The feed-forward organization of anticipatory postural adjustments across multi - directional movement

Ryan H. Brown

BSc, MSc candidate

Department of Kinesiology and Physical Education

McGill University, Montreal

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DEDICATION

This thesis is dedicated to my late grandparents, Ron and Gwen, Carl and Alice.

Thank you for all your inspiration and support, you are examples to live by.

ACKNOWLEDGMENTS

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GLOSSARY

EMG	Electromyography
COM	Center of body mass
COP	Center of foot pressure
APR	Automatic postural responses
APA	Anticipatory postural adjustments
GRF	Ground reaction forces
A-P	Anterior - Posterior plane
M-L	Medial - Lateral plane
msec	millisecond
Sol	Soleus
Tib	Tibialis anterior
Per	Peroneus longus
Gast	Gastrocnemius
Rect	Rectus femoris
Bicp	Biceps femoris
ES	Erector spinae
Abs	Rectus abdominus

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ABSTRACT

Anticipatory postural adjustments (APA's) occurring prior to the initiation of forward whole body movements are characterized by muscular activity of the legs and trunk under feed-forward neural control. Compensatory postural muscle responses to unexpected perturbations of the support surface in multiple directions have been shown to have a directionally tuned organization. This thesis sought to examine whether APA's preceding multi directional pointing movements performed while standing are organized in a similar directionally tuned manner as to feedback postural adjustments. The postural musculature was recorded in seven subjects as they performed discrete pointing movements to targets placed at 15° intervals in the forward plane. The results showed that the postural muscles were active across specific ranges of pointing directions, with maximal activity to only one direction. This tuned muscular response is similar to the organization of compensatory postural adjustments, and is indicative of a strategy of simplifying the neural control of voluntary movement.

SOMMAIRE

Les ajustements posturaux anticipés (APA’s) se produisant avant le déclenchement des mouvements vers l'avant du corps entier sont caractérisés par l'activité musculaire des jambes et du tronc sous une commande neurale en boucle proactive. Il a été démontré que les réponses compensatoires des muscles posturaux suite aux perturbations inattendues de la surface d'appui ont une organisation directionnelle spécifique. Le but de cette étude d’examiner si l'activité musculaire des APA’s des mouvements de pointage multidirectionnels exécutés debout etaient également organisée d'une façon directionnelle. La musculature posturale a été enregistrée chez 7 sujets pendant qu'ils effectuaient un mouvement de pointage vers des cibles placées à des intervalles de 15° vers l'avant. Les résultats ont démontré que les muscles posturaux étaient actifs dans plusieurs directions de pointage, avec l'activité maximale dans seulement une direction. Cette réponse musculaire est semblable à l'organisation des ajustements posturaux compensatoires et est indicative d'une stratégie de simplification de la commande neurale du mouvement.

CHAPTER 1: INTRODUCTION

The control of upright posture is an integral part of every day life that is performed so automatically that the average person neglects to consider its complexity. Maintaining a stable platform enables humans to interact with the world through a multitude of movements such as reaching, lifting objects, and locomotion. All movements, however, create perturbations that threaten upright stability, and must be accounted for by the central nervous system (CNS). Evidence has shown that humans predict postural perturbations that forthcoming movements will cause, and act in a feed-forward control manner to stabilize posture (Bouisset and Zattara, 1981, 1987; Crenna et al., 1987; Crenna and Frigo, 1991; Massion, 1992). Furthermore, humans are adept at responding to perturbations that are inflicted upon the body through extensive sensory feedback control loops (Macpherson, 1991). However, the underlying organization of the complex arrangement of muscular activity and forces of postural adjustments is still heavily under debate.

The majority of postural control research has examined the postural responses of animals and humans to unexpected movements to the support surface upon which they are standing. These feedback based postural responses are produced very rapidly, are highly organized, and are modified across perturbation directions, termed Automatic Postural Responses (APR) (Horak and Nashner, 1986; Macpherson, 1988a, b; Moore et al., 1988; Horak and Macpherson, 1996; Henry et al., 1998). Despite this, there is debate over how the CNS produces an adequate response so quickly when there is no unique solution. In producing any movement, the CNS is faced with the degrees of freedom problem, in that any movement can be performed through many different combinations of joint and muscle actions, and for the CNS to consider all possible actions independently would be very inefficient and computationally costly (Macpherson, 1991). An often-proposed solution to this is to reduce the number of variables the CNS is required to control by creating functional groupings, or synergies, of body segments, muscles or movements (Macpherson, 1991; Massion, 1992; Horak and Macpherson, 1996). Significant attempts at quantifying feedback postural responses through synergy analysis have been performed and indicate there may be loose, modifiable muscle synergies that act together to produce adequate muscular responses and simplify the control strategy of the CNS (Macpherson, 1988a; Henry et al., 1998; Ting and Macpherson, 2005; Torres-Oviedo et al., 2006).

Postural adjustments also occur when the body produces voluntary movements while standing, such as arm reaching. Numerous electromyographic studies have shown that prior to the onset of these movements, postural muscles not involved in the focal movement become active, termed Anticipatory Postural

Adjustments (APA's) (Bouisset and Zattara, 1981; Crenna et al., 1987; Breniere and Do, 1991; Crenna and Frigo, 1991; Massion, 1992; Lepers and Breniere, 1995; Stapley et al., 1998). It is assumed that this anticipatory muscular activity plays a postural role, functioning to maintain postural stability. The APA activity has also been seen to be relatively stereotyped, with similar activation patterns seen across many movement tasks such as reaching, gait initiation, and arm raising (Crenna and Frigo, 1991). Furthermore, APA's are organized in a modifiable fashion according to the upcoming task requirements, similar to the postural responses to perturbations. APA's, however, are produced in a feed-forward control manner, suggesting the CNS is using an internal forward model of the body to predict the resulting postural perturbation of movements, and thus produce an appropriate motor plan (Kawato et al., 2003; Davidson and Wolpert, 2005).

Research into APA's has focused mainly on movements in a single direction (Bouisset and Zattara, 1981; Crenna et al., 1987; Crenna and Frigo, 1991; Massion, 1992; Alexandrov et al., 1998; Stapley et al., 1998; Hodges et al., 1999). However, there has been little research of the muscular organization of the APA period for a single movement across an extensive range of movement directions. Therefore, the purpose of this present study is to examine the feed-forward organization of the postural muscles of standing humans during an arm reach-to-point task to numerous directions in the forward plane, and to examine whether their organization is similar to that seen for feedback postural responses to unexpected perturbations.

This thesis will provide novel information into the organization of anticipatory postural adjustments, and add to the understanding of feed-forward postural control mechanisms. It has been divided into 5 chapters, beginning with this introductory Chapter 1 to illustrate and highlight the rationale for the study. Chapter 2 provides an in-depth review of the literature pertinent to this study, followed with the hypothesis. Chapter 3 outlines the methodology of the experimental paradigm, as well as a complete synopsis of the data analysis procedures. Chapter 4 will present the results of the study; Chapter 5 will discuss the results, experimental issues, and areas for further research.

CHAPTER 2: REVIEW OF LITERATURE

2.1 Equilibrium and Postural Control:

Humans typically adopt an upright, bipedal stance that aligns the body with the earth's vertical axis, determined by gravity. This upright position is inherently unstable, as 2/3 of the body weight lies high up in the trunk over the small base of support of the feet (Gatev et al., 1999). Two behavioural goals are integral for postural control; postural orientation being the relative positioning of body segments with respect to each other and the environment, and postural equilibrium being a state where all forces acting on the body are balanced, enabling the body to remain in a desired location (static equilibrium) (Horak and Macpherson, 1996). When standing quietly, the body remains in the same postural orientation and is in postural equilibrium signifying all forces acting on it are balanced (Horak and Macpherson, 1996). However, the body is never completely motionless, and maintaining stability is a dynamic task under the control of the central nervous system (CNS) based on sensory information from the peripheral sensory systems. Furthermore, to facilitate active movements the body orientation is frequently altered, requiring central nervous system involvement to maintain balance under dynamic conditions (dynamic equilibrium) (Horak and Macpherson, 1996).

2.2 Principles of Balance:

During quiet stance, the body can be considered to function as an inverted pendulum, as is shown in Figure 1A (Winter et al., 1998; Winter et al., 2003; Winter, 2005). In this situation the body acts as a single rigid segment with its center of mass (COM), a theoretical balance point through which forces act upon the body, elevated high in the trunk. The body is free to rotate about the pivot point of the ankles, but to maintain upright stability the vertical projection of the COM must remain within the confines of the base of support (BOS); the area outlined by the feet on the ground. Active force is required to control the position of the COM, created by contractions of musculature surrounding the ankle which generate forces applied to the ground, termed ground reaction forces (GRF). The point of application of these forces is called the center of pressure (COP), which acts to accelerate the COM in the opposite direction (Horak and Macpherson, 1996; Winter et al., 2003). The inverted pendulum model illustrates how the CNS utilizes the COP to regulate the global COM variable. Figure 1B illustrates how both variables show similar movement within the BOS during quiet stance, however, the COP moves with higher velocity and frequency, therefore acting to control the position of the COM (Winter et al., 1998).

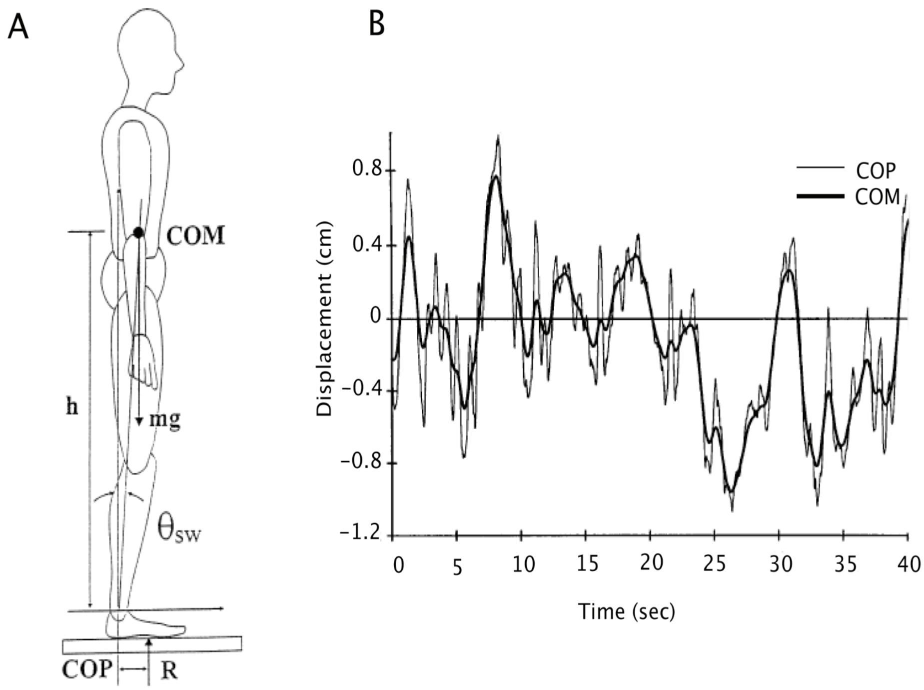


Figure 1: A) The inverted pendulum model of upright human stance. The COM resides high up in the trunk, with the vertical projection within the BOS outlined by the feet. The ground reaction forces, R, act upwards on the body to counter the downward force of gravity (mg). (*Adapted from Winter et al. 2003*) B) A 40-s recording of the A-P COM and COP in a typically quiet standing subject. The COP shows slightly greater movement within the BOS at a higher frequency, acting to accelerate the COM in the opposite direction (*Adapted from Winter et al. 1998*).

2.3 Postural Control During Equilibrium Conditions:

While standing the body is never completely motionless (Nashner et al., 1982). Studies have shown that the body is constantly swaying in the anterior-posterior (A-P) and medio-lateral (M-L) planes (Nashner et al., 1982; Day et al., 1993; Horak and Macpherson, 1996; Winter et al., 1996). In the standing position, the COM lies along the vertical planes of major joints of the body; the shoulder, hip, and knee, and therefore does not create torques about these joints' rotational axes. However, during quiet stance, the COM lies 5mm anterior to the ankle joint, causing a constant dorsi-flexion moment on the body and pulling it anteriorly (Oatis, 2004). To account for this, constant plantar flexion activity is seen in the Soleus (Sol) and Gastrocnemius (Gast) muscles, creating a counter active torque. Thus A-P sway is primarily controlled by the ankle plantar flexors/dorsi flexors, where as M-L sway has been shown to be controlled primarily by hip abductors/adductors, and the ankle evertors/invertors (Day et al., 1993; Winter et al., 1996; Winter et al., 2003). As the COM position fluctuates, the COP is used to control the COM position in combinations of A-P and M-L directions. Figure 2 illustrates the constant feedback control of postural sway in the A-P plane.

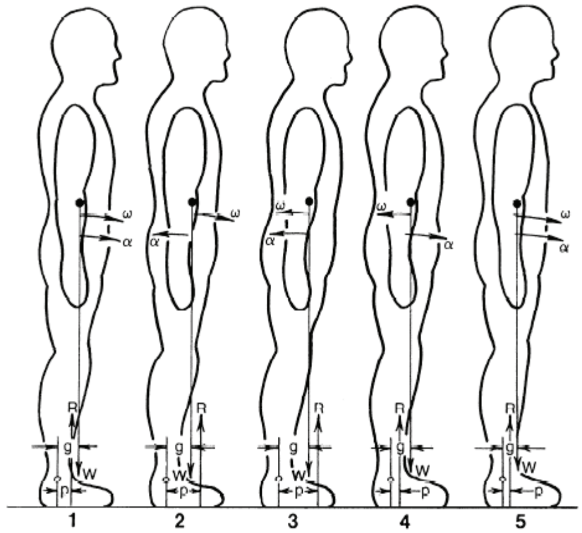


Figure 2: The control of quiet stance through COP (R) manipulation of the COM at 5 different times. (1) The R is posterior to the COM, with the body's angular velocity (ω) and acceleration (α) acting clockwise (forwards) (2) to correct this forward movement, the R is moved anterior of the COM, and α is reversed (3) the ω has now reversed to counter-clockwise and the COM is posterior to the R (4) the R is moved posterior to the COM to reverse the α to clockwise movement again, and (5) the body is back in the original condition. (*Adapted from Winter et al. 1996*)

2.4 Postural Control Muscles:

The control of posture is attained by the contraction of many muscles of the legs and trunk that primarily control the ankle, knee, and hip joints. The following is a description of the function of the primary postural muscles, as they are illustrated in Figure 3 (Marieb, 1995).

The ankle joint primarily allows movement in the A-P plane, with joint rotation in either dorsi-flexion, where the foot moves upwards, or plantar flexion, where the foot moves downwards contacting the support surface. Plantar-flexion movements are produced by the prime movers Sol and Gast muscles, which are considered the prime anti-gravity muscles (Figure 3A). Dorsi-flexion movements are controlled by the prime mover tibialis anterior (Tib) muscle, and to a lesser extent by the peroneus longus (Per). These muscle also attach onto the foot, and respectively invert and evert the foot to keep it flat on the ground.

The knee joint is limited to extension and flexion movements, and is primarily controlled by 2 large groupings of muscles in either the anterior or the posterior portion of the leg (Figure 3 B). The rectus femoris (Rect) muscle from the anterior quadriceps is the prime mover for knee extension. This muscle also spans the hip joint, and aids in flexing the trunk forward. The biceps femoris (Bicp) muscle from the posterior hamstrings is the prime mover for knee flexion. The Gast muscles also spans the knee joint, and act as week knee flexors.

Trunk motion is highly complex, involving many muscles, including several biarticular muscles that cross two joints, such as Rect. However, the two major trunk muscle contributors are the erector spinae longissimus (ES) muscle, the prime mover for hip extension and providing resistance to forward bending, and the rectus abdominus (Abs) muscle which flexes and rotates the trunk about the lumbar vertebrae (Figure 3 C).

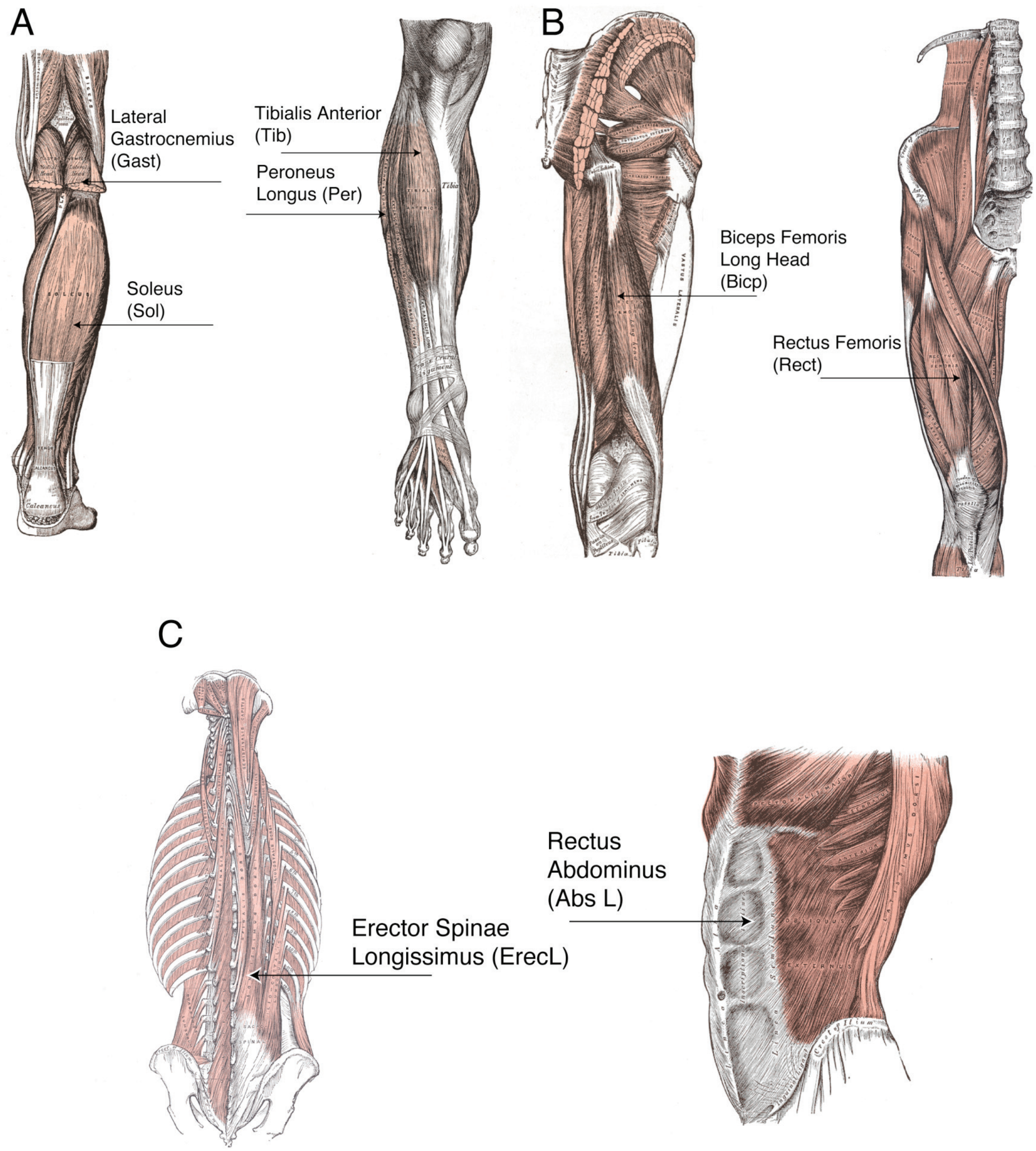


Figure 3: Anatomical diagram showing muscles of the A) Lower leg B) Thigh C) Trunk. (*Adapted from Gray, H. 1918).*

2.5 Feedback Based Postural Adjustments:

Classically, postural control has been studied using a paradigm where standing subjects are subjected to unexpected movements of their support surface, moving the feet and therefore changing the position of the BOS (Horak and Macpherson 1996). When humans are subjected to these perturbations during stance, their postural orientation and equilibrium are altered, and they must respond accordingly to the perturbation to maintain equilibrium (Horak and Macpherson 1996). In such a situation, the postural control mechanisms of the CNS must rely on feedback sensory information to determine changes in the location of the body and its segments in space, as well as the direction and magnitude of the perturbation (Horak and Nashner, 1986; Macpherson, 1988a; Horak and Macpherson, 1996).

In both humans and cats, when their support surface is unexpectedly moved during quiet stance, muscular activity occurs in the muscles of the supporting limbs within 70-100 msec in humans, and 40-60 msec in cats (Horak and Macpherson 1996). These electromyographic (EMG, the recording of the electrical activity of muscles) responses function to maintain posture and produce forces that oppose the COM displacement caused by the perturbation, termed Automatic Postural Responses (APR's). APR's are not a simple reflexive response to muscle stretch as the response occurs too slowly after the onset of the perturbation; however, the responses do occur well in advance of voluntary reaction time of ~200 msec. The responses are generally characterized by an initial activation of distal lower leg muscles, suggesting the muscular responses are under CNS control and not simple reflex pathways, as these muscles have the longest distance for efferent information to travel to from the CNS. (Macpherson, 1988b; Schmidt and Wrisberg, 2004).

2.5.1 Perturbations to Posture in the Anterior-Posterior Plane:

Research into postural responses to perturbations in the A-P plane showed that responses involve particular groups of muscles contracting with distinctive latencies and amplitudes (Nashner et al., 1982; Horak and Nashner, 1986; Moore et al., 1988; Horak and Macpherson, 1996). These responses have been grouped into 3 strategies, and are elicited by varying the amplitude and magnitude of the perturbation (Horak and Nashner, 1986). The first is the ankle strategy, which is the most common response during quiet stance. Nashner (1977) found the muscular response occurred in a distal-to-proximal order, initiating about the ankle and creating a torque to oppose the displacement of the body. For example, Figure 4 A shows a response to a forward surface perturbation, triggering a posterior ankle synergy that involves a distal to proximal activation of the gastrocnemius, hamstrings, and paraspinal muscles, producing minimal movement about the knee and hip

(Horak and Macpherson, 1996). This restores the position of the COM, but is effective only for small, slow perturbations. In responses to larger and faster movements, the ankle strategy is replaced by the hip strategy, involving bending of the trunk segment about the hips, with no muscular activity seen about the ankles (see Figure 4 B). These 2 strategies actually represent extremes in a continuum of postural responses, with the ankle and hip strategies often overlapping with one another, creating mixtures of muscle activation patterns with different proportions of each strategy (Horak and Macpherson, 1996). The third strategy is changing the BOS, generally by taking a step. This occurs for large and fast perturbations, as well as when subjects have no prior experience with the perturbation (Horak and Macpherson, 1996).

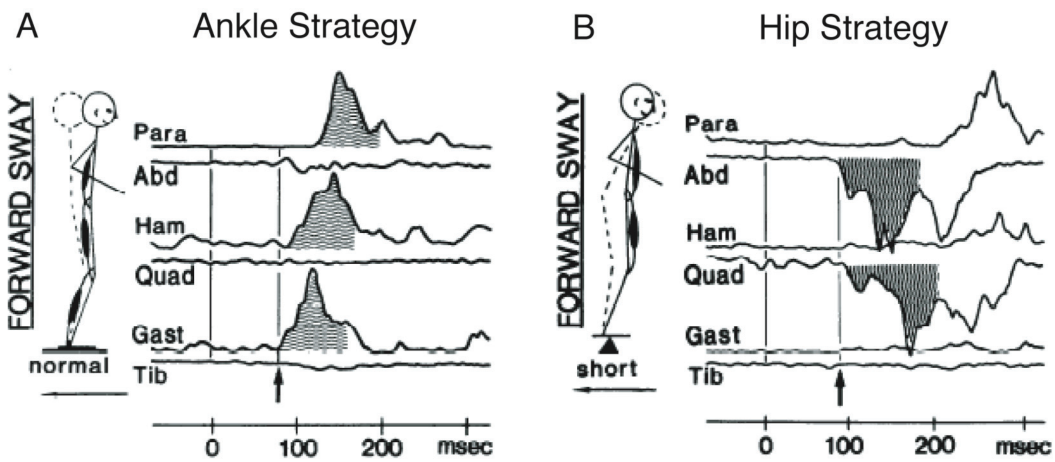


Figure 4: Muscle response patterns to surface perturbations. A) Ankle strategy response to a forward sway on a normal surface. The distal-proximal EMG activation pattern begins earliest with the distal Gastrocnemius muscle and progresses proximally to the thigh and trunk. B) Hip strategy response to a forward perturbation on a short surface elicits the activation of hip and knee muscles, with no ankle muscle activation. The dashed stick figures represent body positioning, and it can be seen the hip strategy causes hip flexion, where as the hip remains in the same relative position in the ankle strategy. (*Adapted from Horak and Nashner 1986*)

The APR patterns can be influenced by many factors; prior experience, surface conditions, intent, and initial body alignment (Horak and Macpherson, 1996). For example, the size of the support surface affects the strategy used for perturbations of equal magnitudes. Perturbations that elicit ankle strategy in normal stance conditions produce hip strategy responses on a narrow surface, as the BOS is functionally smaller, rendering the ankle strategy ineffective to create sufficient GRF's to counteract the COM displacement (see Figure 4). Furthermore, when a person is subjected to perturbation on a narrow stance surface, and then switched a normal stance, prior experience results in the first several perturbations eliciting the hip strategy, with the ankle strategy progressively taking over, thus showing the responses are not ‘hard wired’ synergies, but are modifiable according to the task conditions (Macpherson, 1988b; Horak and Macpherson, 1996; Henry et al., 1998).

2.5.2 Perturbations to Multiple Directions in the Horizontal Plane:

Disturbances to balance occur in many more directions than just the A-P plane, and it has been shown that as the direction of surface perturbations are changed in small increments, the organization of the postural responses systematically change with perturbation direction (Macpherson, 1988a,b; Moore et al., 1988; Henry et al., 1998). Macpherson (1988) examined responses of standing cats to linear perturbations in multiple directions throughout 360° of the horizontal plane. The study found that regardless of the perturbation direction cats produced GRF’s in 1 of 2 responses directions under each paw, with the amplitude of the force response varying according to the perturbation direction (see Figure 5 A). This was termed the force constraint strategy, with the limited force response patterns interpreted as a simplification strategy to reduce the number of degrees of freedom that need to be controlled by the CNS. This force output pattern was the result of a variable pattern of muscle activations, in which muscles showed tuned responses across the perturbation directions (See Figure 5 B). EMG amplitude responses were modulated across specific ranges of perturbation directions, showing a maximal response to a single direction. The response amplitudes decreased as the direction of perturbation was deviated from the maximal response direction, creating a directionally tuned muscular response. Several biarticular muscles showed maximal responses to two perturbation directions separated by roughly 180° to act appropriately about both the joints spanned by the muscle. As well, several muscles were active to perturbation directions that were not along their anatomical line of action, which was unexpected, as muscles are assumed to be most mechanically effective in anatomical alignment (Macpherson, 1988a,b; Moore et al., 1988; Henry et al., 1998). However, combining the response patterns of the muscles produced only 2 constrained force vectors against the ground, which suggest a complex response organization by the CNS.

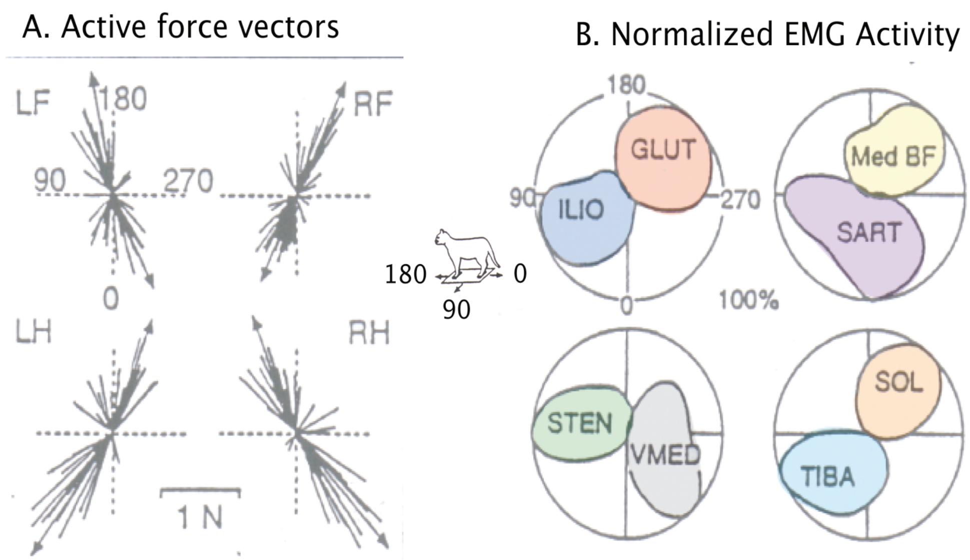


Figure 5: The response patterns of cats to perturbations in multiple directions in the horizontal plane. A) Active force vectors produced under each paw across 16 perturbation directions, the arrows represent the mean response vectors for each grouping. LH, RH, left and right hindlimb; LF, RF, left and right forelimb of the cat. The tight clustering of force vectors is termed the force constraint strategy, as force is exerted in 2 only directions in response to perturbations across 360°. B) EMG tuning curves of several representative muscles at each limb, plotted in polar coordinates against the normalized amplitude. Muscles were active over distinct ranges, with a maximal response to 1 direction, with several active to 2 directions 180° apart (See SART), and yet produced the invariant response forces. Inset is the direction of the perturbation and coordinate system in degrees. (*Adapted from Horak and Macpherson 1996*).

Henry et al. (1998) in a similar study examined the postural responses of humans to sudden perturbations of the support surface in multiple directions. Postural muscles of the lower limb and trunk showed distinct tuning curves, with most showing a maximal response to one perturbation direction and several muscles of the trunk and thighs showing bipolar tuning curves with maximal activity to 2 separate perturbation directions. It was found that generally muscles could be grouped into diagonal clusters according to their direction of maximal activity (See

Figure 6 A). These clusters suggest synergistic relationships between the muscles across those perturbation directions, and a combination of the synergies for directions where the clusters overlap. This implies that the synergies are flexible and can be modified to interact with one another, showing higher level CNS involvement.

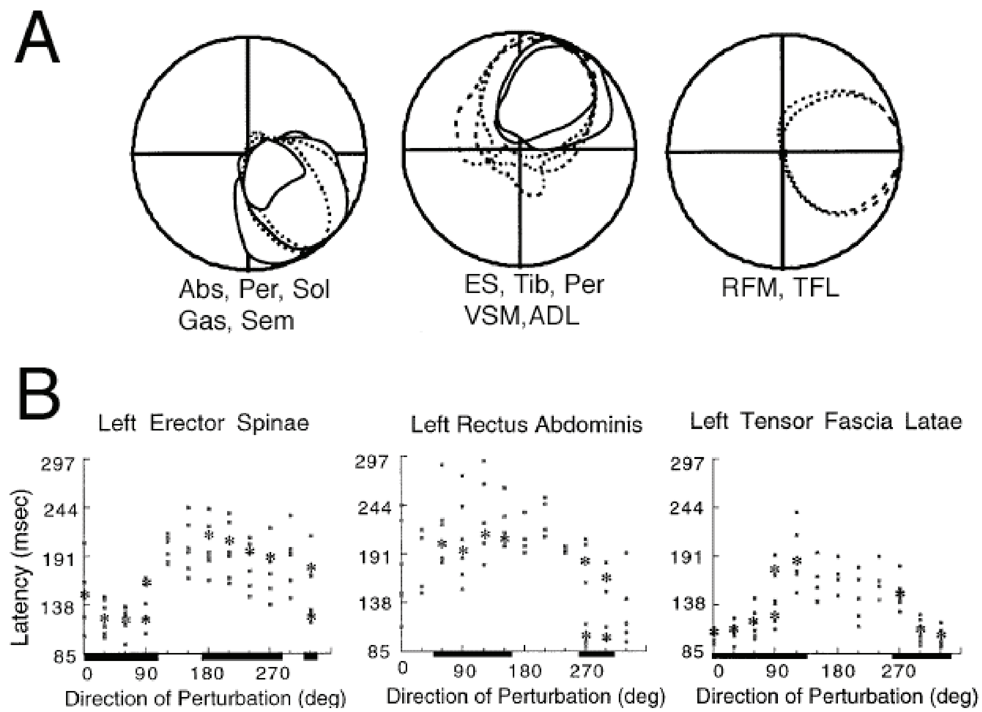


Figure 6: Human postural responses to surface perturbations A) Directionally tuned muscle responses cluster together in 3 groups across perturbation directions. Per acts in more than one cluster as they showed peak amplitudes to 2 directions B) Scatter plot showing the onset latencies for 3 proximal muscles, illustrating the latency changes with perturbation directions. Asterisks represent the mean onset time across for subjects at directions the muscle was significantly active. (*Adapted from Henry et al. 1998*)

The timing of muscle activations after the onset of the perturbation remained constant for lower leg and thigh muscles, showing no effect of perturbation direction, whereas the trunk and hip abductor muscles showed either an early or late onset time according to perturbation direction, with 60°-180° degrees separating the onset periods (See Figure 6 B). Recruitment of the trunk muscles either early or late changed the role of the hip in the movement through altering the hip torque produced, and showed the modification of the muscle synergies according to the perturbation directions. This was similar to the findings of Moore (1988), except they found the trunk muscles showed a continuum of onset times, progressively changing between late and early onsets with changing perturbation directions. However, it has been proposed that these differences are the result of methodological differences, as Moore's subjects were aware of the direction of the impending perturbation. However, that both studies showed changing onset times for the trunk and hip adductor muscles illustrates the directional specificity of the muscle activations.

A further study by Henry et al. (2001) examined the effects of stance width on responses to postural perturbations, as stance width directly affects the BOS and can cause a change in the postural strategy used. Narrow stance has been shown to increase lateral sway in quiet stance and increase trunk movement during APR 's, where as a wide stance results in reduced lateral sway through increased stability from limb geometry and stiffness of the leg and trunk joints (Winter et al., 2003). Henry et al. (2001) showed that at each perturbation direction, the displacement of the COM was equal between the stance conditions due to significantly larger COP displacements in the narrow stance, especially for lateral perturbations, acting to counteract COM movements. The muscular responses patterns were very similar between the stance conditions, with the latency responses of all recorded muscles showing no differences. However, the amplitude of the tuning curves showed higher response magnitudes for narrow stance compared with normal and wide stance width's at the same perturbation direction. This suggests the same muscular organization was used at each perturbation direction for all stance widths, with the CNS just slightly modifying the EMG amplitude. There was also a decrease in the force constraint strategy for wide stance widths compared with the narrow stance, as there was increased stability from the limb geometry, requiring less involvement of the CNS to maintain postural stability.

In summary, perturbations to equilibrium conditions in stance produce automatic postural responses through feedback control to prevent falling. These rapid responses show a complex CNS organization of muscular responses to produce appropriate ground reaction forces in order to oppose perturbation actions on the COM. When the perturbation direction is changed throughout the horizontal plane, a directionally tuned muscular responses pattern is seen, producing a constrained force output which is believed to simplify the CNS's control by reducing the number of DOF that need to be accounted for.

2.6 Feed-forward Control of Posture:

The postural control system must also account for postural perturbations it will cause to itself through voluntary movements. This is necessary as performing movements from the standing position, for example forward arm reaching, alters the orientation of limb segments, relocating the COM, creating a perturbation to postural equilibrium (Latash et al., 1995; Pozzo et al., 2002). Furthermore, muscular contractions of the focal movements create internal forces and torques through the linked joints of the body, disturbing equilibrium (Massion, 1992; Pozzo et al. 2002). It has been well established that prior to the onset of voluntary movements performed while standing, postural muscle activity occurs before the onset of focal movement, termed anticipatory postural adjustments (APA) (Bouisset and Zattara, 1981; Crenna et al., 1987; Crenna and Frigo, 1991). Figure 7 illustrates the APA muscular activity for forward arm reaching, as there is clear EMG activity of several muscles before the onset of the arm movement, indicated by the vertical line.

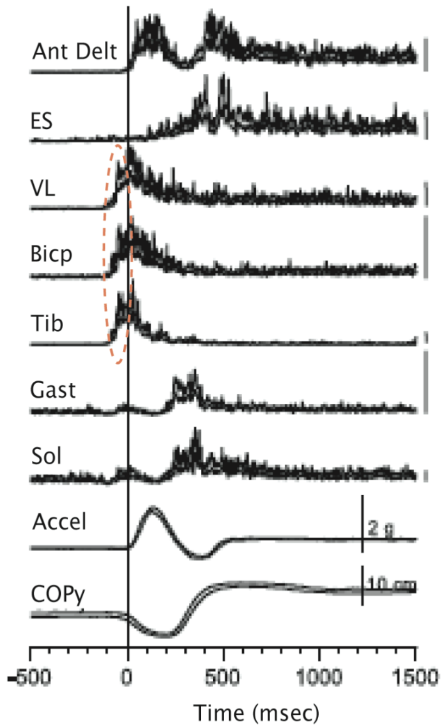


Figure 7: Anticipatory postural adjustment activity during a forward arm reach. The vertical line represents the onset of the voluntary arm movement. There is clear EMG activity in the Tib, Bicp, and the vastus lateralis (VL) muscles (circled) prior to onset of the prime mover Anterior Deltoid. (*Adapted from Tyler and Karst 2004*)

This feed-forward control of posture is traditionally believed to act to predictively counter the expected postural disturbance caused by forthcoming movements (Massion, 1992; Aruin and Latash, 1995; Horak and Macpherson, 1996). Bouisett and Zattara (1987) demonstrated that for uni- and bi-lateral arm raises, during the APA period GRF's were produced in the opposite direction to those created by the arm movements, effectively canceling out the postural perturbation. Furthermore, as mass was added to the hand to induce larger postural perturbations during arm raises, the duration of the APA period increased, thus creating larger

GRF's to counter the increased perturbation to the COM from the loaded arm movement. These results were furthered by Lee et al. (1990) performing a lever-pulling task from standing. They found similar results to that of Bouisett and Zattara, reporting an increased APA period duration corresponded with an increased required task load. It was also shown that fast movements require a larger APA than slow movements, as there is a greater need to accelerate the body to overcome the inertia of the moving segment. Lee et al. suggest that the increased APA duration is not necessarily only to counteract the postural effects of the movement, but that they may also play a role in performing the actual task, thus debating the functional role of the APA's to solely stabilize posture.

An investigation by Crenna and Frigo (1991) into EMG patterns of leg muscles showed a consistent activation pattern of several muscles during the APA period of many fast forward movements, including rising on tip toes, pushing backwards, gait initiation, etc, shown in Figure 8. APA activity was stereotyped by an initial inhibition of the Sol muscle, followed closely by activation of the Tib muscle, displaying a synergistic relationship (see Figure 8 A). This consistently resulted in a backward shift in COP for all examined movements (see Figure 8 B). However, the proposed goal of the APA for forward throwing is to maintain the COM within the BOS, whereas gait initiation is designed to destabilize equilibrium and cause a forward projection of the COM to facilitate walking (Breniere and Do, 1991; Lepers and Breniere, 1995). In both situations, the APA is adjusted to the amplitude of the upcoming movement, with the APA amplitude of EMG activity for gait initiation correlating with the upcoming movement velocity in a similar fashion to the increased force production seen in the APA for movements with higher loads. The discovery of all these forward oriented movements sharing the same APA pattern added to the debate over the functional role of APA's.

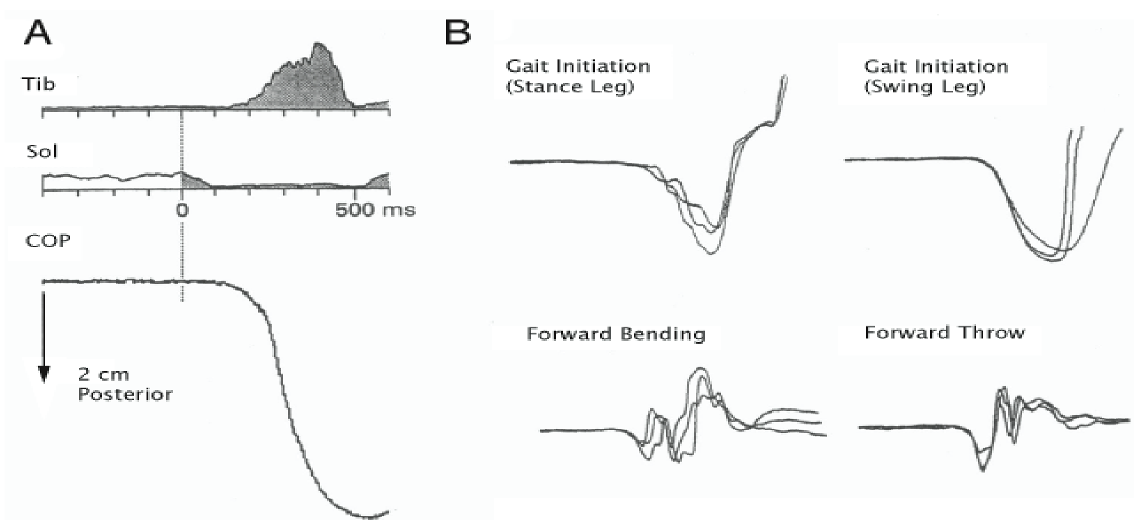


Figure 8: APA activity across several forward oriented movements. A) The EMG traces show the inhibition of the Sol, followed by the activation of the Tib muscle. This can be seen to cause a posterior shift of the COP. B) The same COP movements are seen across a variety of forward oriented movements, showing the wide spread use of the same APA pattern. (*Adapted from Crenna and Frigo 1991*).

More recently, several research groups have produced results that question the classic COM stabilizing role of APA's. Kaminski (1995) examined arm reaching movements from a seated position where the target was placed beyond the arm's length, therefore changing the role of the trunk from a postural stabilizer to being actively involved in the focal movement, propelling the body forward to reach the target. As the target distance was increased beyond arm length, increased trunk flexion and rotation were seamlessly incorporated into the reaching movement, as it became an integral part of positioning the hand to contact the target. In a follow up experiment with standing subjects, when target distance was within arm length there was no consistent APA pattern between subjects (Kaminski, 2001). As the target distance increased beyond arm length, the APA period consistently showed a posterior shift of COP, driving the COM forwards toward the target. The amplitude and duration of the APA increased linearly as target distance increased beyond arm length, suggesting that depending on the task the APA does not solely serve to stabilize posture, but may also be involved in initiating and assisting whole body reaching tasks.

This was furthered when Tyler and Karst (2004) examined the EMG patterns in a similar experiment, where subjects had to reach to targets placed at 4 different distances relative to arm length, -10, 0 , +10 , and + 20 cm, set at shoulder height. They found that as the target distance increased, the EMG of non-focal postural muscles they recorded showed a progressively earlier onset (prior to movement onset). They suggest the non-focal muscles changed from playing a stabilizing role in the APA, to a transport role for farther target distances. The exception to this was the Sol muscle that showed no consistent changes across arm distances, and the erector spinae muscle, which showed progressively later onsets and was active after movement initiation for far distances, potentially changing from a trunk stabilization role to decelerating the trunk as it reaches far the target. This indicates that the APA muscular activity is pre planned by the CNS in accordance with the focal movement distance, and that muscle patterns can be affected on an individual basis. The COP was also found to increase in magnitude with target distance, showing the same initial posterior shift followed by an anterior shift as seen by Kaminiski (2001). Similar results were seen in whole body reaching tasks, wherein the forward movement requires significant displacement of trunk and body forwards to reach and pick up an object placed on the ground (Stapley et al., 1998; Stapley et al., 1999). The APA period produced a backward COP shift, forcing the COM forward within the BOS. EMG analysis of these movements found an early TA burst to exert the plantar flexion moment needed to pull the body forwards, acting in a focal role for the movement as opposed to a strictly postural role.

The pattern of APA activations has been well classified for forward movements, however its functional role remains under debate. Regardless, EMG results indicate APA's for forward movements are initiated by an inhibition of the Sol, followed by an activation of the Tib muscles to actively move the COP posteriorly prior to movement onset. The duration of the APA period has also been shown to correlate with the upcoming task requirements, as it is increased to produce a larger COP displacement for larger movement loads, and the muscle onset pattern is changed according to the postural requirement of the task. However, little research has been performed on APA patterns across multiple directions. Aruin and Latash (1995) examined bi-lateral shoulder movements in directions between 90° and –90° degrees of the sagittal plane (from directly forward to directly backwards). They demonstrated that postural muscles had directionally specific activations, with forward movements producing classic APA activity of posterior muscles (Sol, ES, Bicp), and backwards movements demonstrated APA activity in anterior muscles (Abs, Rect, Tib). The muscular activations were substantially different across the whole range of shoulder motions, showing periods of inactivity. However, this study used a bi-lateral movement which was designed to only elicit postural perturbations in the A-P plane, therefore this does not indicate how APA's are organized for movements that will cause postural perturbations in different directions.

Hypothesis:

It is known that automatic postural responses to multidirectional perturbations of equilibrium show a variable organization of postural muscles, with each muscle producing a broad, directionally tuned response with maximal activation for one characteristic direction. These feedback recruitment patterns suggest there may be a synergistic control of APR's resulting in an invariant force output, which are indicative of a simplification of the CNS's control of the APR to multi-directional perturbations.

It is not known if a similar organization of muscular activity exists for feed-forward postural control in standing man as is seen in feedback control. As both feed-forward and feedback mechanisms function to maintain postural control, we question whether the two are governed by a similar CNS organization of muscular activity. Therefore, the goal of this study was to investigate how standing humans organize their APA's for multi-directional voluntary movements. Our hypothesis is that *as seen for APR's, the central nervous system uses a tuned muscular response that simplifies control of APA's during multi-directional pointing movements.*

CHAPTER 3: METHODOLOGY

3.1 Subjects:

Seven human subjects were used in this experiment; see table 1 for subject measurements. Each was free of any known neurological disorder, severe visual impairment or disease, or musculoskeletal disorders. All gave written consent, and full confidentiality and anonymity were ensured. Subjects were given a brief written description of the experiment prior to participation. The study was approved by the McGill Faculty of Education research ethics board (see Appendix).

Subject	Height (cm)	Mass (Kg)	Arm Length (cm)	Target Distance (cm)	Shoulder height (cm)	Age (Years)
AA	168.0	64.3	65.5	85.0	137.0	23.0
JF	170.0	77.6	69.0	90.0	138.0	21.0
JJ	172.0	62.3	73.5	95.6	143.0	27.0
KM	172.0	52.5	73.0	94.9	135.0	25.0
MF	163.0	53.6	66.0	85.8	137.0	20.0
SJ	168.0	75.4	70.0	91.0	134.4	25.0
WS	172.7	75.3	64.5	83.9	135.0	23.0
Mean	*169.4*	*65.9*	*68.8*	*89.5*	*137.1*	*23.4*
STD	*3.4*	*10.5*	*3.6*	*4.7*	*2.9*	*2.4*

Table 1: Subject measurements

3.2 Apparatus and Subject Set-up:

A custom-built target array consisting of a 180^{o} semicircular array, with 13 illuminating targets placed evenly at 15^{o} intervals was constructed for the experiment, illustrated in Figure 9. The array was fully adjustable in height and target distance to suit each subjects arm length and shoulder height. Each target light was a modified pushbutton gaming switch (model 459512, RP Electronics, Burnaby BC) embedded with a red light-emitting diode (LED) (model KSB-1621, ABRA Electronics, Montreal QC) that lit up by command of the data collection software (see section 3.5). Subjects were aligned in the target array with their shoulders lined up with targets at 0^{o} and 180^{o}, and the xiphoid process at 90^{o}. They stood barefoot centered on an AMTI (Watertown, MA) tri-axial force plate, with their feet at their normal stance position. Tape was used to outline the placement of their feet to ensure that they kept the same foot position for the duration of the experiment. Subjects also wore a chest band with a modified gaming switch embedded to detect movement onset. The activity of 16 muscles was recorded using a 16 channel Delsys Myomonitor III (Delsys, Boston MA) (see Below section 3.3).

Target distance, mean of 89.5 with a standard deviation +/- 45.0 cm, was set at 130% of the subjects arm length (mean of 68.8 +/- 3.6 cm), measured from the acromion process to the tip of their index finger with their arm in 90° shoulder flexion, full elbow extension, and pronation at the wrist. Target distance was set as the distance from the subject's xiphoid process to each target switch while the subject stood upright and centered in the array.

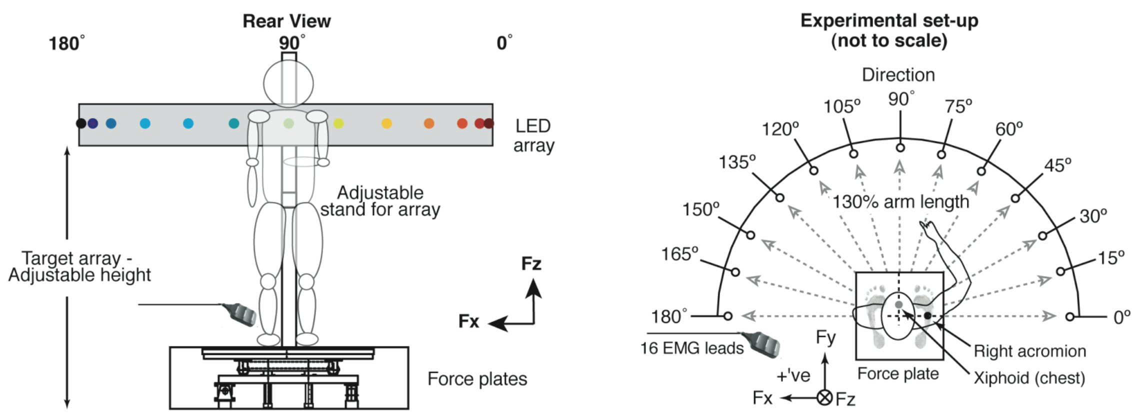


Figure 9: Experimental target array and subject orientation. Targets were placed at 15-degree intervals at subject shoulder level, and at a distance of 130% of arm length. Subjects stood centered in the target array, with the xiphoid process aligned with the 90° target, and the shoulders in line with the 0° and 180° targets, with both feet centered on an AMTI force plate. 16 Delsys EMG leads were attached to the muscle bellies of the specified muscles.

3.3 EMG Placement:

Activity was recorded bilaterally (left and right leg) from: tibialis anterior, soleus, lateral gastrocnemius, peroneus longus, biceps femoris, and rectus femoris muscles. Further muscles were recorded on a single side of the body: left erector spinae, left rectus abdominus (both at the T4 level), anterior and posterior deltoid of the right shoulder (see Table 2 for EMG electrode placements).

Positioning of the EMG electrodes (DE-2.3 Single differential surface EMG electrodes, Delsys) was performed according to the guidelines of SENIAM, (Hermens et al., 1999). Once the location of the muscle belly had been located, the skin was then shaved and scoured with rubbing alcohol to ensure good skin contact with the electrode.

Muscle	Electrode Placement	Orientation
Deltoideus Anterior	One finger width distal and anterior to the acromion.	In the direction of the line between the acromion and the thumb.
Deltoideus Posterior	Centered in the area about two finger breadths behind the angle of the acromion.	In the direction of the line between the acromion and the little finger.
Erector Spinae-longissimus	Two finger widths lateral from the proc. spin. of L1.	Vertical
Rectus Abdominus	Positioned two finger widths laterally at 50% of the line between the xiphoid process and the belly button.	Vertical
Rectus Femoris	Positioned at 50% of the line between the anterior spina iliaca superior to the superior part of the patella	In the direction of the line from the anterior spina iliaca superior to the superior part of the patella.
Biceps Femoris	Positioned at 50% on the line between the ischial tuberosity and the lateral epicondyle of the tibia.	In the direction of the line between the ischial tuberosity and the lateral epicondyle of the tibia.
Gastrocnemius Medialis	On the most prominent bulge of the muscle.	In the direction of the leg
Soleus	2/3 of the line between the medial condylis of the femur to the medial malleolus.	In the direction of the line between the medial condylis to the medial malleolus
Peroneus Longus	Positioned at 25%of the line between the tip of the head of the fibula to the tip of the lateral malleolus.	In the direction of the line between the tip of the head of the fibula to the tip of the lateral malleolus
Tibialis anterior	Positioned at 1/3 on the line between the tip of the fibula and the tip of the medial malleolus.	In the direction of the line between the tip of the fibula and the tip of the medial malleolus.

Table 2: EMG electrode placement directions

3.4 Experimental Procedure:

The experiments took place in the McGill University Balance and Voluntary Movement Laboratory during 3-hour sessions. Subjects were placed within the target array before the onset of the experiments, as described above. Subjects were instructed to stand with their head and gaze facing forwards, their right hand depressing the chest switch. When standing quietly they were instructed to reach and point with their right (dominant) hand to an illuminated target light and depress the target switch as quickly as possible. They were then asked to return to the same initial position and await the next trial.

When ready for a trial, subjects stood vertically, held their right index finger depressing the contact switch placed over their xiphoid process, with their left arm hanging naturally at the side of their body. Once standing quietly at the ready, an experimenter initiated individual trials using an external trigger box (Trigger Module, Delsys, Boston MA). This initiated the data collection software (see section 3.5), and produced an auditory tone signalling the beginning of a trial to the subject. Following the tone at 1000 msec, one of the 13 target LEDs illuminated in a random order. Subjects were to reach as quickly as possible with their right hand and contact the light/target. An acclimatization period was given to each subject, consisting of 1 trial in each pointing direction in a random order, with no data recorded for these trials. Following this, the task was to complete 210 trials in a randomized order, a total of 15 trials in each direction, including 15 null trials where no target was illuminated after the auditory tone to reduce target prediction. Data acquisition occurred for a total 5000 msec, allowing for the recording of quiet background stance and the entire reaching movement. After blocks of approximately 50 trials, subjects were instructed to take a break and relax to reduce effects of fatigue. Subjects were instructed to place their feet back within the tape indicating their initial foot position on the force plate when restarting trials after breaks.

3.5 Data Collection:

Two independent data collection software's (Labview and EMGworks, see below) were used to collect trial data on 1 PC (Intel Pentium 4, 3.40 GHz, 1.0 GB RAM). Both software's were programmed to constantly stream incoming data, but only to begin recording data upon the reception of a 5V pulse on a specific input channel (see Figure 10). An external trigger (Delsys Trigger module) was used to synchronize both software packages for data collection. When the trigger was depressed, it emitted a 5V pulse that was split and interfaced with each software, therefore simultaneously reaching both awaiting software's and synchronizing the initiation of data collection.

3.5.1 Labview:

A custom built Labview (National Instruments, Austin TX) program was created to control the array targets, as well as record all incoming data from target switches and the AMTI force plate (EMG was recorded separately). The PC was interfaced with a National Instruments Data Acquisition Card (NI PCI-6259), which was connected to two National Instrument Connector Blocks (SCB-68). This created a specific output channel for each of the 13 LED targets, a specific input channel for the synchronizing start pulse, each switch (1 chest switch, 13 target switches) and the AMTI force plate (Total = 21 input channels, 13 output channels).

3.5.1.1 Control of the Target Lights:

Upon receiving the 5V input signal from the external trigger, the Labview program was activated. This produced an auditory tone at collection frame 1, signalling the beginning of data collection. 1000 msec after the start pulse a single target light was illuminated in a randomized order.

3.5.1.2 Recording of Input Signals:

3.5.1.2.1 The Chest Switch:

The chest switch was attached to the subject's chest around the xiphoid process. The switch was "normally closed" signifying a pulse of 5V was outputted when it was not depressed. Therefore, until the subject moved the focal arm and released the switch, there was no output signal. Once the chest switch was released, a 5V current was produced that was recorded by the Labview software on a specific channel through the SCB-68 and recorded on the PC, until the chest switch was depressed again.

3.5.1.2.2 Target Switches:

All 13 target switches functioned identically with each having its own input channel through the SCB-68, and were not influenced by the imbedded LED. The switches were "normally open" signifying when depressed they outputted a 5V pulse. Therefore, once hand contact was made with the switch, it outputted a 5V current that was gathered by the

Labview software on a specific channel through the SCB-68, and recorded on the PC.

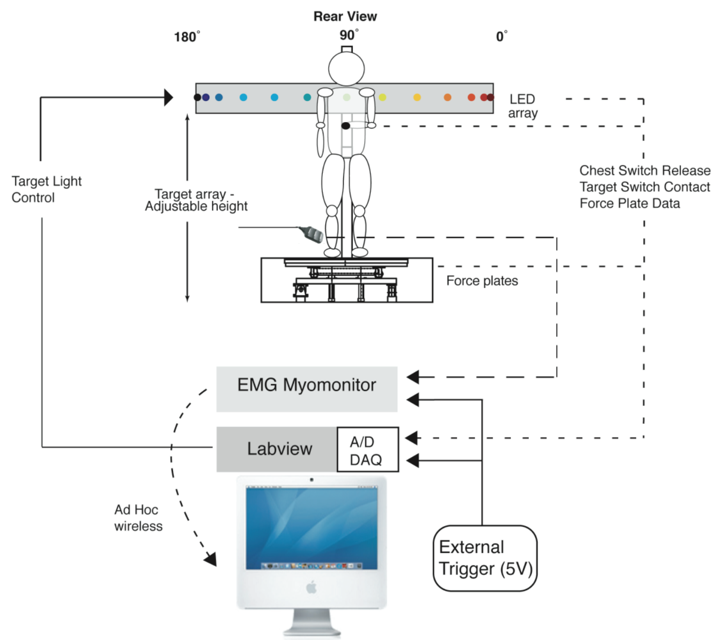


Figure 10: Control of experiment software and data collection

3.5.2 EMG Collection:

EMG data was recorded separately with EMGworks software (Delsys, Boston MA). The electrodes were placed on the muscle bellies and connected to two 8 channel Input modules which connected into the Myomonitor main unit (Delsys Myomonitor III). All signals were recorded at 1000Hz, pre-amplified with a gain of 1000, and bandpass filtered at 20-450Hz. The main unit connected wirelessly to the PC via an ad-hoc direct network, and was connected to the external trigger device. Upon reception of the 5V pulse, the main unit commenced recording of EMG signals and started a real time display of all EMG traces on the PC, where each channel of EMG was recorded and stored.

3.6 Data Analysis:

3.6.1 Movement Time and Trial Rejections:

Focal movement onset and termination were determined from the chest switch and target switches respectively. The movement time (MT) of each trial was calculated as the duration between the onset of the chest switch signal and the onset of the target switch signal. All movement times were pooled for individual subjects. A threshold of 1 standard deviation above the mean was calculated, and all trials with MT exceeding this were immediately rejected. This was based on a roughly normal distribution for most subjects in their MT's (see results 4.1). These slow MT trials were rejected to ensure significant APA muscle activity was evoked, as slow movements have been shown to produce lower amplitude APA EMG signals, as discussed in section 2.6. Further rejection criteria included; any trials where the subject missed a target, trials where a substantial amount of background activity was found in a muscle signifying non-quiet stance prior to target light illumination, or trials were the subject showed anticipation of the target direction by initially moving towards an incorrect target.

3.6.2 EMG Signal Processing:

All EMG signals were recorded and analyzed offline using custom built MATLAB scripts (The MathWorks, Natick MA). A power spectrum analysis was performed on pilot data, and a 100Hz cut-off was chosen. All trials and recorded muscles were treated using identical methods. Trials were de-meaned to return them to a 0 (DC) offset by subtracting the mean value of the entire vector of data from each data point. Trials were then rectified, and filtered with a 100Hz lowpass, second order butterworth filter. Filtering was performed using the filtfilt function of Matlab, which processes the data forwards, and then in the reverse direction to prevent any phase shift from occurring.

3.6.3 EMG Event Tagging:

Events in the EMG data were found using a standardized protocol. The mean EMG background value was determined over 500 ms of quiet stance for each muscle of every trial, beginning 250 msec after the start tone and ending 250 msec prior to the target light onset. Two cut-off values were then created:

- Activation threshold: two standard deviations above the mean of the background.
- Inhibition threshold: one standard deviation below the mean of the background.

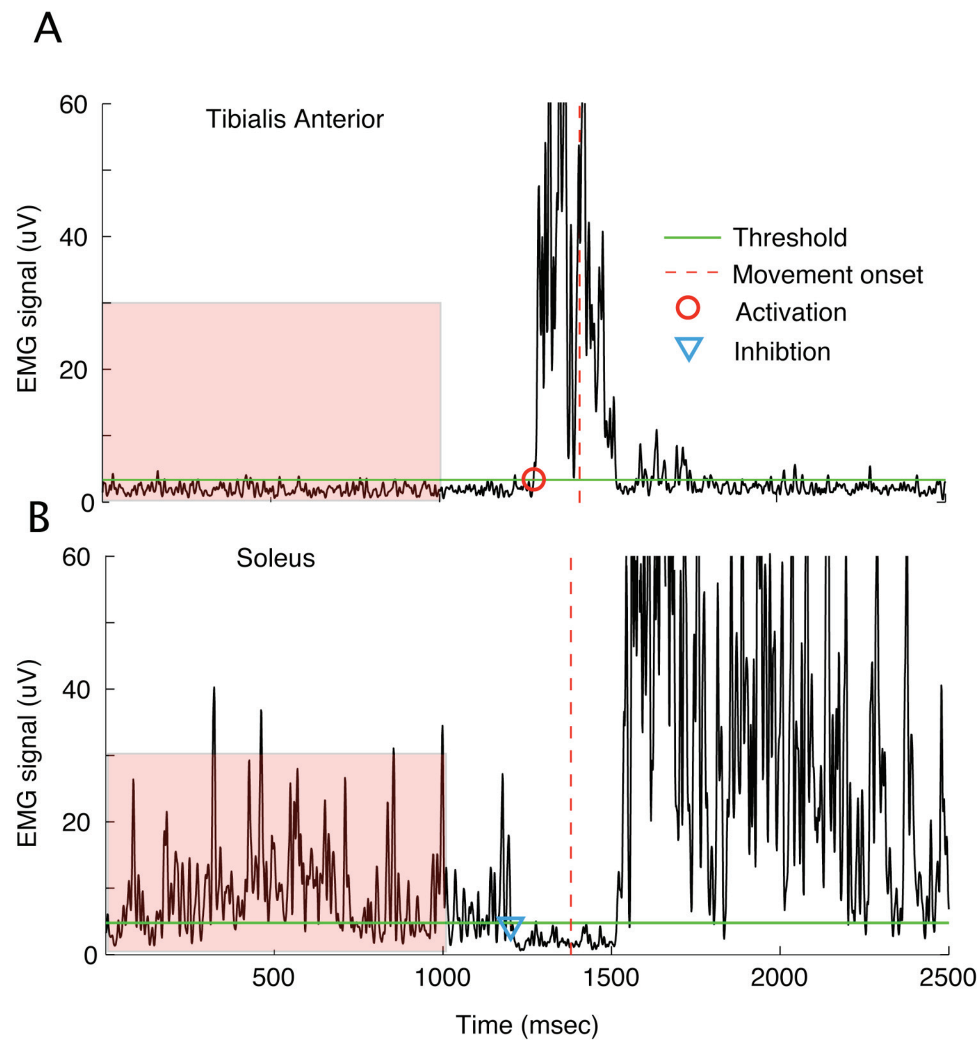


Figure 11: Typical EMG traces showing A) Activation threshold and B) Inhibition threshold, and algorithm determined onset points

Cut-off values were set as a threshold for a search algorithm used to determine the first frame in a processed EMG that surpassed the threshold value, and remained above for a minimum of 25 msec. Figure 11 illustrates typical EMG traces with their determined activation (Figure 11A) and inhibition (Figure 11B).

The background period prior to target light onset is highlighted in red, with the calculated cut-off thresholds clearly indicating the onset of EMG activity. Two separate search algorithms were used, one for activations and the other for inhibitions.

Algorithms searched each EMG trace independently, initializing at the onset of the target light (1000 msec) and tagged the first frame where the threshold conditions were satisfied. Inhibitions were also tagged visually by a single investigator in the Soleus muscles, using a custom Matlab program, as inhibitions thresholds were often not sensitive enough to determine inhibitory activity. All trials were then inspected visually to determine the accuracy of the tagged events by a single experimenter.

3.6.4 Determination on EMG Activation Onset:

Onset times for all muscles were determined as the difference between the tagged onset of EMG activity and/or inhibition, and the onset of the chest switch. All activity occurring between the onset of the target light and the triggering of the chest switch was deemed anticipatory. The APA duration for each trial was set as the earliest onset of all muscles in that particular trial.

3.6.5 Calculation of Amplitude:

EMG amplitudes were calculated as the Root Mean Square (RMS) of the EMG signal between the determined APA onset of the trial and the chest switch onset. The mean background period RMS amplitude was then subtracted to show only the increase in amplitude during the APA period. For individual subjects and muscles, the mean amplitude value was calculated at each pointing direction, and the highest mean response was then used to normalize the muscles responses across all pointing directions. This created a maximum amplitude response of 1 for each muscle at a specific pointing direction, with all other amplitudes being a relative fraction of this peak. The normalized amplitudes of muscles could then be plotted as tuning curves in polar coordinates, allowing comparison between all subjects and pointing directions for each muscle.

3.6.5.1 Calculation of EMG Amplitude in 4 Phases:

The EMG amplitude was also calculated across 4 equal phases of the APA period. The APA period was divided into 4 equal periods, 25% of the entire period. The same RMS calculations were applied to each phase as in section 3.6.5. The values were then plotted as tuning curves in polar coordinates for each phase.

3.7 Statistics:

As subjects performed the same movement under different conditions, or pointing directions, muscle onset times were compared across pointing directions using a Repeated Measures ANOVA using SAS 11 (SAS Institute Inc, Cary NC). The level of significance was set at $p < 0.001$, and a Post-hoc Tukey test was performed to determine differences between individual pointing directions.

CHAPTER 4: RESULTS

4.1 Movement Time:

The duration of the pointing movement (MT) was calculated for all trials as the duration between the onset of focal movement (chest switch), and contact of the target switch with the pointing finger. All subjects were instructed to move as quickly as possible; however, subjects showed a fairly large range of mean movement times from 380 - 725 msec. The grouped MT's for all subjects showed a normal distribution (Figure 12 A), with an over all mean of 560 +/- 135 msec. This distribution shows the MT's were similar across the subjects, and are a good representation of the greater population. There was a significant affect of pointing direction ($F = 7.95$, $P < 0.01$) on MT. Generally, MT increased from targets 0° to 180°, and left side targets showed significantly longer MT than ride side targets (see Figure 12 B).

4.1.1 Trial Rejection Cut-off:

As there was variability between subject MT's, a rejection cut-off was calculated for each subject as the mean MT plus 1 standard deviation to eliminate very slow trials (Figure 12 C). The cut-off values had a range of 448 - 810 msec, with a mean of 646 +/- 113 msec. All trials with MT's beyond this cut-off range were removed from further analysis. The number of rejected trials from each subject ranged between 22 and 63, with a mean of 44 +/- 10. This also included trials where the subjects did not make contact with the target, had a significant amount of body sway or showed significant EMG activity prior to the target illumination.

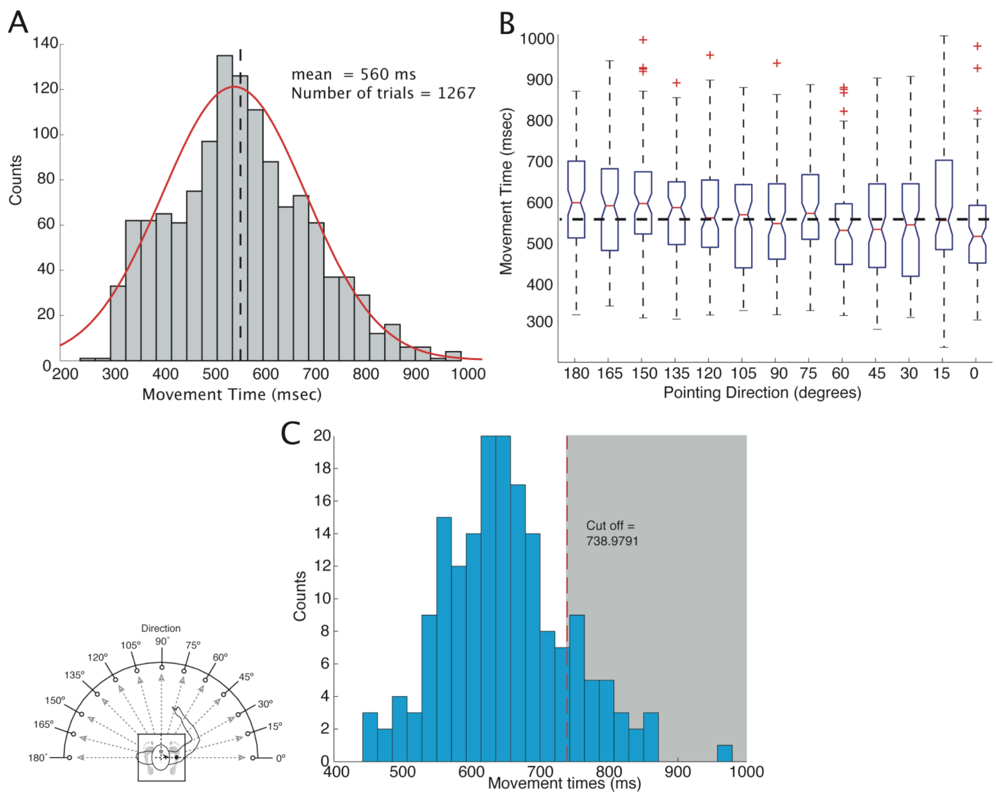


Figure 12: A) Distribution plot of grouped movement times across all subjects and pointing directions. B) Box plot of movement times across pointing directions for all subjects grouped C) Distribution plot of all calculated MT for subject SJ. The trial rejection cut-off of the men MT + 1 Standard deviation is shown, and all trials in the grey shaded region were removed from further analysis.

4.2 General Pattern of EMG Activation in the APA Period:

Individual muscles exhibited changing APA activity throughout the range of pointing directions, from which general activation patterns could be seen. Figure 13 illustrates these typical changes in muscle activity, showing representative EMG traces for individual muscles across all pointing directions for one typical subject (AA). The TibL and TibR muscles are active during the APA period for pointing directions 30° - 150° and 30° - 135° respectively, with no APA activity occurring for extreme side reaches (0° and 180°). The SolL and SolR both showed clear inhibitory activity during the APA period across most pointing directions, with the exception of far contralateral directions for each leg where no APA inhibition occurred. Instead, at these contralateral pointing directions the SolR showed active bursts, and the SolL showed increased tonic activity.

The ESL and BicpL showed similar activation patterns to one another, with APA activity to left side targets only, the BicpR active over 90° - 180°, and the ErecL active over 135° - 180°. The RectL and RectR show reciprocal APA activation patterns, with Rect L active for 30° - 180°, and RectR active for 0° - 105°. The PerL and PerR showed similar APA activation patterns to with each other, active over ranges of 60° - 135° and 60° - 120° respectively.

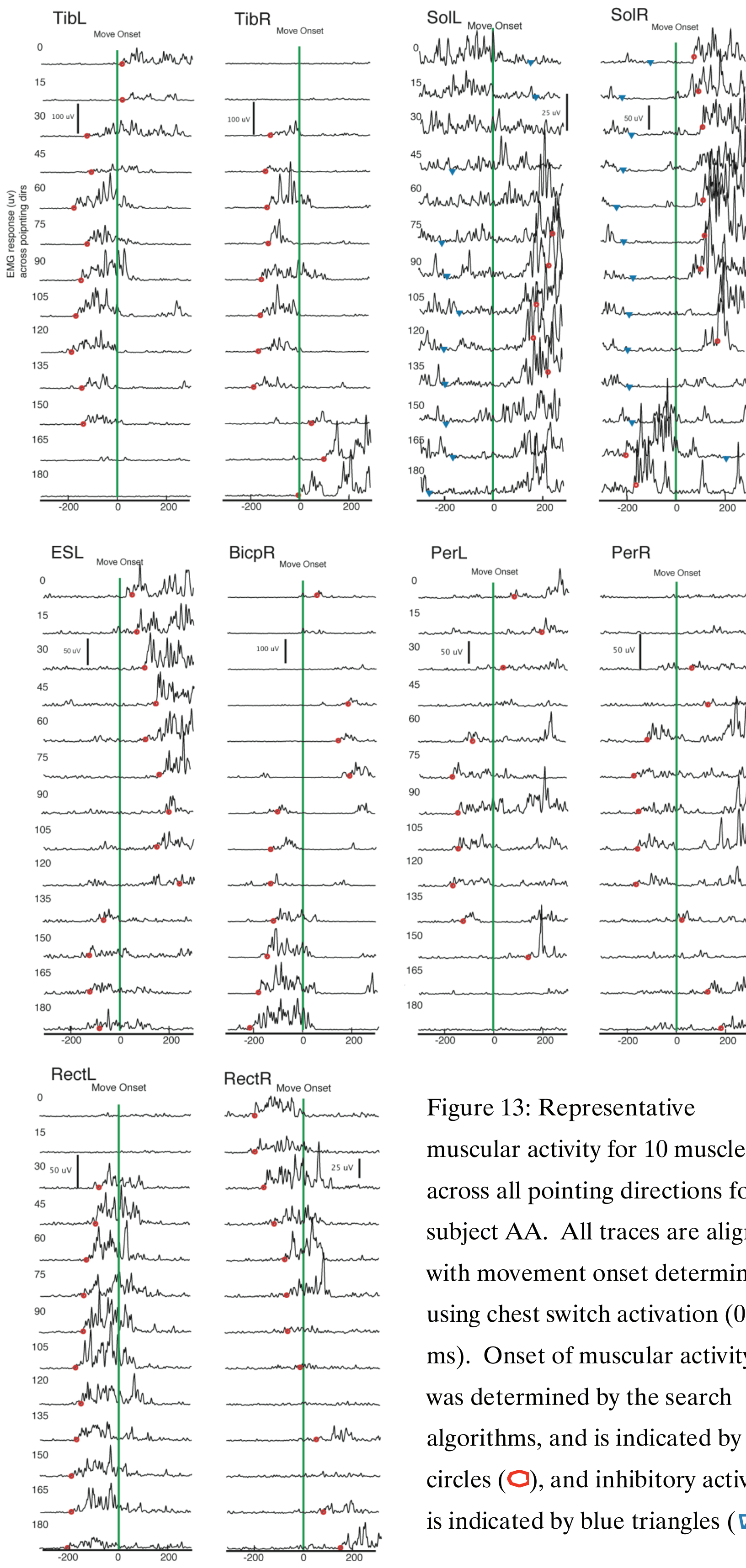


Figure 13: Representative muscular activity for 10 muscles across all pointing directions for subject AA. All traces are aligned with movement onset determined using chest switch activation (0 ms). Onset of muscular activity was determined by the search algorithms, and is indicated by red circles (○), and inhibitory activity is indicated by blue triangles (▽).

4.2.1 Ratio of EMG Onset Activity Across Pointing Directions:

The pattern of EMG activity in the APA period was quantified for each muscle by determining to which pointing directions individual muscles showed consistent APA activity. All trials were pooled at each pointing direction for a muscle, and the number of trials for which the muscle exhibited APA activity was divided by the total number of trials retained for that pointing direction. Thus;

$$\text{Ratio} = \frac{\text{Number of trials showing APA activity for pointing direction}}{\text{Total number of trials retained for pointing direction}}$$

A muscle was required to show APA activity in at least %60 of trials at a particular pointing direction to be considered for further analysis, therefore a cut-off ratio of at least 0.6 was set. Figure 14 shows the calculated activation ratios for each muscle at all pointing directions for the same subject as the representative traces (AA). These plots reflect the pattern of activation and inhibitions seen in the representative traces, as only the directions where a muscle surpassed the 0.6 ratio show APA activity in Figure 13.

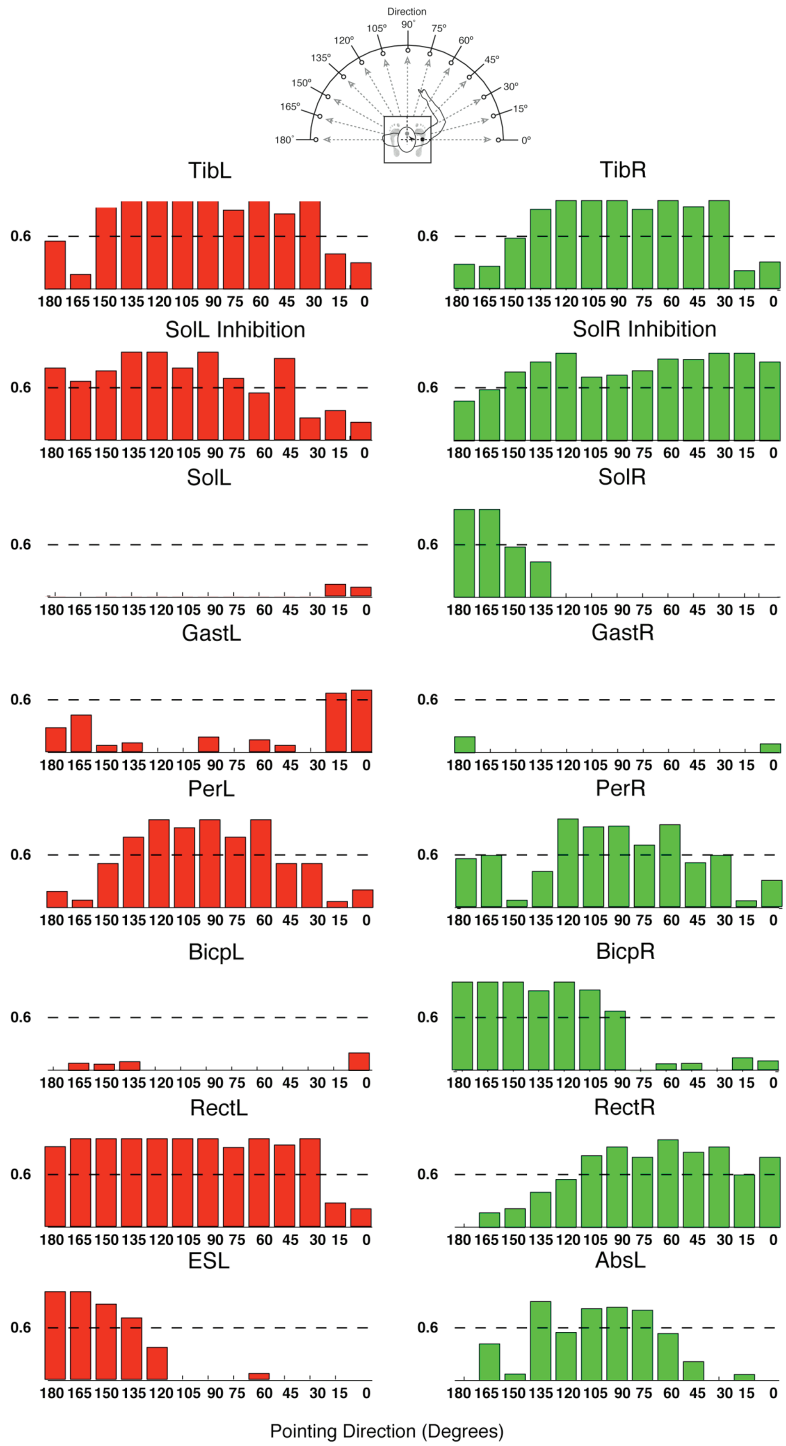


Figure 14: The calculated activation ratio of EMG APA activity across pointing directions is shown for all muscles for subject AA. For each muscle, the number of trials showing APA activity is divided by the number of retained trials for each pointing direction. Muscles we considered to be functionally active at a pointing direction if their activation ratio was > 0.6 (shown as a dotted horizontal line in all plots). This was used to define the range of pointing directions a muscle was activated for in the APA period, and builds the general activation pattern.

4.3 Grand Mean EMG Ratio:

The activation patterns presented in Figure 13 and 14 were a very good representation of the subject population as a whole. The activation ratios were calculated across all subjects to produce a grand mean activation profile of muscle contributions (Figure 15). All trials per pointing direction were pooled for all subjects, and the same 60% activation cut-off was applied. The overall pattern of APA activations for each muscle can be clearly seen in Figure 15, with individual muscles showing significant activations across distinct ranges of pointing directions. The following is a summary of the pattern of activity recorded across the sampled muscles.

Tibialis Anterior: The TibL and TibR showed significant EMG activity across a large portion of the reaching directions, 30° -150° and 45° -180° respectively. The range of active pointing directions of the TibL was very similar across all subjects, where as TibR showed higher variability in its distribution of activity.

Soleus: The Sol muscles showed consistent inhibition across most pointing directions. There was no inhibition for far contralateral pointing directions (165° and 180° for SolR, and 0°-30° for SolL), and the SolR also showed significant burst activity for the contralateral reaching direction (180°). All subjects exhibited very similar patterns of Sol inhibition for both the left and right legs, whereas only 4 of 7 subjects showed SolR bursting activity for the far contra-lateral reaching directions.

Peroneus Longus: both Per muscles showed a general activation range from 60°-120°, with PerR also active at the far contralateral pointing direction (180°). There was high variability between subjects for both peroneal muscles, with one subject showing no activation at all (MF), and another subject showing activation across almost the entire range of pointing directions (JJ).

Rectus Femoris: The RectL muscle was active for all subjects, and exhibited APA activity over the range of 60° - 180° for 5 of the subjects, with activity over a smaller portion of this range for the remaining 2 subjects. The RectR was active in only 6 subjects, and showed high variability in its range of activity. 3 subjects showed significant activity to the ipsilateral and forward pointing directions (0° - 120°), where as 2 others showed activity to the forward and controlateral directions only (75° - 165°). This accounted for the grand mean showing significant activity only over the 60° -105° pointing range, as it was the area of overlap between the subjects.

Biceps Femoris: BicpR exhibited consistent activity during the APA period, over the range of 135° - 180° degrees of pointing directions. All subjects showed significant activity in the BicpR in that range, and three subjects had activity over an increased range of pointing directions. There was no consistent activity in BicpL.

Erector Spinae: ESL was found to be active only across pointing directions 135° - 180°. All subjects had ESL activity within this range, however the amount of significant EMG activity was variable as 2 subjects showed 3 pointing directions of activity (150° - 180°), and 1 subject showed activity over a range of 10 pointing directions (45° - 180°).

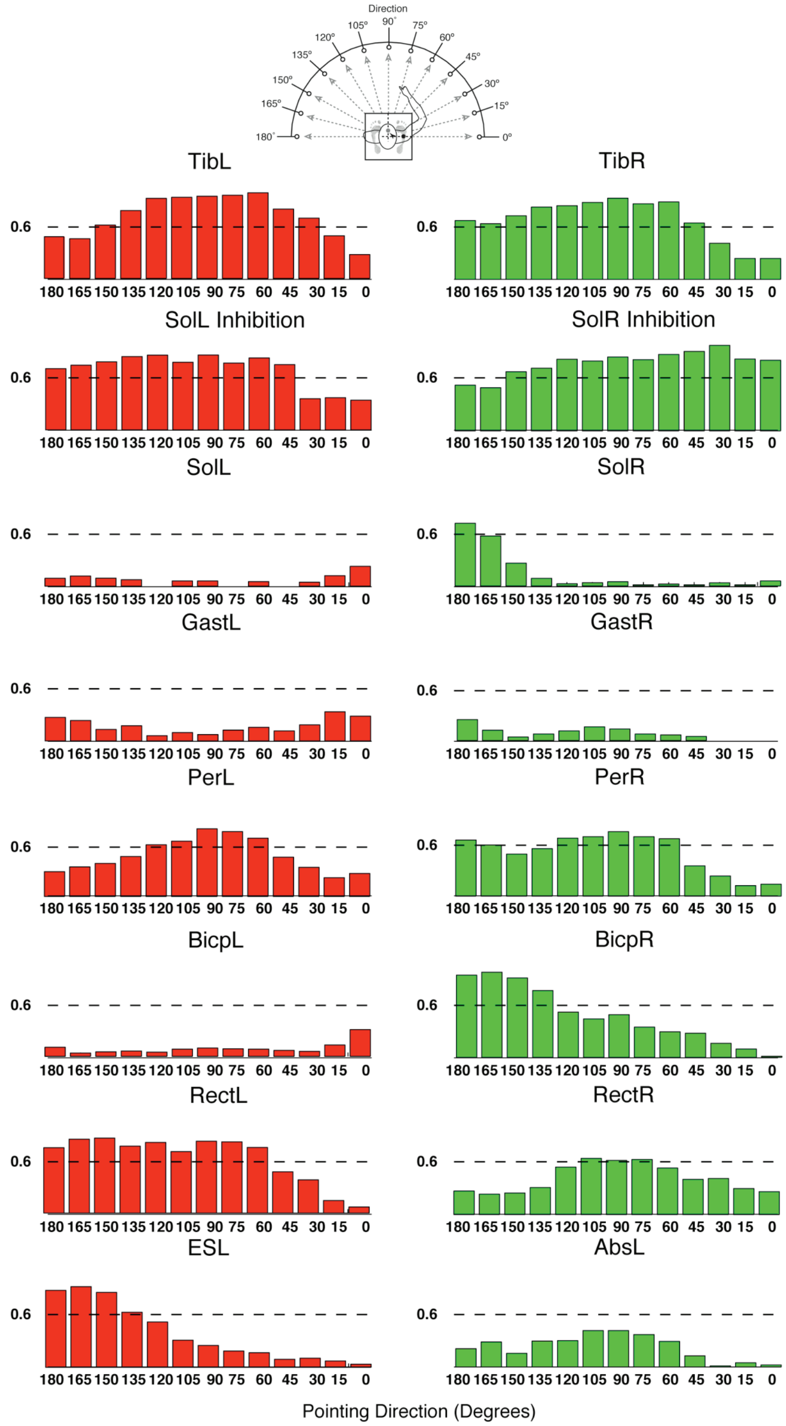


Figure 15: The calculated grand mean activation ratio of EMG APA activity across pointing directions is shown for all muscles across all subjects. For each muscle, number of trials showing APA activity is divided by the number of retained trials for each pointing directions. Muscles are considered to be functionally active at a pointing direction if their activation ratio is > 0.6 (shown as a dotted horizontal line in all plots). This is used to define the range of pointing directions a muscle is activated for in the APA, and builds the general activation pattern.

Examining the activity of the muscles across the subjects, it was found that 7 muscles showed consistent activation in all subjects; TibL, TibR, SolR, SolL, BicpR, ESL, RectL, and a further 3 muscles showed activation in 6 of 7subjects; PerL, PerR, RectR. However, all muscles showed inter-subject variability in the range of pointing directions over which they were active.

Furthermore, 4 muscles were found not to be involved at any pointing direction, GastL, GastR, BicpL, AbsL. Examining the activity of these muscles across individual subjects, the AbsL showed significant activity in only 3 subjects, and the remaining muscles showed very limited activity (maximum of 2 pointing directions) in 1 or 2 subjects.   This lack of activity allowed for these muscles to be removed from further analysis of the directional tuning of APA's.

4.3.1 Variability in EMG Activation Ranges:

The patterns of muscle activation showed a degree of variability between subjects. Several subjects had very similar activation ratio patterns to that of the grand mean, while other subjects showed greater deviation in their range of APA activations across muscles, as well as the combination of muscles being activated. The activation ratio pattern presented in Figure 14 (subject AA) was very similar to the grand mean activation profile with TibL, SolL inhibition, SolR inhibition, ESL having the same activation ranges as the grand mean. Small differences were found for PerR, PerL, and RectL, as each differed from the grand mean ratio by 1 or 2 pointing directions. The largest difference between subject AA and the grand mean can be seen in the RectR and BicpR, each showing an increased range of active pointing directions, with RectR being active to 5 more pointing directions (0° - 60°) and BicpR active to 3 more directions (90° - 120°).

Several subjects showed greater differences in their activation ratio patterns when compared against the grand mean, but many similarities remained.
For example, Figure 16 shows representative traces for subject JJ, and Figure 17 shows their APA activation ratio pattern. These figures illustrate clearly that the SolL, SolR, and ESL have very similar activation ranges to the grand mean. However, substantial differences between this subject and the grand mean can be seen for the TibL, TibR, PerL, PerR and BicpR; these muscles were active to larger ranges of pointing directions. The Rect muscles, however, showed a substantial reduction in the number of pointing directions showing significant APA activity. The RectL was active over 2 pointing directions that also overlapped with the grand mean, and the RectR was active to 3 left lateral pointing directions which showed no significant activity in the grand mean.

Thus, the grand mean results represent a relatively common pattern of muscular activation across pointing directions. The finding that 7 muscles were active in all subjects, 3 muscles were active in 6 subjects, and 4 muscles showed no activity signifies that there was consistency in the muscular activation patterns across subjects for these tasks. Even though there was variability between individual subjects and the grand mean, the amount of similarity between these subjects and the grand mean was much greater that the amount of difference.

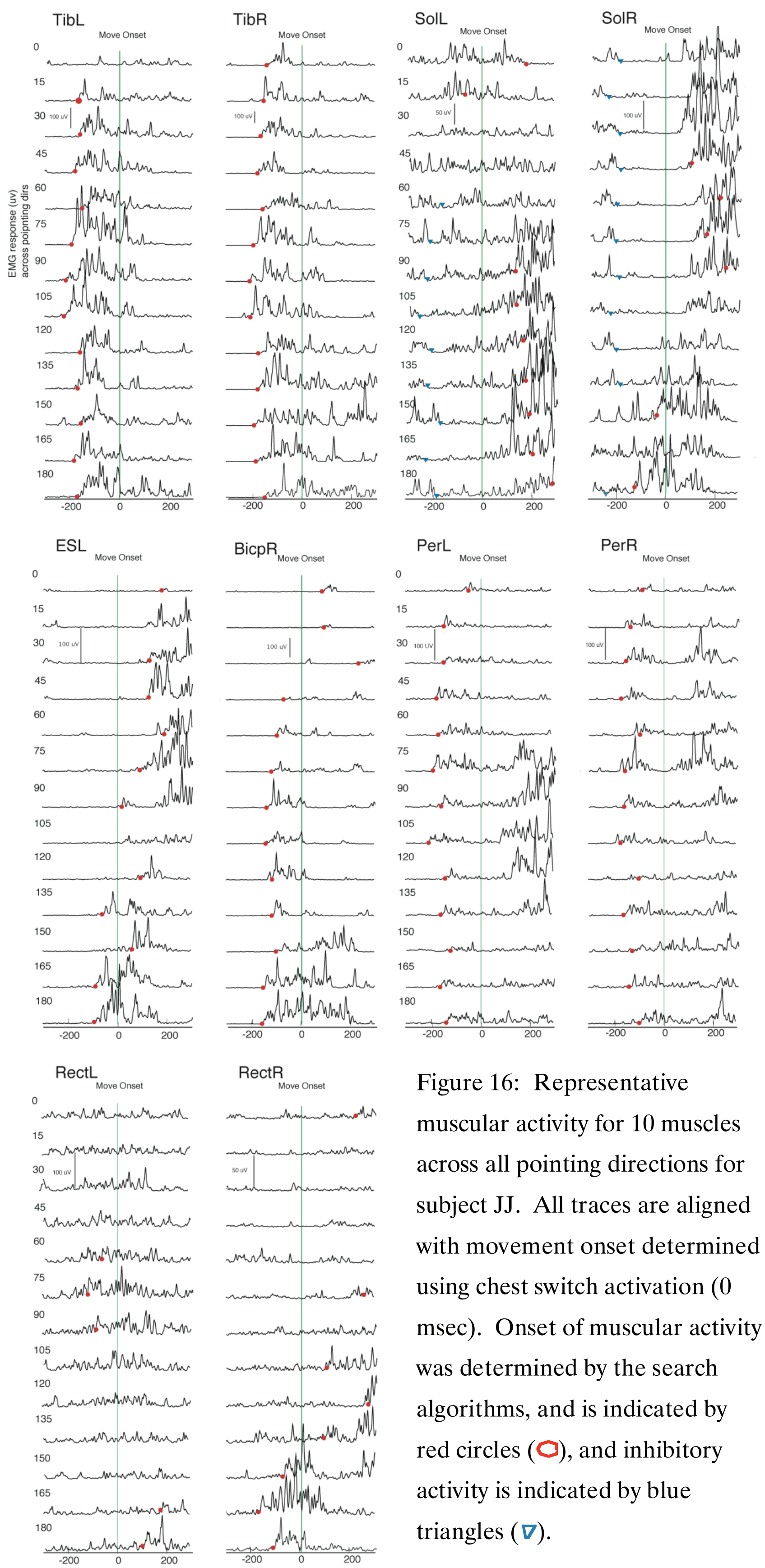


Figure 16: Representative muscular activity for 10 muscles across all pointing directions for subject JJ. All traces are aligned with movement onset determined using chest switch activation (0 msec). Onset of muscular activity was determined by the search algorithms, and is indicated by red circles (⭘), and inhibitory activity is indicated by blue triangles (▽).

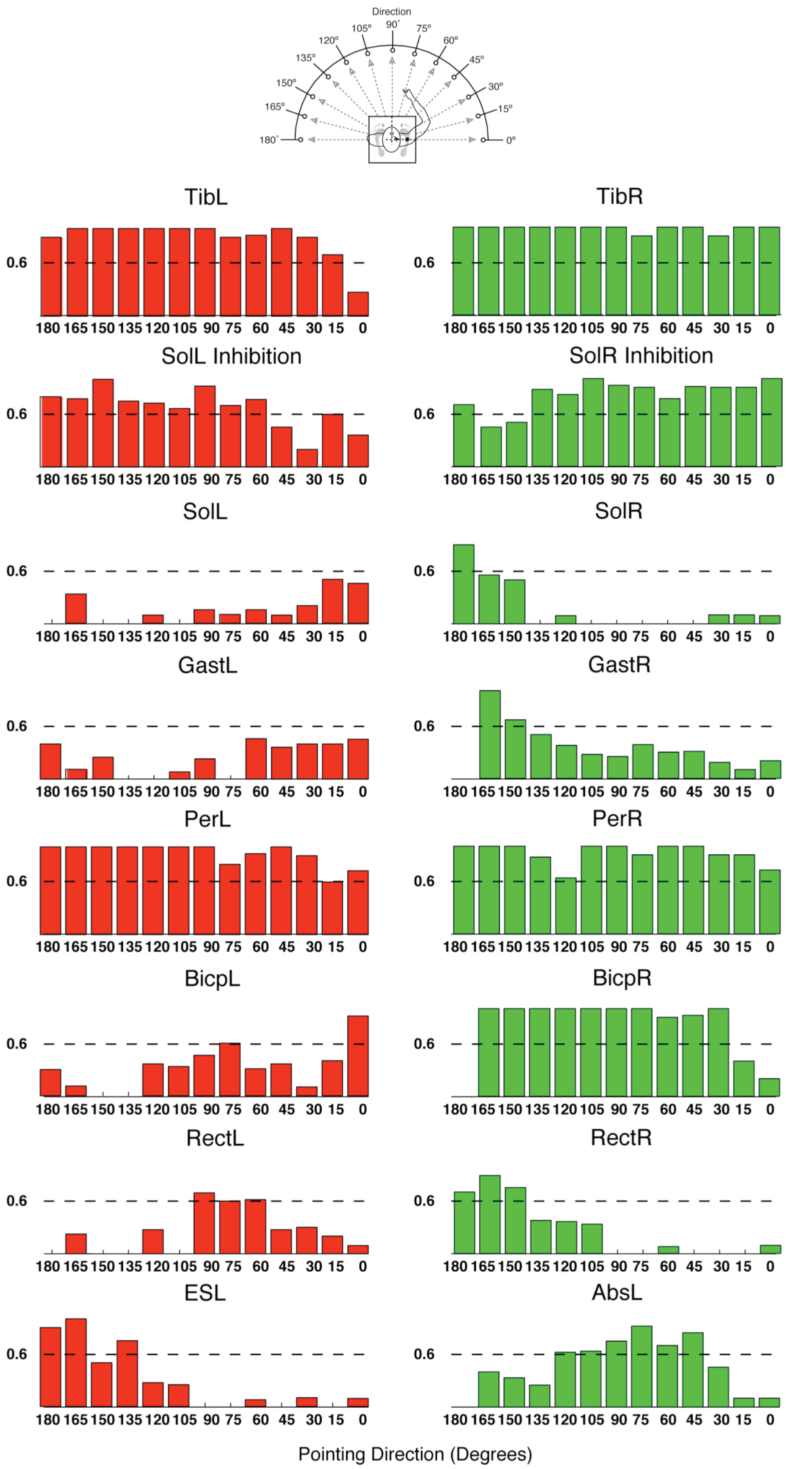


Figure 17: The calculated activation ratio of EMG APA activity across pointing directions is shown for all muscles for subject JJ. For each muscle, the number of trials showing APA activity is divided by the number of retained trials for each pointing direction. Muscles we considered to be functionally active at a pointing direction if their activation ratio was > 0.6 (shown as a dotted horizontal line in all plots). This was used to define the range of pointing directions a muscle was activated for in the APA period, and builds the general activation pattern.

4.4 Onset of the APA Period:

The onset of the APA period was set using the earliest determined EMG `activity, and was calculated from that moment to the onset of the focal movement (chest switch) for every trial. The range of mean APA onset times across subjects was - 201.8 to - 299.7 msec, with a mean of -239.6 +/- 63.8 msec. The pooled APA onset times showed a normal distribution (Figure 18 A), however, there was a significant affect of pointing direction on APA onset (F = 8.57, P < 0.001, Figure 18 B). The trend was for the APA onset to occur earlier as the pointing direction increased to 180°, with post hoc Tukey test showing the main differences occurring between 15° and 120°- 180°, and 30° to 105° - 180° (P < 0.05).

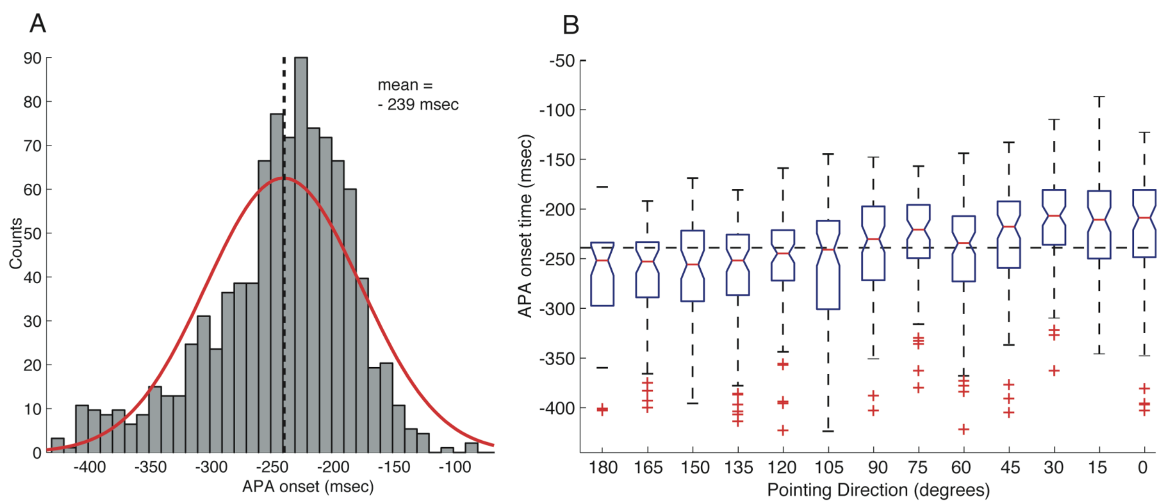


Figure 18: APA onset characteristics. A) Distribution plot of grouped APA onset times across all subjects and pointing directions. B) Box plot of APA onset times across pointing directions for all subjects grouped.

4.5 Muscle Onset Timing:

All muscles showed distinct onsets of activity during the APA period, with some showing significant changes in their onset times as the pointing direction changed. Figure 19 illustrates the mean onset of muscles for each subject at pointing directions where they showed significant activity. As well, for directions where muscles were found to be significantly active in the grand mean activation ratio, the mean onset times across subjects are shown with an asterisk. Generally, APA onset was initiated by an inhibition of a Sol muscle, with both left and right sides having earlier mean onset times than all other muscles (SolL -222 +/- 39 msec, SolR - 211 +/- 50 msec). Across the pointing directions for which they were recruited, the group mean onset times for SolL showed a consistent onset timing of inhibitory activity, whereas the SolR showed significantly later inhibition onset for right side targets (-146 msec) than for 45° -135° (- 213 +/- 50 msec). The SolR also exhibited active bursting for 180 degrees targets, and was active at -156 +/- 76 msec.

This Sol inhibitory activity was generally followed by activation of the Tib muscles (TibL = -172 +/-39 msec, TibR = -196 +/- 54 msec). The TibL showed fairly consistent activation times across active pointing directions, but the TibR showed a significant effect of pointing direction ($F = 7.67$, $P < 0.01$) with the trend for this muscle to be active later for right side targets (45°-60°, mean onset = -128 +/- 28 msec) than forward targets (75°-135°, mean onset = -179 +/- 9 msec).

The RectL showed similar activity to the Tib muscles with a mean onset of -183 +/- 44 msec. The muscle also showed a significant effect of pointing direction on onset time ($F = 12.99$, $P < 0.01$), with onsets for forward directions (60°-90° mean -132 +/- 5 msec) being significantly later than left side targets (105°-165°, mean = -174 +/- 4 msec). 2 subjects showed very late activations to only 3 target directions, one for left lateral directions and the other for forward directions (highlighted in Figure 19).

The onset activity of the RectR muscle was very inconsistent between subjects with a mean of - 138 +/- 43 msec. This was similar to the variability seen in terms of its activation ratio and overall recruitment across subjects, as no clear activation pattern could be seen.

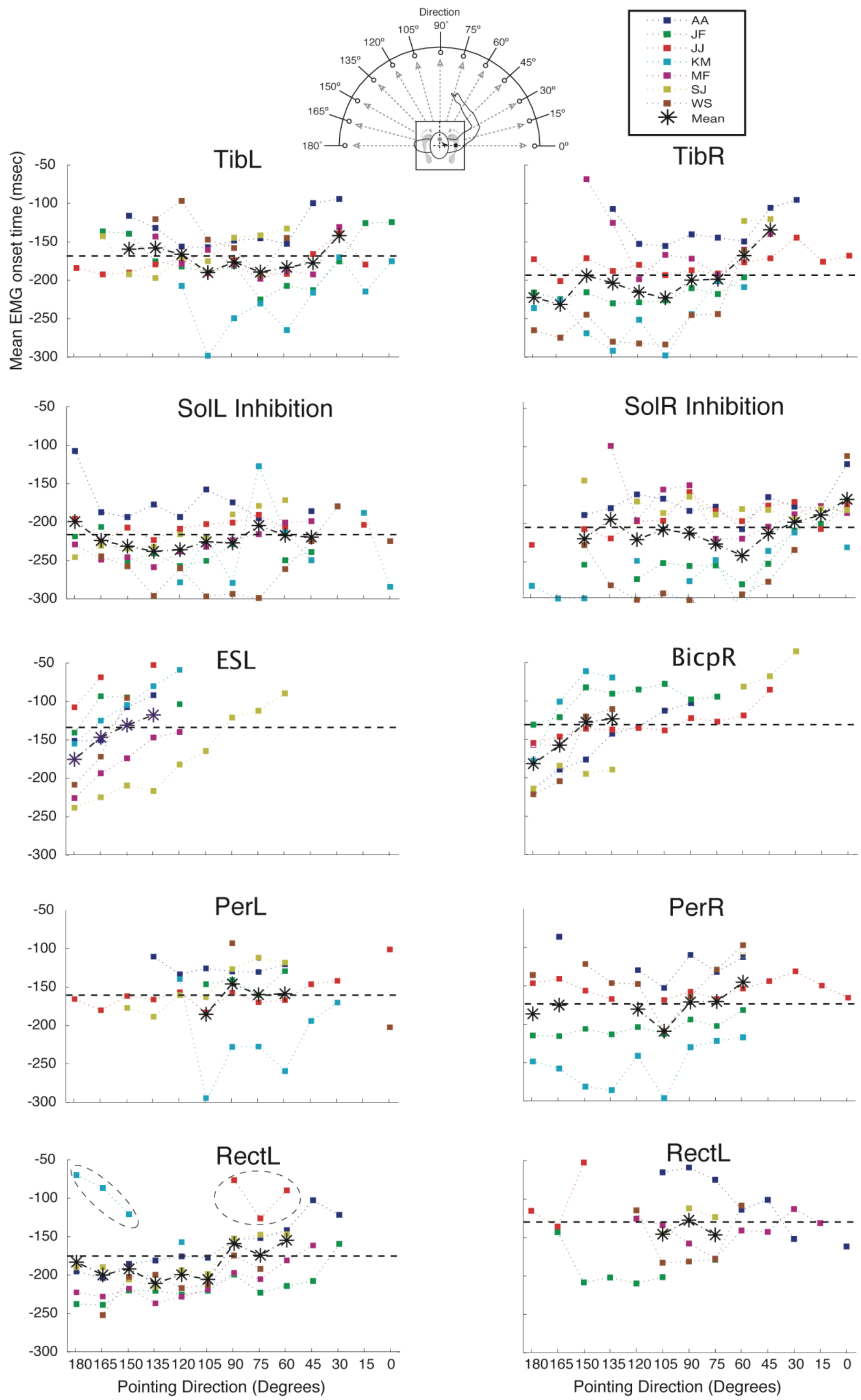


Figure 19: Calculated onset time of 10 individual muscles across all pointing directions for all subjects. Scatter plots represent the mean onset time for each subject at pointing directions for which they showed significant activation ratio activity (>%60). The asterisk represents the group mean for directions muscles showed grand mean activation ratio > %60, and the dashed horizontal line is the overall mean across subjects. All times are relative to the onset of the focal movement as determined by the chest switch.

The BicpR (-131 +/- 46 msec) and ESL (-139 +/- 52 msec) showed progressively earlier activation onset for left side targets from 135°-180°. The ESL muscle was also active significantly closer to movement initiation for directions 135° and 150° ($F = 20.73$, $P < 0.01$) with a mean onset of -106 +/- 10 msec, compared with lateral directions (165° and 180°) at -141+/- 18 msec. The BicpR had a similar onset pattern, with pointing directions 135° and 150° having a mean onset time of -123+/- 41 msec compared with 165° and 180° at -167 +/- 36 msec. For 3 subjects, BicpR had a larger range of active pointing directions, with the same trend of an earlier onset as the pointing direction increased leftwards towards 180°.

Both PerL and PerR were considered significantly active across the forward oriented pointing directions, and had mean onset times of -160 +/- 43 msec and -177 +/- 52 msec respectively. The PerL was very consistent across 5 subjects; however, 1 other subject showed very early onset activity, and the 1 remaining subject showed no APA activity. The PerR was much more variable, with 2 subjects showing little to no activity, and the remaining 5 subjects with onset times very spread out.

4.6 EMG Response Amplitude in the APA Period:

For each muscle, the EMG amplitude during the APA period was continuously modulated across their range of active pointing directions. The normalized amplitude response of 8 muscles is shown in Figure 20 for all subjects (Sol inhibition was not illustrated as the inhibition amplitude was not considered significant). The Root Mean Square of EMG activity during the APA period was calculated for individual muscles in each trial. To illustrate the amplitude variation between pointing directions, mean amplitude responses were calculated for all active pointing directions, and the maximal responses was used to normalize against all others. All muscle examined were active over a distinct range of pointing directions, and showed maximal amplitude response to a single pointing direction, illustrated in Figure 20 with an asterisk for each subject.

The Tib muscles were maximally active to forward oriented reaches, with TibL showing maximal response to directions on the right side of centre (75°) for 5 of 7 subjects. All subjects were tightly grouped for TibL, but TibR showed increased variability between the subject amplitude responses, as the max responses was primarily spread across the left side of centre (90°-135°).

The ESL and BicpR were both maximally active to 180° pointing directions for 6 of 7 subjects, with the remaining subject maximally active at 165°. A clear progression from 90° to 180° degrees can be seen, with a consistent increase in amplitude for both muscles over that range. The polar plots for both muscles showed very similar responses from all subjects.

The Per muscles showed similar amplitude patterns with the Tib muscles, with PerL maximally active to right side targets at 75°, and PerR maximally active to the left side of centre. However, there was more variability seen between subjects than seen for the Tib muscles.

RectL showed maximal activity to forward pointing directions as well, spread evenly between the range of 75°-105°. The amplitude did remained high across the left side pointing directions to 180° for 6 of 7 subjects, and was mostly inactive at right side directions. The RectR was again inconsistent between subjects, with 3 subjects showing maximal activity to forward pointing directions similar to the RectL, 1 subject maximally to the right side targets, 2 subjects to far left targets, and 1 subject with no significant activity at all. The RectR muscle would seem to be functioning differently for each subject.

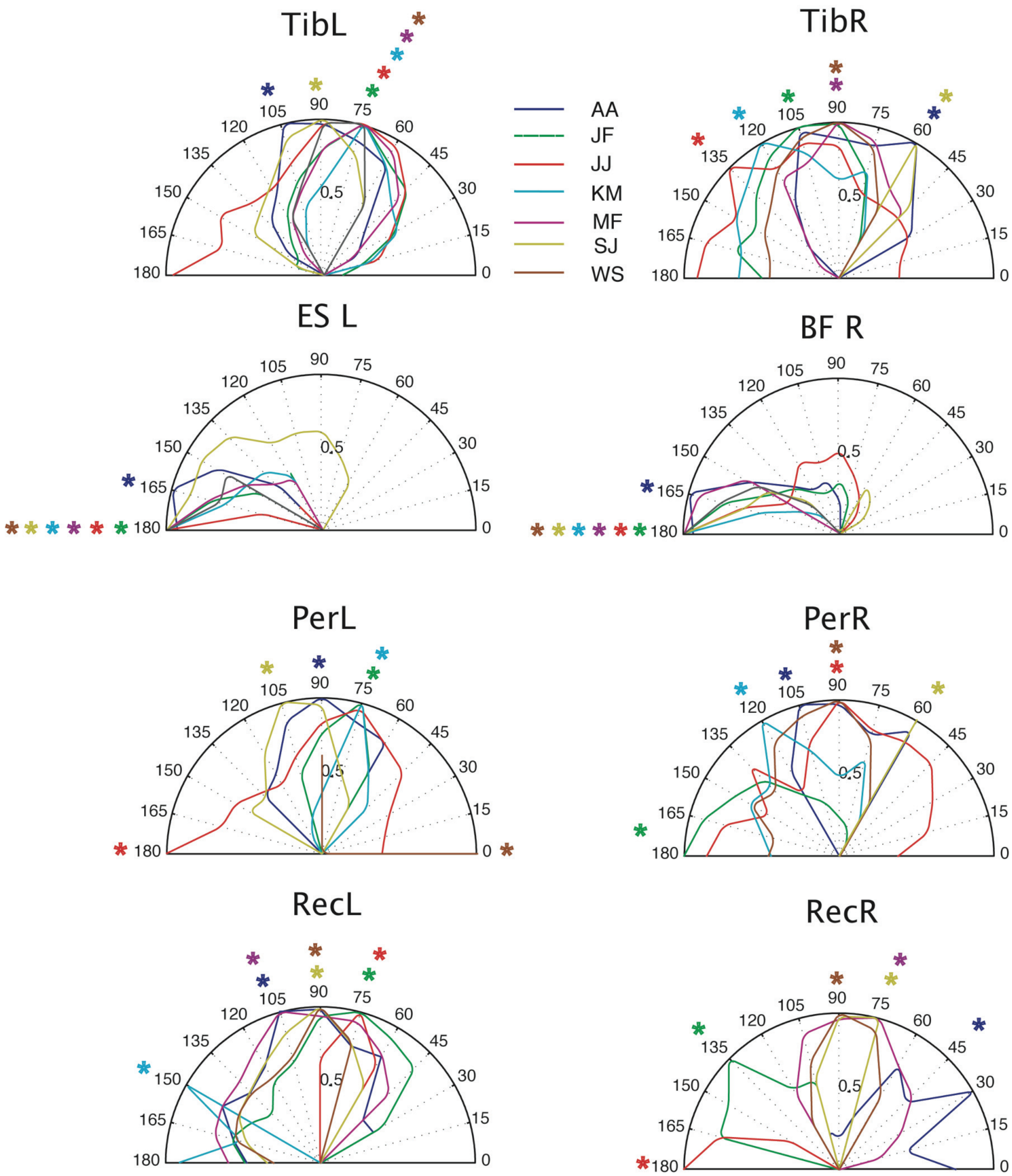
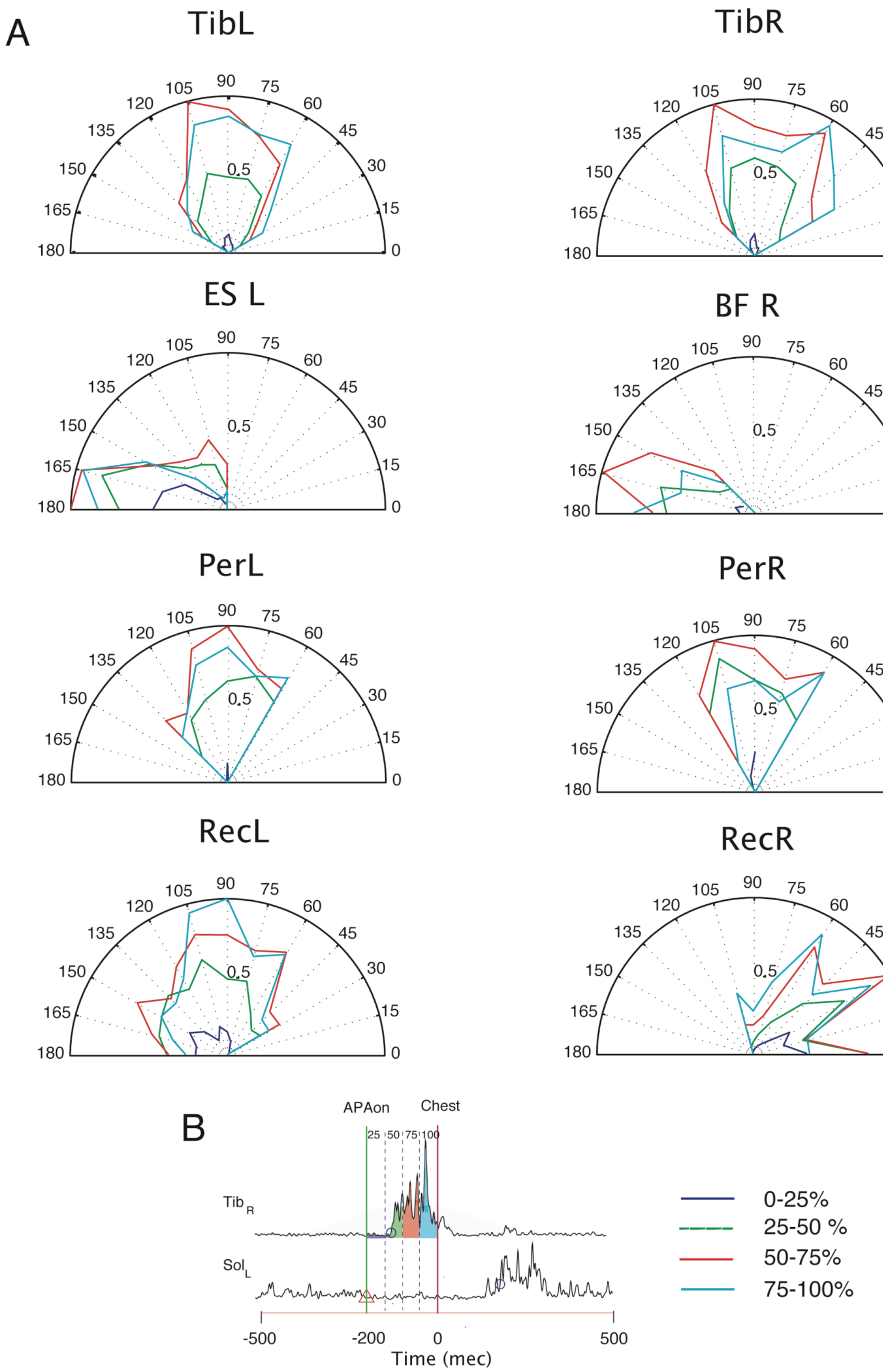


Figure 20: Normalized amplitude response of 8 muscles across pointing directions. All subjects are represented in each polar plot with their mean, normalized amplitude shown in polar coordinates for each pointing direction for which they showed significant activation ratio (>60%). For each muscle, the RMS of the APA period was calculated, and with the direction showing the highest mean value used to normalize all other directions for each muscle. The direction of maximum amplitude responses if represented by an asterisk for each subject.

4.6.1 Progression of EMG Amplitude Over the APA Period:

APA's are active adjustments under direct control of CNS commands, and the EMG amplitude showed significant differences with time. Furthermore, muscular contractions do not reach maximal amplitude instantaneously (see Figure 21 B), as the EMG trace takes time peak. Therefore the production of force from a muscle is not constant over time. To examine the progression of amplitude in muscles, the APA period was divided into 4 equal phases of 25% increments, and the normalized RMS was calculated for each muscle across pointing directions. Figure 21A represents the amplitude response of a single subject (AA) for all phases of the APA period. Across all muscles, peak amplitude responses occurred in the 3rd and 4th phases, representing the period closest to the onset of the movement. However, the spatial tuning of the amplitude remained constant across the phases, with the shape of the tuning curves consistent across phases.



°Figure 21: Amplitude response of a representative subject (AA) calculated in 4 equal phases of 25% of the APA period. A) The RMS amplitude of the 4 phases plotted in polar coordinates, showing the progression of the amplitude response over the duration of the APA period. B) A representative EMG trace of the TibR and SolL muscles, showing the phase divisions and relative amplitude of each phase. Note, SolL is included to show the onset of the APA period and the beginning of the first phase.

The Tib muscles showed consistent early onset in the APA period (Figure 21), however their peak amplitude responses occurred in the later phases of the movement, suggesting initial burst activity continued to increase throughout the APA period. This pattern remained the same for all pointing directions.

The ESL, however, showed an increase in early phase amplitude as the pointing direction increased to 180°. This increase indicates that the ESL produced earlier and higher magnitude burst at lateral directions.

CHAPTER 5: DISCUSSION

As humans are capable of performing many movements during stance that are not solely in the forward plane, this study sought to characterize the underlying organization of feed-forward postural adjustments throughout multiple movement directions. The results showed that the muscular activation during the APA period followed established patterns for forward movements, and distinct patterns of organization were seen with regard to the focal movement direction. Thus, following the original hypothesis, anticipatory muscular activity was organized in a directionally tuned pattern, as previously seen with the organization of feedback driven APR's to surface perturbations across multiple directions.

5.1 The Nature of the Anticipatory Postural Activity:

The results of the study showed that the APA period had similar characteristics to what is established in the literature. APA onset times, with a mean of -239 +/- 63.8 msec across all subjects and movement directions, were found to be well within the range of previously reported onset times, which generally ranged between -150 to - 300 msec depending on the task (Bouisset and Zattara, 1987; Massion, 1992; Stapley et al., 1998; Stapley et al., 1999; Tyler and Karst, 2004). The muscular activity of the APA period for forward pointing directions, 60° - 120°, followed the classic pattern of an initial Sol inhibition followed closely by Tib activation, as is seen across many forward movements (Crenna and Frigo 1991). This activity was ascribed to cause a posterior displacement of the COP, believed to either stabilize posture or initiate the movement depending on the task requirements (Lee et al. 1990, Massion 1992, Stapley et al. 1998). Although the goal of this study was not to quantify the mechanical effects of the APA, Figure 22 shows the EMG activity and the recorded GRF's for 1 typical subject, at 5 principal directions. Briefly, it can be clearly seen that for each movement direction, the muscular activity of the APA period (the shaded region) produces the dynamic changes in the GRF's to initiate the focal movement. For example, at 180° the burst of the SolR and BicpR induced a rightwards force to actively propel the body leftwards. This is opposite to that seen at 0°, where SolR inhibition and SolL tonic activity acted to displace the body rightwards. Thus, the mechanical effects of the APA were to initiate movement towards the target.

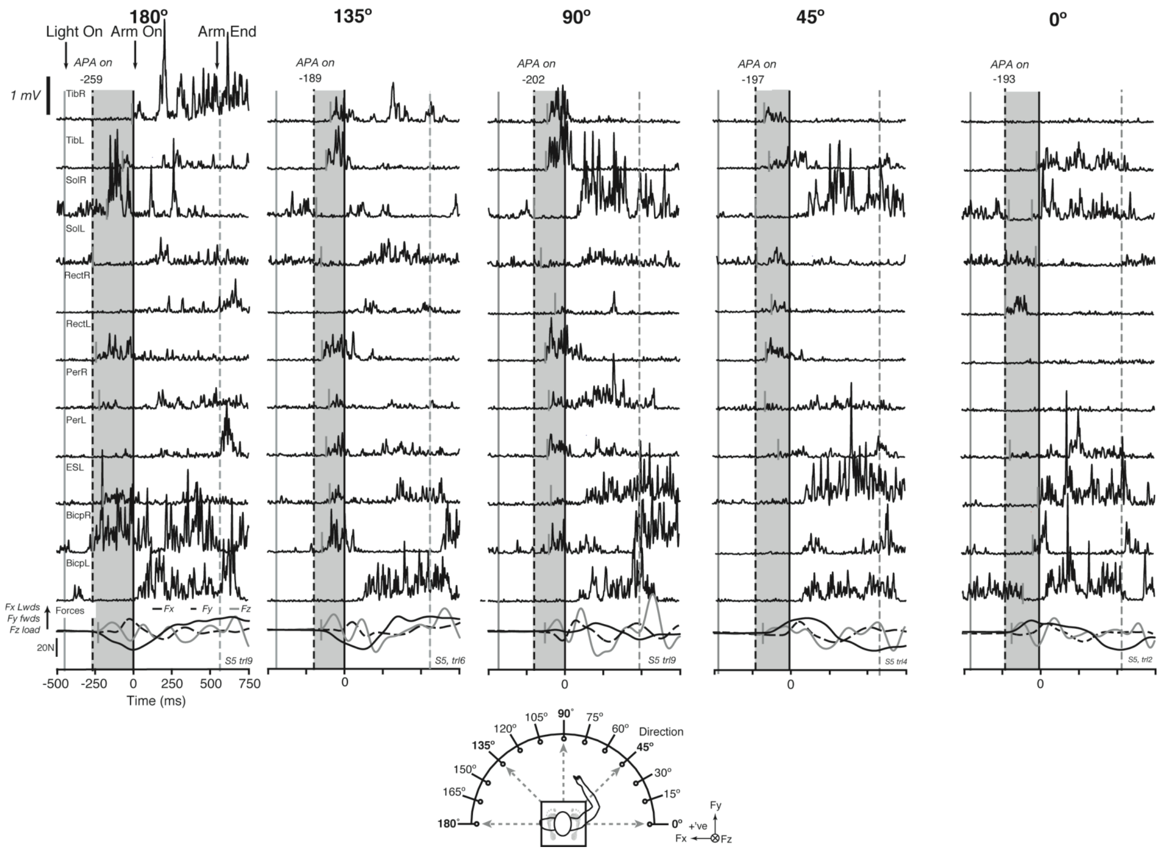


Figure 22: EMG and forces at 5 principal pointing directions for 1 typical subject. Muscular activity initiates the APA period, shown with a vertical dotted line. The mechanical effects occur shortly after onset, shown as ground reaction forces; Fx, Fy, and Fz. The changes in force during the APA can be seen to create the dynamic events to initiate movement in the direction of the intended target.

5.2 The Influence of Target Direction on APA Characteristics:

The primary focus of this study was to characterize the APA period of a movement across multiple directions, and to examine the feed-forward control of posture. A reach-to-point task was used in this study as it has been repeatedly shown to elicit APA activity, with increased target distances producing larger APA's to account for increased perturbations to posture as trunk movement becomes a functional requirement to complete the task (Stapley et al., 1998; Tyler and Karst, 2004). The reaching task also enabled us to examine the directionality of APA's, as subjects are able to perform the same movement across multiple directions. The nature of the focal movement in this study, however, is asymmetrical, as projecting the right arm to left side targets required a much greater body rotation than pointing to right side targets. This is clearly illustrated in Figure 23, which shows kinematic representations of pointing movements to 3 directions, 0°, 90°, and 180°, recorded from one subject. The influence of this extra rotation could be seen in the duration of the pointing movement, as MT increased progressively across the pointing directions (see Figure 12). This effect was also seen across the duration of the APA period, which became progressively longer throughout the target range from 0°- 180° (see Figure 18). Increased APA duration is known to occur for increased task loads (Bouisset and Zattara, 1987; Lee et al., 1990), gait velocity (Breniere and Do, 1986), and reaching distance requirements (Stapley et al., 1998b; Kaminski, 2001; Tyler and Karst, 2004). Thus, it is likely the increased APA duration was to produce greater GRF's to rotate the body and project the COM to left side targets, whereas the shorter APA period seen for right side targets would produce smaller GRF's, as the body is able to rely more on the force of gravity to passively fall towards the target.

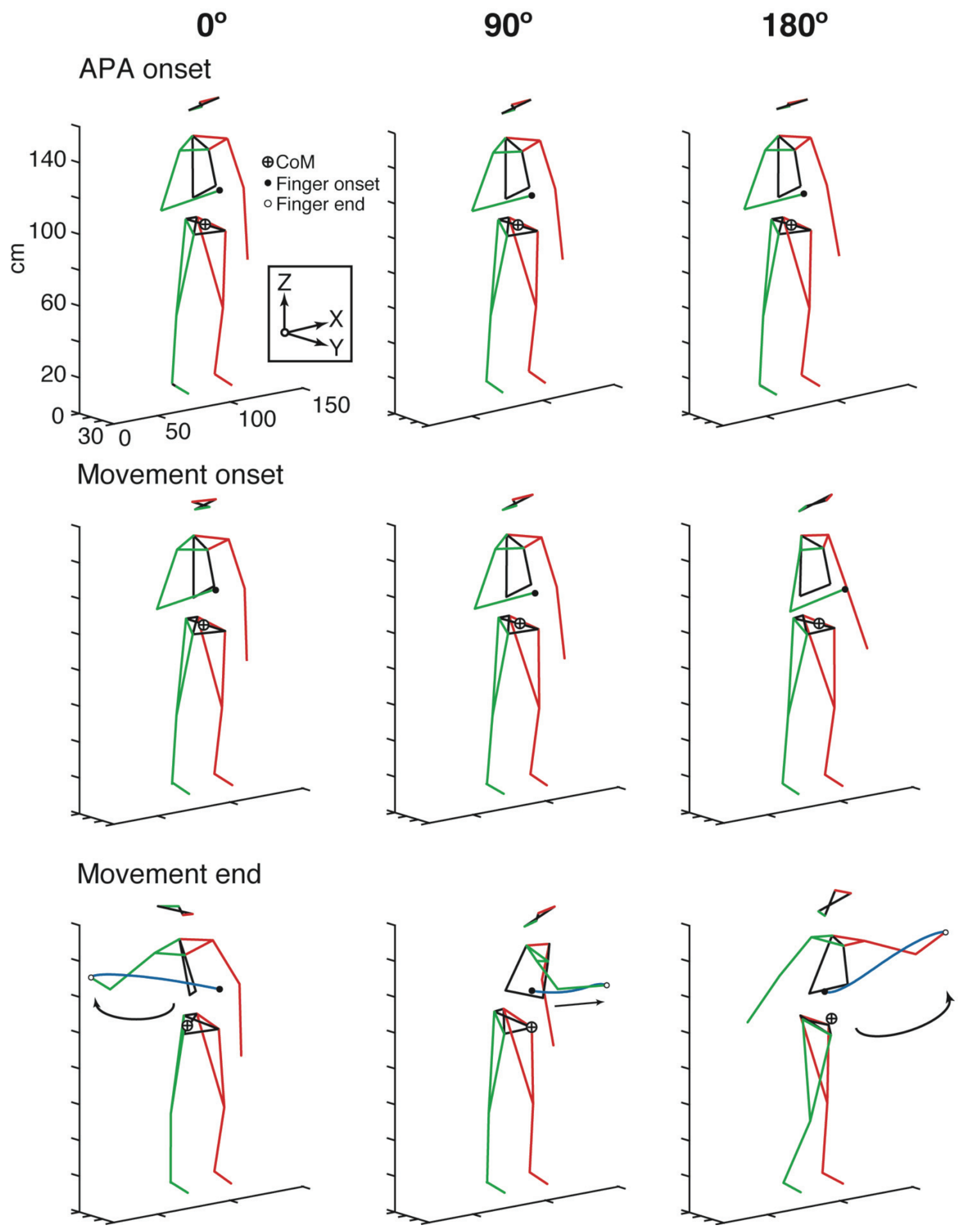


Figure 23: Kinematic representations of the pointing task for 3 periods of the movement; APA onset, movement initiation, and movement end at target contact, across 3 pointing directions 0°, 90°, 180°. The trajectory of the finger is shown by the blue trace, which clearly shows greater range of movement for the 180° targets. The alteration of the leg orientation can be seen as well, with a greater rotation of the legs being required for the 180° target.

5.3 Muscle Involvement Across Pointing Directions:

Forward oriented reaches between 60° - 120° followed stereotypical APA onset patterns; consistent Sol inhibition followed by Tib activation in both the left and right legs, coupled with the activity of the PerL, PerR, RectL, and RectR muscles that function primarily to move the body forward in the A-P plane. Beyond this forward range as the pointing directions moved laterally, the involvement of active muscles progressively changed. However, this change was not symmetrical about both the left and right lateral sides, as there was a greater amount of active muscles for leftward directions as opposed to the right side, as can be seen in the grand mean activation ratio presented in Figure 15.

Right side targets involved a steady decrease in the number of muscles involved from 60°- 0°, as can be seen in the Figure 15, with only the Tib and Sol muscles showing consistent activity across subjects for several pointing directions. The activity of the TibL ceased at 30°, which is the limit of its optimal line of pull for peak torque production (Henry et al., 1998). This coupled with the TibR being inactive beyond 45° indicates the COP is no longer being shifted posteriorly, as this has been tightly linked with Tib muscle activity (Stapley et al. 1998). Indeed, with little more than SolR inhibition across 15° - 0° the body is no longer pulling itself forwards, and is simply decoupling the stabilizing muscles about the ankle and may be relying on the force of gravity to move the COM laterally towards the targets. It should be also noted that examinations of the data showed an increase in the tonic background of SolL, which would act to create stiffness in the left leg and reduce A-P movement about the ankle, thus creating a stable base to ensure postural stability (Horak and Macpherson 1996; Stapley et al. 1998).

The trend for the onset of the SolL inhibition to occur significantly closer to movement initiation at right side targets, as well as for the TibR at 45°, suggests there was less of a need to generate force to these directions, as the body was required less rotation, and could rely more on the force of gravity. A possible explanation for the lack of muscle activity at these pointing directions could be the result of not examining all the required muscles for the movement, as the right side trunk muscles were not included in the experimental set up. For example, no hip abductors were recorded which would act to pull the trunk laterally. There was also greater variability between subjects of muscle activations for these directions, suggesting the movement strategy was not unified among subjects.

Across left side pointing directions between 135°- 180°, there was an increase in the number of active muscles compared to right side directions, with several muscles showing a trend of progressively earlier onset times as the pointing direction increased towards 180°. Similar activity was seen in the Tib and Sol muscles as for right side movements, except that the Sol muscles showed reciprocal activity, with SolL demonstrating consistent inhibitions across the lateral pointing directions. SolR ceased inhibitory activity beyond 135°, but actively participated at 180°, showing consistent APA burst activity. This SolR burst activity was coupled with consistent TibR activity that showed a progressively earlier onset time, along with the PerR exhibiting significant activity again across 165°-180°.

The RectL was active across the forward and left lateral pointing directions, and its onset time become progressively earlier as the pointing directions increased towards 180°. The BicpR and ESL were exclusively active in this range, and showed increasingly earlier onsets as the direction moved from 135° - 180°. This is the opposite of what Tyler and Karst (2004) found for ES onset, which showed onset activity during the APA period for short reaches and moved progressively later until ES onset occurred after movement initiation for reaches beyond arm length. They attributed the earlier APA onset to function to stabilize the trunk and resist the destabilizing effects of the arm movement, whereas the later ES onset may represent slowing down the trunk during the movement, thus changing the role of the muscle according to the task requirements. Therefore, this progressively earlier onset of the ESL in our task may represent increased trunk stabilization to accommodate the rotational moment to left side targets. Furthermore, the earlier RectL activity may have related to this earlier ESL onset, as it spans the hip joint and may have acted to prevent over extension of the back, and to act to flex the trunk forwards to reach the target. The late SolL inhibition would remove the tonic plantar flexion moment it creates, allowing the left leg to freely move about the ankle, similarly to the inverted pendulum model (Winter et al., 1998).

The activity of the right leg muscles suggests they initiated the rotational moment for the movement. The BicpR showed progressively earlier onset that would flex the knee joint, loading the right leg and shifting the COP to the right. This was in parallel with the TibR being active earliest across the left directions, actively pulling the right leg forward and laterally left. Following the TibR activation, at 180° the SolR showed active bursting at -157 msec, thus creating a large plantar flexion force, which is also seen in gait initiation to propel the COM forwards and accelerate the swing leg of the first step (Breniere and Do, 1986; Brunt et al., 1999)

5.4 Muscle Tuning Curves:

The results of this study indicate that for feed-forward postural adjustments, muscles produced a directionally tuned amplitude response across a distinct range of pointing directions. This supports our original hypothesis. The results illustrate that APA's are directionally specific, with each muscle having a direction of preferred maximal activity. The direction of peak amplitude response was generally in line with each muscles functional alignment, as the majority of the muscles were maximally active for forward directions. However, the ESL and BicpR were maximally active to 180°, which is orthogonal to their forward line of action. Similar results were reported in studies of APR's, where muscles were often maximally active along a diagonal axis (Macpherson 1988; Henry et al. 1998). These authors suggested that the muscle activation patterns are not necessarily based on the best mechanical advantage of the muscles and a more global control variable, such as forces during the force constraint strategy, is used to govern the muscular activation patterns (Macpherson 1988a; Henry et al., 1998). This may be the case in this study, but a detailed analysis of the forces would be needed.

The muscle tuning curves of this study can be placed into 3 groups based on their range of active pointing directions; Forwards (TibL, PerR, PerL), Left lateral (ESL, BicpR), and Forward lateral (RectL, TibR). The forwards group follows the anatomical line of action for the muscles, as they primarily control A-P ankle force, whereas the lateral group is maximally active to pointing directions that are orthogonal to the muscles line of action. The Forward lateral group overlaps with the other 2 groups, as the muscles show peak amplitudes for forwards pointing directions, but maintain high amplitude responses across to 180°. These groupings illustrate that multiple muscles show similar patterns of activity, however, they do not necessarily perform similar anatomical roles. The ESL and BicpR show very similar activation patterns but have very different functional roles, as they are not physiological agonists or antagonists. This illustrates the possible synergistic activity of the muscles, as they are controlled together in functional groupings. These groupings then overlap to produce a continuum of muscle activation patterns to create feed-forward postural adjustments (Moore et al. 1988; Henry et al. 1998).

5.5 Why a Directionally Tuned Muscular Organization of Feed-forward Postural Adjustments?

The tuned muscular responses found represented a modulation of the muscular responses across the focal movement directions. Directionally tuned responses seen during feedback postural responses to perturbations in multiple directions were considered to be a method employed by the CNS to simplify the control of the musculature. Directionally tuned responses are thought to result from a synergistic control of muscles by the CNS, wherein a synergy can been defined as a group of muscles constrained to act in a concerted manner with similar activation gains and spatial activation patterns (Macpherson, 1991, Henry et al., 1998, Torres-Oviedo et al., 2006). Synergistic muscular control allows for the rapid activation of appropriate muscles by a single neural command, thereby reducing the required control of the CNS through decreasing the number of variables, degrees of freedom, that it must account for (Ting and Macpherson, 2005; Torres-Oviedo et al., 2006). The extreme alternative to synergy control is the independent activation of each muscles response, which would place a large computational strain on the CNS. Henry et al. 1998 found muscles could be grouped into three functional clusters based on their direction of peak amplitude, and the range of perturbation directions for which they were active. However, muscles were not ‘hard wired’ into synergies, meaning muscle are not fixed into a single functional group, as muscular responses have proven to be highly modifiable and adapt to changes in postural alignment, stance width, etc. (Macpherson, 1988b, 1991; Henry et al., 1998, 2001)

Using recent computational techniques, several groups have shown that the muscular patterns of postural responses can be accounted for by multiple, overlapping synergy groupings, wherein a muscle may belong to more than one synergy at any given time (Ting and Macpherson, 2005; Torres-Oviedo et al., 2006). Within each synergy, the muscle has a fixed proportion of activation, and the CNS produces movements by altering the strength of the motor command to activate each synergy. Therefore, the ensuing EMG response of a muscle represents the sum of the weighted activation from each synergy (Ting and Macpherson 2005). Torres-Oviedo et al. showed that 5 functional synergies were robust across multiple perturbation directions and several postural alignments, accounting for > 80% of variability in the EMG and force tuning curves, and were similar across subjects.

They propose that synergy control forms part of the neural control apparatus for balance maintenance, and that synergies should underlie the organization of other automatic postural responses, as well as voluntary movements (Torres-Oviedo et al. 2006).

The APA responses seen in our results show a similar directionally tuned activity, suggesting there may be a synergistic organization for feed-forward control of posture as well. Furthermore, the spatial tuning of the muscles was consistent across 4 phases of the APA period (Figure 20) showing the amplitude responses patterns were not variable, and were consistently scaled throughout the APA. This consistent directionally tuned response further supports the idea that APA's are pre-planned according to the forthcoming movement. The ability of the CNS to predict the outcome of a movement is thought to occur through the use of internal forward models, which act to predict the sensory consequences of a movement and the future state of the motor system (Kawato et al., 2003; Davidson and Wolpert, 2005). Forward models are developed through motor learning, which occurs progressively throughout life using movement experience, the resulting sensory feedback, and further adaptation to create an internal representation of the body (Kawato et al., 2003; Shadmehr and Wise, 2005). Thus, the estimate of the sensory consequences of a movement from the forward model facilitates the CNS producing an appropriate APA motor command. Therefore, feedback information received from movements is drawn upon to update the internal model, allowing upcoming APA's to be modulated accordingly.

5.6 Conclusions:

Feed-forward postural adjustments are pre-planned with reference to focal movement requirements. As the movement direction changes, our results showed that the musculature is organized in a directionally tuned manner, indicating that feed-forward adjustments are produced in accordance with the directional component of the movement. This supports our hypothesis that feed-forward and feedback postural control mechanisms show a similar central nervous system organization.

5.7 Further Research:

This study provided the framework from which much further research can be performed. Our results of tuned muscular responses across movement directions provided evidence of simplification of muscular control by the CNS for postural adjustments. However, more work is required to examine the involvement of other muscles that may be involved, particularly for the lateral pointing directions which have been examined much less in previous research. This study examined muscles that control primarily forward oriented movements, which may be a partial explanation for the limited muscular responses seen for right lateral targets.

An examination of the effects of stance width on the organization of APA's in our research paradigm would shed light on how the postural strategies are adopted in different postural configurations. Assuming a similar CNS organization to APR's, we would expect to see an amplitude modification in muscular responses across stance widths, with the muscles showing similar spatial tuning patterns. This would supply further evidence for a simplified synergistic control of muscles; however, a computational analysis would be necessary to determine if a robust synergy organization exists across pointing directions and stance widths.

5.8 Limitations:

This study has two experimental issues that have become known over this process. The first issue relates to the recorded muscles, as it would appear that there was insufficient EMG recording of right side muscles. This is an inherent difficulty with EMG analysis on whole body movements, as it is impossible to take into consideration all muscles of the body that may have been involved in the movement. Previous studies examining whole body movements have limited EMG placements to a single side of the body, and assumed symmetry between the left and right side of the body. However, this is clearly not possible in our experiment, as has been highlighted by the differences between several bilaterally recorded muscles, predominantly the Rect and Bicp muscles. Regardless, we would predict that additional muscles would show similar tuned amplitude responses and onset timing.

The second issue is the placement of the subjects feet, as they were asked only to stand at a natural stance width. This may influence each subject's postural strategy, as stance width is associated with an alteration in muscular organization. This may have been a factor into the large discrepancies seen between subjects for several muscles. Forcing subjects into a measured stance width, proportional to their shoulder width may allow tighter control of subject positioning. However, this may force the subject into an unnatural position and create an alteration of their postural strategy as well.

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APPENDIX

McGill

Faculty of Education – Ethics Review Board
McGill University
Faculty of Education
3700 McTavish; Room 230
Montreal H3A 1Y2

Tel: (514) 398-7039
Fax: (514) 398-1527
Ethics website: www.mcgill.ca/rgo/ethics/human

Faculty of Education – Review Ethics Board
Certificate of Ethical Acceptability of Research Involving Humans

REB File #: 605-1005

Project Title: ***The Coordination of Posture and Voluntary Movement***

Applicant's Name: Paul Stapley **Department**: KPE

Status: Faculty **Supervisor's Name: n/a**

Granting Agency and Title (if applicable): NSERC

Type of Review: Expedited ✓___ Full _____

This project was reviewed by: Stringer/McAlpine/Bracewell

Approved by R Bracewell Oct 19, 2005
____
Signature/Date
Robert Bracewell, Ph.D.
Chair, Education Ethics Review Board

Approval Period: Oct 19/05 **to** Oct 19/06

All research involving human subjects requires review on an annual basis. An Annual Report/Request for Renewal form should be submitted at least one month before the above expiry date. If a project has been completed or terminated for any reason before the expiry date, a Final Report form must be submitted. Should any modification or other unanticipated development occur before the next required review, the REB must be informed and any modification can't be initiated until approval is received. This project was reviewed and approved in accordance with the requirements of the McGill University Policy on the Ethical Conduct of Research Involving Human Subjects and with the Tri-Council Policy Statement on the Ethical Conduct for Research Involving Human Subjects.

10/19/05