the top row show peak agonist amplitude, whereas panels in the second-row show agonist Q30. Panels on the left show results for the grip release task and panels on the right show results for the calf raise task. Significant differences between SCM + and SCM- conditions are indicated with an asterisk (*). Circle markers represent data points from a sample of 200 individual trials. Error bars represent quartiles.

3.3 Startle-related EMG Characteristics

Startle-related EMG characteristics were compared between stimulus conditions and postural context for grip release (Fig. 3A-D) and calf raise tasks (Fig. 3E-H). Analysis of incidence of the startle reflex in the grip release task (Fig. 3A) found a significant main effect of Context ($t(29) = -3.42$, $p = .002$, $d = -0.64$) on proportion of SAS trial in which a startle reflex was observed such that a larger incidence of the startle reflex was observed for the supported grip release task (supported mean = 0.489, 95% CI [0.357, 0.620]; unsupported mean = 0.339, 95% CI [0.207, 0.471]). Analysis of SCM onset latency in the grip release task (Fig. 3B) found a significant main effect of Context ($F(1, 178) = 4.28$, $p = .040$) such that shorter SCM onset latencies were observed for the unsupported task (mean = 78.6, 95% CI [70.7, 86.5]) compared to the supported task (mean = 84.3, 95% CI [76.8, 91.7]). Analysis of peak SCM amplitude in the grip release task (Fig. 3C) found a significant main effect of Context ($F(1, 1182.38) = 9.58$, $p = .002$), such that a larger peak SCM amplitude was observed for the supported (mean = 0.1004 mV, 95% CI [0.0609, 0.1399]) compared to the unsupported task (mean = 0.0524 mV, 95% CI [0.0609, 0.1399]). Analysis of SCM Q30 in the grip release task (Fig. 3D) found no significant main effect of Context ($F(1, 183.26) = 3.06$, $p = 0.082$).

Analysis of incidence of the startle reflex in the calf raise task found no significant main effect of Context ($t(29) = -0.48$, $p = .637$, $d = -0.09$) on the proportion of SAS trials in which a startle reflex was observed (seated mean = 0.461, 95% CI [0.334, 0.589]; standing mean = 0.433, 95% CI [0.306, 0.561]) (Fig. 3E). Analysis of SCM onset latency in the calf raise task found a significant main effect of Context ($F(1, 188.88) = 9.99$, $p = .002$) such that the standing task (mean = 82.0, 95% CI [74.1, 89.9]) had shorter SCM onset latencies than the seated task (mean = 88.7, 95% CI [80.8, 96.5]) (Fig. 3F). Analysis of peak SCM amplitude in the calf raise task found

a significant main effect of Context ($F(1, 195.3) = 15.19, p < .001$), such that a larger peak SCM amplitude was observed for the seated (mean = 0.1478 mV, 95% CI [0.0949, 0.201]) task compared to the standing task (high postural mean = 0.0524 mV, 95% CI [0.0609, 0.1399]) (Fig. 3G). Analysis of SCM Q30 in the calf raise task found a significant main effect of Context ($F(1, 198.9) = 21.46, p < .001$), such that a larger SCM Q30 was observed for the seated task (mean = 0.001771, 95% CI [0.001259, 0.00228]) compared to the standing task (mean = 0.000809, 95% CI [0.000287, 0.00133]) (Fig. 3H).

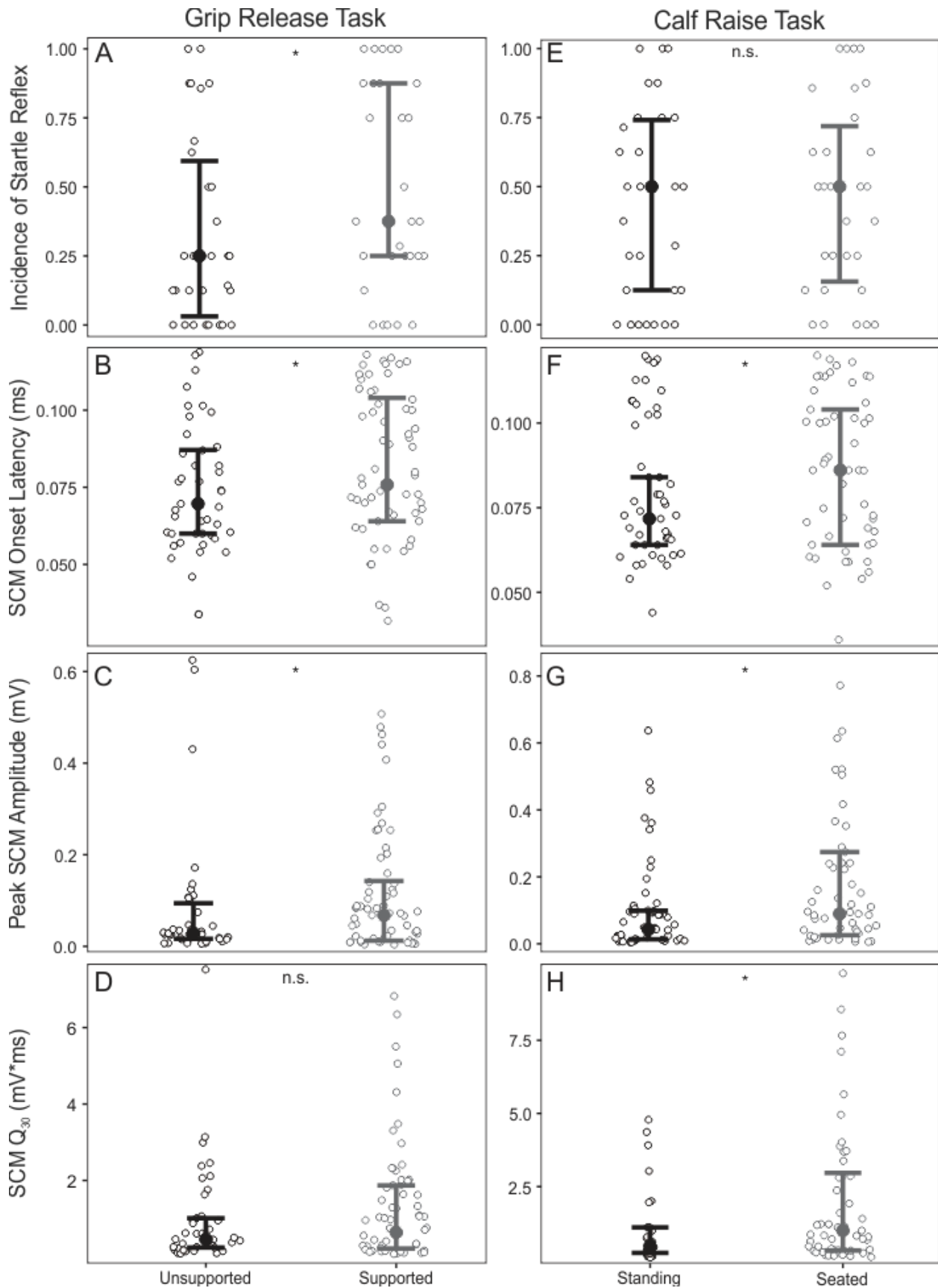


Figure 3: Startle-related EMG characteristics showed for high and low postural contexts. Panels in the top row show incidence of the startle reflex, panels in the second-row show onset latency of the SCM, panels in the third-row show peak SCM amplitude, and panel in the last row show SCM Q30. Panels on the left show results for the grip release task and panels on the right show results for the calf raise task. Significant differences between postural contexts are indicated with an asterisk (*). Circle markers represent data points from a sample of 200 individual trials (all data shown for incidence of startle reflex). Error bars represent quartiles.

3.4 Time to Peak Ground Reaction Forces

Time to peak positive and negative GRFs in the anterior-posterior direction were compared between stimulus conditions and postural context for the calf raise tasks (Fig. 4). Analysis of time to peak negative force found significant main effects of Context ($F(1, 2284.1) = 12672.57, p < .001$) and Condition ($F(2, 2291.5) = 23.64, p < .001$). Moreover, these effects were superseded by a significant interaction between the factors ($F(2, 2286.1) = 35.09, p < .001$). Post-hoc analysis revealed that in the standing task a significantly shorter time to peak positive force was observed for SCM+ compared to SCM- trials (SCM+ mean = 148.18 ms, 95% CI [134.87, 161.5]; SCM- mean = 171.11 ms, 95% CI [158.63, 183.6]; $p = .006$). No difference was observed in the seated task (SCM+ mean = 18.73 ms, 95% CI [5.61, 31.8]; SCM- mean = 6.88 ms, 95% CI [-5.77, 19.5]; $p = .451$; Fig. 3A). Similar results were found for analysis of time to peak positive force, such that significant main effects were found for Context ($F(1, 2284.1) = 3902.05, p < .001$) and Condition ($F(2, 2291.5) = 44.44, p < .001$). These effects were superseded by a significant interaction effect between the factors ($F(2, 2286.2) = 31.29, p < .001$). Post-hoc analysis revealed a significant difference in time to peak positive force between SCM+ and SCM- trials for the standing task (SCM+ mean = 241.5 ms, 95% CI [226.9, 2561]; SCM- mean = 264.2, 95% CI [250.4, 277.9]; $p = .020$) but not the seated task (SCM+ mean = 59.6 ms, 95% CI [45.2, 74.0]; SCM- mean = 48.0 ms, 95% CI [34.1, 61.9]; $p = .582$) (Fig. 4B).

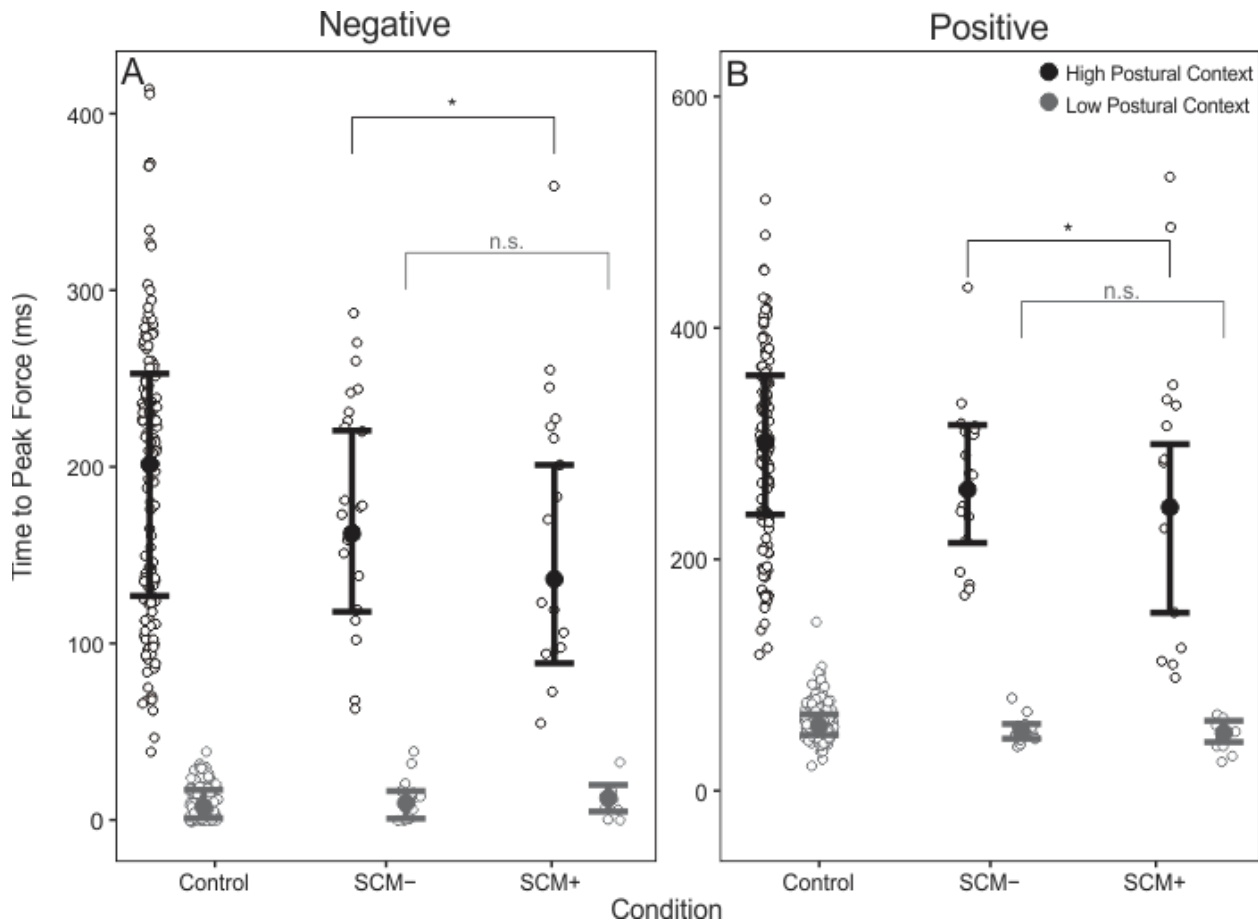


Figure 4: Times to peak negative (A) and positive (B) force (ms) showed for Control and SAS stimulus conditions. The SAS stimulus condition is divided into responses with a startle reflex (SCM+) and ones without (SCM-). Significant differences between SCM + and SCM- conditions are indicated with an asterisk (*). Circle markers represent data points from a sample of 200 individual trials. Error bars represent quartiles.

3.5 Postural Adjustments

3.5.1 Onset Latency

Onset latencies of postural adjustments were compared between stimulus conditions and postural context for the grip release (Fig. 5) and calf raise tasks (Fig. 6). Postural adjustments in the grip release task were grouped as either anticipatory postural adjustments (APAs) if suppression in the BB muscle was observed prior to voluntary movement onset or compensatory postural adjustments (CPAs) if increased activation of the TB muscle was observed after

voluntary movement onset. Analysis of onset latency of APAs in the grip release task found a significant main effect of Condition ($F(2, 92.61) = 10.5328, p < .001$), but no significant effect of Context ($F(1, 297.77) = 0.7054, p < .402$). Furthermore, a Condition by Context interaction effect was found ($F(2, 291.52) = 3.80, p = .023$). Post-hoc analysis revealed in the unsupported grip release task APA onset latency was significantly shorter for SCM+ compared to SCM- trials (SCM+ mean = 92.5 ms, 95% CI [63.9, 121]; SCM- mean = 139.2 ms, 95% CI [116.5, 162]; $p = .9995$). Alternatively, in the supported grip release task, no difference in APA onset latency between SCM+ and SCM- trials was found (SCM+ mean = 151.8 ms, 95% CI [85.1, 218]; SCM- mean = 140.3 ms, 95% CI [109.0, 172]; $p = .0399$) (Fig.5A). Analysis of onset latency of CPAs in the grip release task found significant main effects of Context ($F(1, 910.88) = 20.7029, p < .001$) and Condition ($F(2, 911.81) = 178.9059, p < .001$). No interaction effect between the factors was found ($p = .7079$). Post-hoc analysis revealed that CPA onset latency was significantly shorter for SCM+ compared to SCM- trials in the supported (SCM+ mean = 128, 95% CI [112, 143]; SCM- mean = 155 ms, 95% CI [139, 170]; $p = .0114$) and unsupported (SCM+ mean 143 ms, 95% CI [122, 163]; SCM- mean = 180 ms, 95% CI [164, 196]; $p = .0053$) grip release tasks (Fig.5B).

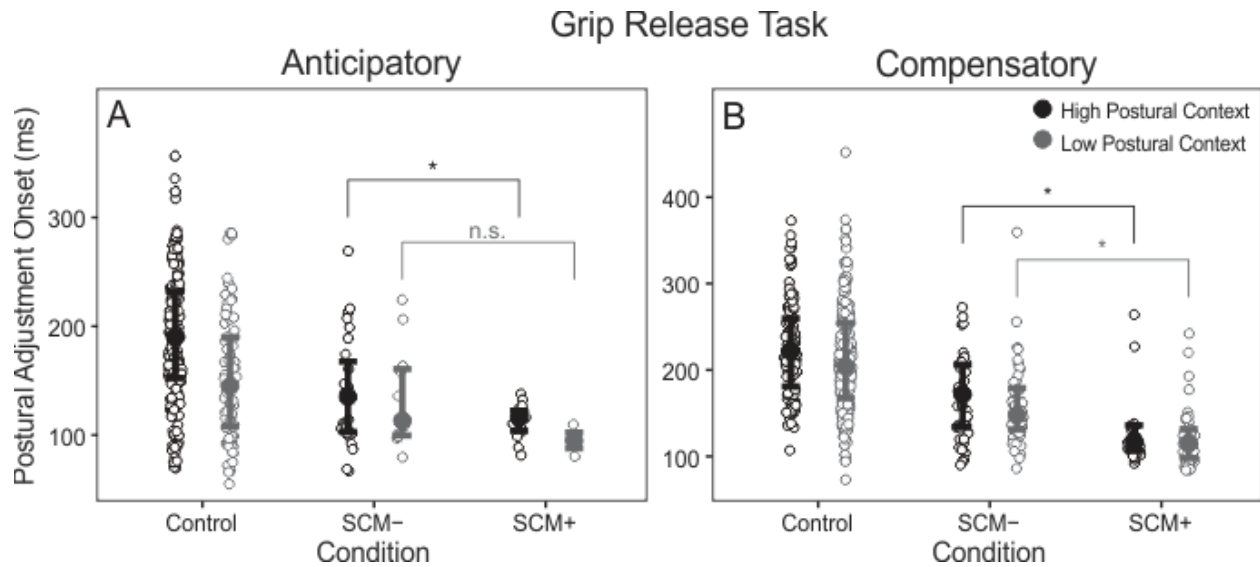


Figure 5: Onset latency for anticipatory (A) and compensatory (B) postural adjustments (ms) for the grip release task showed for Control and SAS stimulus conditions. The SAS stimulus condition is divided into responses with a startle reflex (SCM+) and ones without (SCM-). Significant differences between SCM + and SCM- conditions are indicated with an asterisk (*). Circle markers represent data points from a sample of 200 individual trials. Error bars represent quartiles.

Analysis of onset latency of postural adjustments in the calf raise task found significant main effects of Context ($F(1, 2284.1) = 229.40, p < .001$) and Condition ($F(2, 2291.6) = 204.87, p < .001$). These effects were superseded by a significant interaction effect between the factors ($F(2, 2286.2) = 5.10, p = .006$). Post-hoc analysis revealed no significant difference in postural adjustment onset latency between SCM+ and SCM- conditions for both the standing (SCM+ mean = 87.6 ms, 95% CI [76.2, 99.1]; SCM- mean = 95.3 ms, 95% CI [76.2, 99.1]; $p = .748$) and seated (SCM+ mean = 122.3 ms, 95% CI [111.1, 133.6]; SCM- mean = 132.1 ms, 95% CI [121.3, 143.0]; $p = .501$) calf raise tasks (Fig. 6).

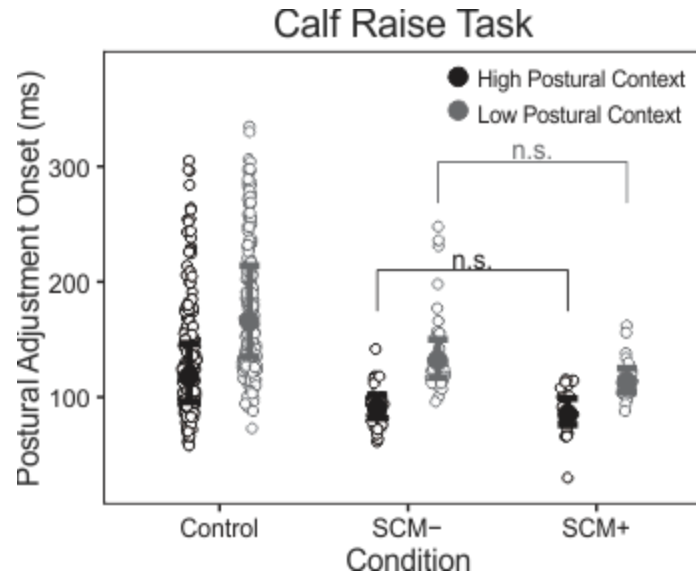


Figure 6: Onset latency for postural adjustments (ms) for the calf raise task showed for Control and SAS stimulus conditions. The SAS stimulus condition is divided into responses with a startle reflex (SCM+) and ones without (SCM-). Significant differences between SCM + and SCM- conditions are indicated with an asterisk (*). Circle markers represent data points from a sample of 200 individual trials. Error bars represent quartiles.

3.5.2 Incidence of Postural Adjustment Types

The incidence of postural adjustment types was compared between postural contexts for the grip release (Fig. 7A-B). Analysis found a larger proportion of APAs for the unsupported (19.8%, 95% CI [12.7, 27.0]) compared to the supported (8.0%, 95% CI [0.8, 15.1] task ($t(29) = 2.48, p = .019, d = 0.46$; Fig. 7A). Analysis of the incidence of CPAs in the grip release task found a significantly smaller proportion of CPAs for the unsupported (30.5%, 95% CI [20.4, 40.5]) compared to the supported (55.8%, 95% CI [45.8, 65.9]) task ($t(29) = -5.45, p < .001, d = -1.01$; Fig. 7B).

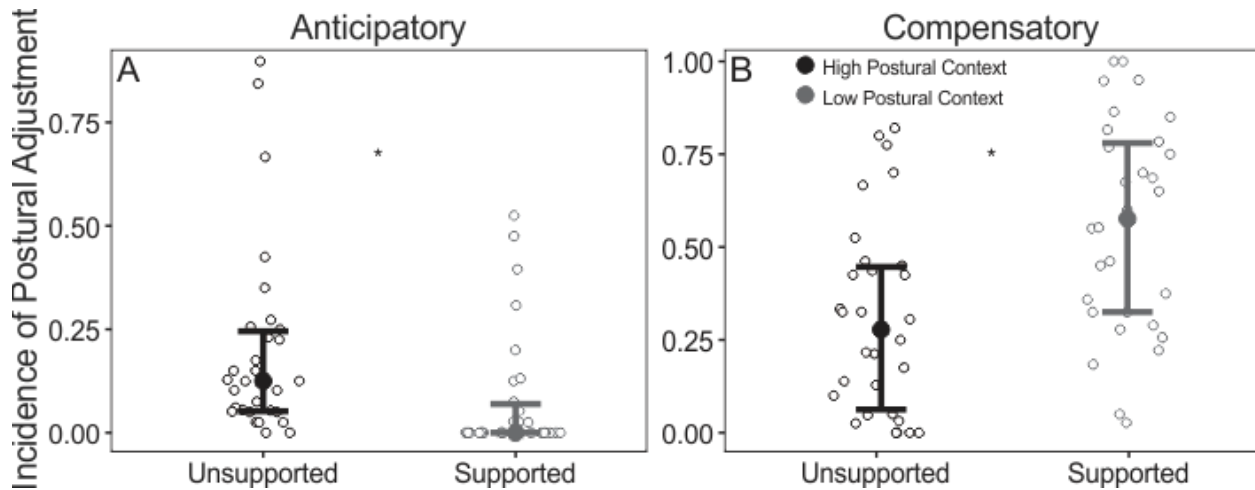


Figure 7: Incidence of anticipatory (A) and compensatory (B) postural adjustments for the grip release task showed for high and low postural contexts. Significant differences between contexts are indicated with an asterisk (*). Note: The incidence of anticipatory postural adjustment includes responses with only APAs and not those with both APAs and CPAs. Circle markers represent data points from a sample of 200 individual trials. Error bars represent quartiles.

3.5.3 Premotor RT as a function of Postural Adjustment Type

Premotor RT was compared between stimulus conditions and postural adjustment types for the grip release task (Fig. 8). Since no significant main effect of Context was found ($F(1, 1214.7) = 0.48, p = .491$), it was removed from the model. Analysis of premotor RT found significant main effects of Condition ($F(2, 1219.9) = 8.62, p < .001$) and Postural Adjustment Type ($F(1, 1238.0) = 30.92, p < .001$). No interaction effect between the factors was observed ($F(2, 1219.4) = 0.52, p = .596$). Premotor RT was significantly longer for responses with an APA (158 ms, 95% CI [145, 172]) compared to those with a CPA (130, 95% CI [120, 141]; $t(1238) = 5.553, p < .001$; Fig. 8). Post-hoc analysis revealed that premotor RTs were significantly longer for Control (182 ms, 95% CI [172, 193]) compared to SCM- (140 ms, 95% CI [127, 152]; $t(1219) = 10.29, p < .001$) and SCM+ (110 ms, 95% CI [95, 125]; $t(1226) = 12.11, p < .001$) conditions. Furthermore, premotor RTs were significantly longer for SCM- compared to SCM+ conditions ($t(1229) = 4.16, p < .001$; Fig. 8).

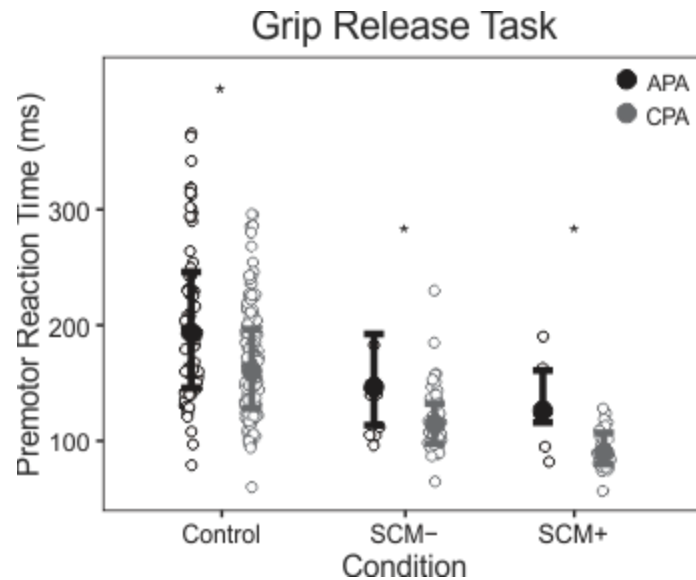


Figure 8: Premotor reaction time (ms) as a function of postural adjustment type (anticipatory postural adjustment, APA; compensatory postural adjustment, CPA) for the grip release task showed for Control and SAS stimulus conditions. The SAS stimulus condition is divided into responses with a startle reflex (SCM+) and ones without (SCM-). Significant differences between postural adjustment types are indicated with an asterisk (*). Circle markers represent data points from a sample of 200 individual trials. Error bars represent quartiles.

4. Discussion

The present study aimed to determine whether a task which requires the maintenance of a specified posture resulted in a larger magnitude of the StartReact effect as compared to a task without this postural demand. If the magnitude of the StartReact effect is modulated by postural requirement, this would provide evidence to suggest that reticulospinal drive is influenced by postural demand. The reticulospinal tract is a known contributor to postural control thus, it was hypothesized that tasks with greater postural demand would have a larger magnitude of StartReact effect (i.e., greater SCM+/- difference in RT) compared to tasks with less postural demand. Premotor RTs were compared between trials where a SAS was presented and a startle reflex was observed in SCM (SCM+), and trials where a SAS was presented and no startle reflex was observed (SCM-). These conditions were comparable since the same SAS was presented; however, the difference lies in whether evidence of the activation of reticular formation was

observed (i.e., the startle reflex). A significant difference in RT was observed between SCM+ and SCM- trials in both postural contexts of the grip release task. However, no difference in the magnitude of the effect between postural contexts was found. This suggests that although the reticulospinal tract was involved in the execution of both tasks, its contribution was not different between postural contexts. On the other hand, in the seated calf raise task, no difference in RT was observed between SCM+ and SCM- conditions; yet an SCM+/- difference *was* found in the standing calf raise task. However, the mean latency in the SCM+ condition was > 200 ms, which may suggest that this task was less susceptible to facilitation by the startle. Thus, it cannot be confirmed that a StartReact effect was observed for the standing calf raise task. Taken together, the results comparing RTs of high and low postural demand contexts of grip release and calf raise tasks do not provide evidence for greater reticulospinal drive for tasks with greater postural demand.

4.1 Is the magnitude of the StartReact effect modulated by postural demand?

Previous studies have shown that the magnitude of the StartReact effect (i.e. the difference in premotor RT between SCM+ and SCM- trials) can be modulated by certain task parameters. For example, Maslovat et al. (2020) found that response latency of a bimanual finger abduction task was significantly shortened on SCM+ as compared to SCM- trials, however, no StartReact effect was found in a unimanual finger abduction task. Similarly, a larger SCM+/- difference in RT has been observed for a bilateral arm abduction task as compared to a bilateral finger abduction task (Maslovat et al., 2023). Therefore, it has been suggested that the task parameters of bilaterality and involvement of proximal musculature allow for greater recruitment of the reticulospinal pathway. Given that the reticulospinal pathway is known to be involved in postural control, the present study expected tasks with a higher postural demand to have a greater

decrease in RT between SCM+ and SCM- trials (i.e., StartReact effect) than tasks with lower postural demand.

In the grip release task, a StartReact effect was observed for both high (unsupported) and low (supported) postural contexts, suggesting that *both* contexts receive contributions from the reticulospinal pathway. However, the magnitude of the StartReact effect was not found to be different *between* contexts, which suggests that reticulospinal drive between the postural contexts was not different. Further evidence of this comes from examination of the startle reflex itself. Specifically, since the startle reflex is known to be mediated by the reticulospinal tract and the reticulospinal tract has important contributions to postural control, it was hypothesized that a startle reflex would be elicited in a larger proportion of SAS trials for the unsupported task as compared to the supported task. Interestingly, the opposite was found in that incidence of startle was 15% larger for the supported task as compared to the unsupported task.

Previous studies have also shown a synergistic relationship between the startle reflex and task-related EMG characteristics, in that larger bursts of agonist activity are often seen with greater reticulospinal contributions (Maslovat et al., 2023). In the present study, a larger peak amplitude and larger Q30 in agonist muscle were seen on SCM+ trials compared to SCM- trials during the unsupported grip release task, but no difference was observed for the supported grip release task. These data provide some support for the hypothesis that the unsupported task receives greater reticulospinal drive given the larger postural demand. However, this support should be considered in the context of the main results presented above, which demonstrated no difference in magnitude of the StartReact effect between conditions of postural demand and a smaller incidence of startle. In terms of the EMG characteristics of the startle reflex, a task that receives greater reticulospinal drive would be expected to exhibit shorter onset latencies of the

startle reflex alongside a larger peak amplitude and Q30 in the SCM muscle. However, the data for the grip release task do not allow for definitive conclusions to be drawn as an earlier SCM onset was observed for the unsupported task, but larger peak amplitude was observed for the supported task, and no difference in Q30 was observed between task contexts. In summary, analyses of task-related and startle-related EMG characteristics for the upper limb tasks do not suggest that one task had greater reticulospinal drive over the other.

The results from the lower limb calf-raise tasks showed similarly conflicting findings. Specifically, there was no difference in premotor RT between SCM+ and SCM- trials (i.e., a StartReact effect) for the seated context, suggesting that the addition of startle-related activation arising from the reticulospinal tract was not sufficient to affect the production of this task. Although a difference in premotor RT between SCM+/- trials was observed for the standing context, a StartReact effect could not be confirmed as RTs were not short enough for involuntarily triggering by SAS to be certain. Moreover, the proportion of SAS trials in which a startle reflex was observed was not different between postural contexts of the calf raise task, providing further evidence that reticulospinal drive was not different between these contexts. Startle-related characteristics also provided mixed findings in that a shorter SCM onset latency was observed for the standing calf raise task compared to the seated task which would suggest greater reticulospinal drive for the standing task. Furthermore, it was hypothesized that if the calf raise task had greater reticulospinal drive, then larger peak SCM amplitude and Q30 would be observed. However, the opposite was found in that a larger peak SCM amplitude and Q30 were observed for the seated task as compared to the standing task. One speculative possibility is that the startle reflex in the SCM was reduced to prevent a change in head position which would be caused by bilateral contraction of the SCM muscles in the startle reflex, although no direct

evidence of this has been previously reported. Nevertheless, GVS studies have shown that head position is an influential factor in standing posture (Britton et al., 1993), although these studies normally use rotation about the longitudinal plane. A startle reflex that changes head position while standing may disturb whole-body postural control; therefore, it is reasonable to suggest that the amplitude of the startle reflex may have been reduced when standing in order to minimize effects on posture.

Analysis of the GRFs during the standing calf raise task indicated that the time to peak positive and negative forces was significantly shorter for SCM+ trials as compared to SCM- trials. This would suggest that the movement was being performed faster on SCM+ trials, which is expected to be a result of increased EMG activity in prime movers. However, analysis of agonist EMG activity in the standing calf raise task demonstrated that peak amplitude and Q30 were not different between SCM+ and SCM- trials. Similar to the RT results, times to peak forces was also too long to be certain that the SCM+ trials showed involuntary triggering by startle, therefore faster movement execution during SCM+ trials is not likely due to increased reticulospinal drive in the standing calf raise task. In the seated calf raise task, times to peak positive and negative force was not different between SCM+ and SCM- trials, supporting the RT finding that additional activation from the reticulospinal tract may not have been sufficient to affect the task production. However, for the seated calf raise, agonist peak amplitude and Q30 were larger for SCM+ as compared to SCM- trials. As previously stated for the grip release task, although these secondary analyses provide support for the hypothesis, they must be taken in the context of the main RT findings which do not support the hypothesis.

Overall, findings of the present study suggest that the magnitude of the StartReact effect was not larger for high postural demand contexts compared to low postural demand contexts –

either in the upper limb or in the lower limbs. Furthermore, the proportion of trials where a startle reflex was elicited was not larger for high postural contexts of the grip release and calf raise tasks. Although some secondary analyses provided evidence in support of the hypothesis, they do not overshadow the main findings. Therefore, the overall results of the present study suggest that postural demand may not influence reticulospinal drive in a similar way as do other task parameters. Nevertheless, for the upper limb grip release task, examining premotor RT in the Control condition showed significantly longer RTs for the unsupported grip release task compared to the supported task. If differences in reticulospinal drive did not lead to these differences, there must be an alternative explanation. In the following section I argue that a greater task complexity of the unsupported task may be the cause of this difference, as response complexity has long been shown to increase RT (F. M. Henry & Rogers, 1960) Specifically, increased RTs in tasks with increased complexity has been argued to result from an inability to prepare some portion of the response in advance. This explanation is supported by the startle reflex response data in the current thesis, as tasks that are less well prepared seem to be less susceptible to the StartReact effect (Carlsen et al., 2004; Maslovat et al., 2015; Sadler et al., 2022).

4.2 Task complexity as a confounding factor to postural demand

Tasks with greater movement complexity are less susceptible to startle as the response is not sufficiently prepared. This relationship between preparation and startle was first described in comparing RTs between simple and choice tasks with a startle paradigm (Carlsen et al., 2004). It was found that the SAS shortened response latencies for a simple RT task, but not when a choice was required. Since the correct response is known in advance for the simple task, it is thought that the response can be preplanned whereas in choice RT the response must be selected after the

imperative stimulus (Donders, 1969). Therefore, the authors suggested that less-prepared responses are not as susceptible to startle. Similarly, in a dual-task paradigm, a SAS does not decrease onset latency of the secondary task to the same extent as when the task is performed in a single-task paradigm (Maslovat et al., 2015). This suggests that the secondary task within a dual-task paradigm is not as well prepared. Therefore, additional task complexity resulting from the requirement to perform multiple actions may lead to lower motor preparation, thus making these tasks less susceptible to a SAS. Similar results were seen within the context of a probe reaction time paradigm. Specifically, when an isometric wrist extension task was performed in response to an auditory imperative stimulus while a continuous tracking task was simultaneously performed with the opposite hand, longer RTs for the isometric wrist extension are observed when the tracking hand is in the middle of movement compared to when the tracking hand is at endpoints of movement (Sadler et al., 2022). Furthermore, the researchers found a low percentage (17%) of trials in which the SAS elicited a startle reflex. These results led the authors to conclude that the requirements of a continuous task influenced the preparation of a second, discrete task. In single-task paradigms the addition of response elements (F. M. Henry & Rogers, 1960), as well as complexity of the timing of muscle activations (Klapp & Maslovat, 2020; Maslovat et al., 2019) has been shown to increase RT as a result of increased task complexity.

In the present study, high postural-demand tasks may be considered to have multiple response elements, one involving postural maintenance (whole-body or within-limb) and a second requiring a discrete motor response (calf raise or grip release). The low postural demand tasks had minimal postural demands such that the primary focus of the task was the discrete response. The seminal work of (Henry & Rogers, 1960) used a paradigm which added a component to the motor response, thus increasing movement complexity and found that as task

complexity increased, so did RT. This paradigm which added responses elements can be applied to the performance of discrete motor task while maintaining a specified postural as a recent study showed that measures of postural stability (i.e. task performance) decreases when the difficulty of the discrete task increases (Saraiva et al., 2023). Thus, in the present experiment the high postural contexts (i.e., standing calf raise, unsupported grip release) likely incur greater task complexity than the low postural contexts (i.e., seated calf raise, supported grip release). RT in the Control (non-SAS) conditions seem to confirm a task complexity effect as the high postural demand context tasks (more complex) exhibited longer RTs than the low postural demand counterparts (less complex tasks).

The high postural demand task contexts used in the present study required maintenance of whole-body or within-limb posture whereas the low postural demand contexts reduced postural demand by supporting posture externally. Postural demands were confirmed using EMG on muscles which elicit postural adjustments. In the calf raise tasks, increased activation in the TA prior to voluntary movement onset (i.e., an APA) was observed when standing, whereas no APA was observed when seated. In comparing onset latencies of the MG and TA muscles, it was found that the TA had a significantly shorter onset latency than the MG in the standing calf raise task, but the onset latencies of the two muscles were not different in the seated calf raise task (Fig. 1B & 7). These results suggest that postural demand was indeed required for the standing calf raise task and not for the seated task. In the grip release task, postural adjustments were categorized as either an APA if suppression of the BB was observed prior to premotor RT or a CPA if increased activation of the TB was observed after premotor RT. Since a larger proportion of APAs were observed for the unsupported compared to the supported task in the upper limb, it can be argued that the unsupported task required higher postural demand.

To summarize, tasks with greater postural demand appear to have had greater response complexity, and this increased response complexity likely reduced the ability to prepare the motor response in advance. Since preparation level was decreased, the high postural demand contexts were not as susceptible to startle.

4.3 The impact of postural adjustments on task complexity: exploratory findings

Some of the first studies that paired as SAS with RT tasks suggested that the APA and voluntary movement were planned and executed as one motor “program” as both latencies were similarly shortened by the presentation of the SAS as compared to a control auditory stimulus (Valls-Solé et al., 1999). However, a more recent study comparing the motor planning of imagined and executed movements found that a SAS triggered the release of an APA for both imagined and executed movements but only triggered the release of the voluntary movement in the executed condition, thereby suggesting that postural and focal components are planned independently (Eagles et al., 2015). In the present study, a StartReact effect (i.e., difference in RT between SCM+ and SCM- trials) was observed for the voluntary movement onset (MG) but not the APA (TA) in the standing calf raise task. This result supports Eagles et al. (2015)’s finding that focal and postural components of a response may be prepared independently.

Previous studies have shown that APAs and CPAs result in biomechanically different outcomes. For example, Chen et al. (2015) found that APA responses to an asymmetric reaching task resulted in co-contraction and reciprocal activation of the different sides of the body, whereas CPA responses resulted in co-contraction of both sides of the body. In the present study, postural adjustments in the grip release task were categorized as APAs when a suppression of activity in the BB was observed prior to voluntary movement onset, and CPAs when an increase in activation in the TB was observed after voluntary movement onset. Interestingly, responses

that exhibited an APA showed significantly longer RTs than those with a CPA. Moreover, a RT difference was observed between SCM+ and SCM- trials for responses with a CPA, however, no SCM+/- difference was observed for responses with an APA. This may suggest that the inclusion of an APA in a task increases task complexity as compared to a CPA, since the SAS only led to decreased RT for responses with a CPA. One reason this might be is that APAs are planned independently from the focal task, as previously mentioned, however, CPAs may be planned as part of the focal task. In turn, responses with a CPA would have fewer independent components and thus less complexity, allowing for a higher level of preparation to be attained, and thus larger influence of a SAS on the response.

To determine whether the CPA was planned as part of the upper limb focal response in the present study, CPA and voluntary movement onsets were examined as a function of Condition. A difference in EMG onset between SCM+ and SCM- trials was found for both the CPA onset and voluntary movement onset, providing evidence that these components of the motor response may in fact be planned together. However, it should be noted that when the same analysis was done for APA and voluntary movement onsets, a significant difference in onset latency between SCM+ and SCM- trials was found for the APA onset but not the voluntary movement onset which is contrary to what was found in the calf raise task of the present study and in previous studies. This may be due to the limited sample size for APA trials as compared to CPA trials.

5. Conclusion

The present study compared the magnitude of the StartReact effect between tasks with high and low postural demand to determine whether reticulospinal drive is modulated by postural demand. It was hypothesized that a larger magnitude of the StartReact effect would be

observed for high postural demand contexts as the reticulospinal tract is an important contributor to postural control. However, the results did not find a larger decrease in RT for SCM+ compared to SCM- trials for the high postural demand contexts compared to the low ones. Therefore, postural demand may not be a task parameter which increases reticulospinal drive. The rationale presented for this finding was that increasing the postural demand of a task also increased task complexity, as evidenced by the longer response latencies of high postural demand tasks compared to low demand ones. Tasks with greater complexity exhibit reduced motor preparation prior to the imperative stimulus and are therefore not as impacted by a SAS. Finally, exploratory findings suggest that postural adjustments occurring prior to voluntary movement onset may increase complexity more than those occurring after voluntary movement onset.

Chapter 3: General Discussion

The present study hypothesized that the addition of a postural requirement to a discrete motor task would increase the magnitude of the StartReact effect as the reticulospinal tract, which is activated when a startle reflex is observed, contributes to postural control. However, the results of the present study did not find that the magnitude of the StartReact effect was larger for these high postural demand contexts, which suggests that reticulospinal drive was not modulated by postural demand. The tasks used in the present study were confirmed as either high or low postural demand by analyzing postural adjustment characteristics, such as onset and type. These analyses did indeed suggest that the tasks manipulated postural demand appropriately such that the high postural demand contexts required greater postural demand than the low postural demand contexts. Given the evidence from previous studies suggesting that some task parameters can influence reticulospinal drive, the present study considers that postural demand may not follow this pattern as postural demand is confound by task complexity demands.

It has been suggested that performing a discrete motor task while maintaining a specified posture is comparable to a task paradigm with multiple response elements. Paradigms with multiple response elements have been shown to allow for less motor preparation to occur prior to the imperative stimulus which in turn reduces susceptibility to startle. Therefore, in the present study postural demand did not increase reticulospinal drive as this task parameter increased task complexity which, in turn, reduced the effect of the SAS.

1. Limitations & Future Directions

The standing calf raise task used in the present study was modeled off the one used by Valls-Solé et al. (1999), however, RTs for the standing calf raise task were longer in the present study. Specifically, Valls-Solé et al. (1999) reported a Control mean RT of 237.6 ms \pm 98.0, and a mean SAS RT of 122.6 ms \pm 25.3. In the present study the Control mean RT was 311 ms, 95% CI [298, 325], the SCM- mean RT was 251 ms, 95% CI [235, 267], and the SCM+ mean RT was 213 ms, 95% CI [196, 230]. These large RT differences between studies might be due to the difference in instructions given to participants. Valls-Solé et al. (1999) allowed participants to begin the task with a forward lean, as they found this increased the muscle activity in the triceps surae muscles which ensured that the silent period prior to motor activity was clearer. However, in the present study participants were instructed to maintain an upright posture until the presentation of the imperative stimulus. Participants were given this instruction as it was thought a forward lean would displace COP anteriorly. Displacement of COP anteriorly was considered an essential component to the APA and therefore we did not want it performed prior to the voluntary movement. Although instructing participants to lean forward would have allowed RTs to be much faster, it may have reduced the postural demand of the task which was necessary to answering the research question of the present study.

The present study was interested in increases in reticulospinal drive as a result of increased postural demand, however, other descending pathways are also involved in postural control. Notably, vestibulospinal and rubrospinal pathways are imperative to posture and locomotion (Grillner et al., 1970; for review see Grillner & El Manira, 2020). Although these pathways were not investigated in the present study, the manipulation may have impacted their contributions to the tasks.

It is important to keep in mind that the objective of the present study was not to investigate APAs, and that tasks with APAs were used in order to be able to confirm the increased postural demands. However, we believe it worthwhile to report APA findings to help guide future research questions. That is, all analyses of APAs were exploratory in nature and not hypothesis-driven, therefore confirmatory, hypothesis-driven research should be done prior to drawing any strong conclusion regarding the APA results.

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