An Examination of the Effects of Equilibrium Constraints on the Control of Goal-Directed Reaching in Humans

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DEDICATION

This document is dedicated to my favorite kid in the world, my brother Justin.

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LIST OF ABBREVIATIONS

aAPA	associated anticipatory postural adjustment
APA	anticipatory postural adjustment
BoS	base of support
CoG	centre of gravity
CoM	centre of mass
DA	anterior deltoid
DF	degree of freedom
GRF	ground reaction force
ISI	inter-stimulus interval
MT	movement time
pAPA	preparatory anticipatory postural adjustment
PD	preferred direction
PPC	posterior parietal cortex
RT	reaction time
TA	tibialis anterior

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ABSTRACT

Goal-directed reaching movements executed from seated positions exhibit rapid, automatic corrections in response to a change in target position. In the standing posture, corrections in arm trajectory during reaching movements are accompanied by feedforward corrections in postural activity which create the dynamical conditions necessary for successful task execution. However, it is unknown how equilibrium constraints associated with standing as opposed to sitting, which has little or no equilibrium constraints, influence the neural processes underlying online corrections of goal-directed movements. This thesis aimed to address this question. Eight healthy adult subjects (3 males, 5 females) performed regular reach-to-point movements and an online arm correction task when seated and when standing. It was hypothesized that the increased equilibrium constraints during stance would influence the online control of goal-directed reaching, resulting in differences in focal movement endpoint kinematics. The focal reaching movement was described using spatiotemporal kinematics of the reaching hand. Whole-body kinematic analyses were also performed to compare the movement strategies utilized in each postural configuration. It was found that the postural configuration (seated vs. standing) in which the movements were executed generally did not affect focal movement parameters (velocity profile, movement time, time to correction, and peak velocity), despite resulting in different whole-body kinematic strategies (i.e. extent of elbow flexion-extension, shoulder adduction-abduction, trunk rotation, pelvis rotation, pelvis obliquity, and pelvis translation). These results highlight the efficacy of the neural processes underlying the end goal of arm reaching movements and their online control. The processes of control do not appear to be affected by the higher demands placed on the CNS required for the maintenance of postural equilibrium during stance.

ABRÉGÉ

En position assise, les mouvements de pointage sur une cible visuelle démontrent des corrections rapides et automatiques lors d’une perturbation spatiale de la cible. En position debout, des corrections posturales anticipent les corrections de la trajectoire de la main et créent les conditions dynamiques requises pour le déroulement du mouvement. Cependant, nous ne savons pas comment la position debout, qui pose plus de contraintes d’équilibre sur le mouvement que la position assise, affecte les processus neuraux à la base des corrections en ligne des mouvements de pointage. Le but de cette étude est d’aborder cette question. Les sujets (3 hommes, 5 femmes) ont pointé une cible visuelle en étant assis et en étant debout. Pour 33% des essais, la cible a été déplacée vers la droite sans prévenir le sujet, exigeant une correction en ligne du mouvement. La configuration posturale (assise/debout) n’a influencé ni la trajectoire de la main ni la correction en ligne du mouvement de la main, bien que les stratégies cinématiques du corps entier décrivant ces deux conditions posturales soient différentes. Ces résultats soulignent l’efficacité des processus neuraux à la base de mouvements de pointage et de contrôle en ligne; il semble que ces processus ne soient pas influencés par la demande neurale augmentée requise pour garder l’équilibre en restant debout.

CHAPTER 1: INTRODUCTION

Goal-directed reaching is fundamental to many of our interactions with the external environment, yet is a highly complex task: It necessitates calculation of the precise spatial location of the target to be reached or grasped based on available sensory information and the programming of appropriate motor responses required for attaining the target. These processes are complex when humans are seated, but become even more difficult to program and control when executed in the standing position: The nervous system must control not only the arm and hand to the target, but also produce the necessary postural adjustments in the legs and trunk to conserve equilibrium. The task can be even further complicated if, for example, the target location is not constant, for example when the target location changes after the onset of movement. In the seated position, the nervous system can produce rapid, automatic corrections in hand trajectory in response to a change in target location without conscious perception of the target change (Pelisson, Prablanc, Goodale, & Jeannerod, 1986; Sarlegna, et al., 2003). However, little is known about whether the processes underlying rapid, online corrections are influenced by equilibrium constraints, since most of the studies that have contributed to our knowledge on this subject have employed seated reaching paradigms.

The process of voluntarily responding to an external stimulus involves three general stages: 1) stimulus identification (e.g. seeing a target object), 2) response selection (e.g. deciding to reach to touch the target object), and 3) motor programming (e.g. generating the neural commands necessary to bring the arm to the target object; Schmidt & Lee, 1999). During goal-directed reaching, at least the initial part of the motor response is executed as pre-programmed, i.e. in a feedforward manner. Later in the movement, however, sensory feedback may be used to modify the movement trajectory during the reach (i.e. “online”), correcting for errors in initial motor programming. The earliest time at which a reaching movement can be modified online is uncertain, but has been suggested to be less than 100 ms after a change in target position (Fautrelle, Prablanc, Berret, Ballay, & Bonnetblanc, 2010; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991).

Online corrections during goal-directed reaching movements require error signals generated from comparisons between locations of the target and of the reaching limb. In seated reaches, continuous visual feedback about target location is important for online control, whereas continuous visual feedback from the moving hand is not (Pelisson, et al., 1986; Prablanc, Pelisson, & Goodale, 1986). Information about hand position is thought to be primarily estimated from efferent copies of the motor command using a forward internal model, bypassing delays inherent to visual or proprioceptive feedback (Desmurget & Grafton, 2000; Gritsenko, Yakovenko, & Kalaska, 2009). The mechanisms underlying the online control of movement have yet to be fully understood. Furthermore, most of the research on the online control of reaching utilizes reaching tasks performed when the subject is seated, which places fewer demands on postural equilibrium.

Goal-directed reaching tasks during stance are commonly utilized to study the feedforward control of posture. Anticipatory postural adjustments (APAs) that precede the focal reaching movement (pAPAs) and those that accompany the reaching movement (aAPAs) have been extensively studied. Until only recently (Fautrelle, et al., 2010; Leonard, Gritsenko, Ouckama, & Stapley, 2011), however, only reaches made to stationary targets have been employed to study aAPAs, unlike much of the research on the online control of reaching. Double step reaching paradigms, in which the target unexpectedly changes location following reach initiation, are useful for studying the online control of movement by artificially creating errors in response programming (thus requiring an online movement correction) without altering the subject’s sensory signals. Leonard et al. (2011) used a double step reaching paradigm to study the online control of aAPAs during stance and found that corrections in postural muscles always occurred before those of the reaching arm following a target shift. The results thus demonstrate the predictive nature of posture with respect to the focal movement during online control of the overall movement.

Whether or not the nature of the online corrections of aAPAs during stance (e.g. the nature of the involved error signals, the effect of voluntary intent) is comparable to that of goal-directed reaching movements performed when seated remains, however, to be investigated. It is possible that equilibrium constraints imposed by the standing configuration (i.e. limited excursion of the body centre of mass) influence online movement control. Further research on the online control of aAPAs using double step or online correction paradigms necessitates an understanding of whether or not these effects exist. The overall aim of this research, therefore, was to investigate whether the processes underlying the online corrections to sudden changes in target position are dependent upon the postural context (seated or standing) under which they are performed. This research provides a basis for further research that will adopt online correction paradigms to study the control of aAPAs during stance by investigating the effects of standing on the online control of movement.

CHAPTER 2: LITERATURE REVIEW

2.1. Goal-Directed Reaching

Much of our daily activities require the ability to localize and reach towards target objects, allowing for interaction with others and with our external environment. That all healthy individuals can perform goal-directed reaching reasonably well without difficulty illustrates the efficacy with which the CNS executes this complex motor skill. Research on goal-directed reaching has provided insights into processes underlying its planning and online control.

2.1.1 The Speed Accuracy Trade-off

A well-known characteristic of goal-directed aiming is the speed-accuracy trade-off: Decreased movement time occurs at the expense of reduced movement accuracy. Woodworth (1899) was first to report and explain this relationship; he proposed a two-component model of reaching, whereby goal-directed reaching movements first consist of an "initial impulse phase" that brings the hand to the vicinity of the target and operates in a feedforward manner before visual feedback can contribute. This is followed by the "current control phase", which utilizes visual feedback to compare hand location with target location to make corrections to the movement trajectory, allowing the hand to come to rest at the target. The rationale for having two phases, one operating in a feedforward manner and the other operating with feedback, was that when movement speeds were above a certain threshold, the availability of vision did not improve movement accuracy compared to movements made without vision (Keele & Posner, 1968; Woodworth, 1899; Zelaznik, Hawkins, & Kisselburgh, 1983). Woodworth's two-component model has provided a framework for guiding experimentation into goal-directed movements (Elliott, Helsen, & Chua, 2001).

2.1.2 Movement Planning

2.1.2.1 Visual and Proprioceptive Contributions to the Planning of Reaches

The successful planning of goal-directed reaching movements requires knowledge of the initial state of the hand and its desired end position. In most cases, the latter is provided by vision, since most reaching movements are made to visual targets. Though the former can be provided through either vision or proprioception, when both sources of information are present, the extent to which each modality interacts with the other and contributes to movement planning has yet to be well understood (Sarlegna & Sainburg, 2009).

To determine whether visual or proprioceptive information about hand location is used to plan reaching movements to visual targets, Rossetti et al. (1995) used prismatic lenses to create a virtual displacement of the LED representing finger position without affecting perception of target position. Based on their results, they suggested that the estimate of initial hand position is encoded by a weighted integration of the visual and proprioceptive information. Sarlegna and Sainburg (2009) suggested an alternative explanation for how vision and proprioception are used during the planning of goal-directed movements. They proposed that vision and proprioception contribute differentially to the planning of goal-directed reaching to visual targets: The kinematic plan of the reaching movement is defined within an extrinsic coordinate system based primarily on visual information of hand position. The transformation of this kinematic plan into the neural commands for the desired motion, given the initial state of the limb, relies on proprioception. This idea is supported by evidence from experiments examining both movement direction (Lateiner & Sainburg, 2003; Sainburg, Lateiner, Latash, & Bagesteiro, 2003; Sober & Sabes, 2003) and movement amplitude (Bagesteiro, Sarlegna, & Sainburg, 2006; Sarlegna & Sainburg, 2007). Regardless of the exact mechanisms by which these sensory modalities are utilized, it is evident from the above-mentioned studies that both vision and proprioception are important for reach movement planning, and that a lack or distortion of either one could result in an incorrect motor plan.

2.1.2.2 Neural Correlates of Reach Direction

The firing patterns of individual cells in the mammalian motor cortex have been found to correlate with certain hand movement parameters, particularly hand movement direction and force output. Neurons in the motor cortex and area 5 of the posterior parietal cortex (PPC) tune broadly to movement direction during 2-dimensional (Georgopoulos, 1983; Georgopoulos, Kalaska, Caminiti, & Massey, 1982) and 3-

dimensional (Kettner, Schwartz, & Georgopoulos, 1988) reaching tasks. These neurons also tune broadly to the direction of an external load for which the arm must compensate (Kalaska, Cohen, Hyde, & Prud'homme, 1989). It has been suggested that each neuron encodes the activity, and consequently torque output, of its corresponding muscle (Kalaska, et al., 1989).

Georgopoulos et al. (Georgopoulos, 1983; Georgopoulos, et al., 1982) found that a vector representing the cell population discharge pattern (population vector) derived from the preferred direction (PD) and change in activity of constituent cells for a given 2-dimensional reach target corresponded reasonably with movement direction (within 11°; Georgopoulos, 1983). Scott et al. (2001) attributed the notable deviation of Georgopoulos et al.'s (1983) population vector from hand movement direction to a non-uniform distribution of cell PDs, which were clustered in two opposing movement directions such that the distribution of cell PDs covaried with peak joint power at the shoulder and elbow. The activity of motor cortical neurons therefore accounts for mechanical anisotropies of arm movement.

2.1.2.3 Segmental Coordination During Goal-Directed Aiming

The execution of aiming movements to visual targets involves a sequence of segmental movements of the eye, head, and arm. Eye and head movements orient gaze to the target to provide the motor system with information about the desired end location of the limb. To examine the pattern of coordination of segmental movements during goal-directed aiming movements, Biguer et al. (1982) instructed subjects to track visual targets of various eccentricities with the eye, head, and hand as quickly and as accurately as possible. They found that following target appearance, the eye would be first to move in the target direction, followed by the head, and then the arm. This sequence of eye, head, and hand movements was found to be unaffected by visual feedback, since it occurred whether the task was performed under normal visual conditions or in the dark, with only targets visible. However, the same authors also found that a sequential pattern of eye, head, and arm movements was absent when movement onsets were determined based on the latencies of muscle EMG. Latencies of the brachial muscles and right posterior neck muscles were very similar to each other and to eye movement latencies. Consequently, Biguer et al. (1982) concluded that neural commands sent to different movement segments are generated in parallel as part of a centrally generated motor pattern. With respect to a serial type organization, this allows for faster mobilization of several motor commands related to the goal.

Differences in overt movement onsets of the different segments despite synchronous EMG latencies can be explained by differences in inertial and gravitational forces acting on the eye, head, and limb (Biguer, et al., 1982; Pelisson, et al., 1986). The sequential onsets of gaze and limb movement makes it possible for foveal or parafoveal fixation of the target to occur before or around the time of arm movement onset, providing cues for a precise guidance of the arm to the target (Biguer, et al., 1982; Pelisson, et al., 1986). Indeed, Vercher et al. (1994), who used a similar movement paradigm, found that movement accuracy decreased when target fixation was not stabilized before the target was extinguished at arm movement onset. In summary, the motor system coordinates body segments during goal-directed aiming movements such that the efficiency of motor programming is maximized (i.e. parallel processing of eye, head, and hand responses) while still allowing for foveal information on target location to update the hand motor program at reach onset (Vercher, et al., 1994).

2.1.3 The Online Control of Reaching

The online control of movement can be defined as a mode of control that can produce modifications to the movement during execution (Khan, Lawrence, Franks, & Buckolz, 2004). The role of online control in goal-directed aiming could include the correction of errors in planning and/or the adjustment of trajectory when targets change location during a programmed movement (Gritsenko, et al., 2009). The correction of an ongoing movement requires a comparison of the system’s desired state and actual (or predicted) state, generating an error signal that is used to modify the outgoing motor command (Latash, 2008). This has classically been termed closed-loop control. For goal-directed reaching movements, the desired state of the system (i.e. spatial location and orientation of the hand) is based on information of the target, which is usually provided by vision. Two possible sources of information exist for the estimation of the actual state of the arm: 1) peripheral sensory feedback (vision and/or proprioception) resulting from movement, termed *reafference*; and 2) a centrally-generated copy of the outgoing motor command, termed efferent copy.

A disadvantage of using reafference for the determination of movement error is the delay associated with transmission of the sensory signals from the periphery to the CNS, especially when the state of the effector undergoes rapid changes during movement. This feedback delay can be bypassed using forward internal modeling (Desmurget & Grafton, 2000; Miall & Wolpert, 1996). An internal model is a system which mimics the behaviour of a natural process (Miall & Wolpert, 1996). Forward models form a class of internal models that represent the normal behaviour of the motor system in response to outgoing motor commands (Miall & Wolpert, 1996). Accordingly, forward models can be used to estimate the state of the system by using the efferent copy of the motor command to generate an internal sensory signal (corollary discharge), which in turn generates an error signal that can be used for closed-loop control (Miall & Wolpert, 1996). This internal, centrally-generated feedback loop, which bypasses delays associated with signal transmission along peripheral nerves, could even be used to predict the future outcome of an ongoing motor command, completely negating feedback delays in corrective pathways (motor predictive control; Miall & Wolpert, 1996). Several models of human voluntary arm control incorporate both reafference and forward modeling for the estimation of the state of the arm (Miall & Wolpert, 1996).

2.1.3.1 Movements to Stationary Targets

For reaches made to stationary targets, the static (and therefore predictable) nature of the target enables the motor system to program the entire movement before movement initiation. There is no doubt that the initial part of all goal-directed movements must be executed without use of sensory feedback to correct the movement (i.e. in a feedforward or open-loop manner) due to delays inherent to the processing of sensory feedback. However, even for movements to stationary targets, research has provided support for an online control of goal-directed movements.

A typical goal-directed reaching movement is characterized by a bell-shaped tangential velocity profile comprised of an acceleration phase (before peak velocity) and deceleration phase (after peak velocity; Fig. 2.1). The shape of the velocity profile is often characterized in terms of its symmetry ratio, the ratio of time spent in acceleration to time spent in deceleration (e.g. Jaric et al., 1998). A perfectly symmetric velocity profile, which equal time spent in acceleration and deceleration, would have a ratio equal to one. While some studies have found velocity profiles of goal-directed reaching movements to be nearly symmetrical (e.g. Pelisson, et al., 1986), it is more common for these movements to have velocity profiles where time spent in deceleration is greater than time in acceleration (e.g. MacKenzie, Marteniuk, Dugas, Liske, & Eickmeier, 1987; Soechting, 1984).

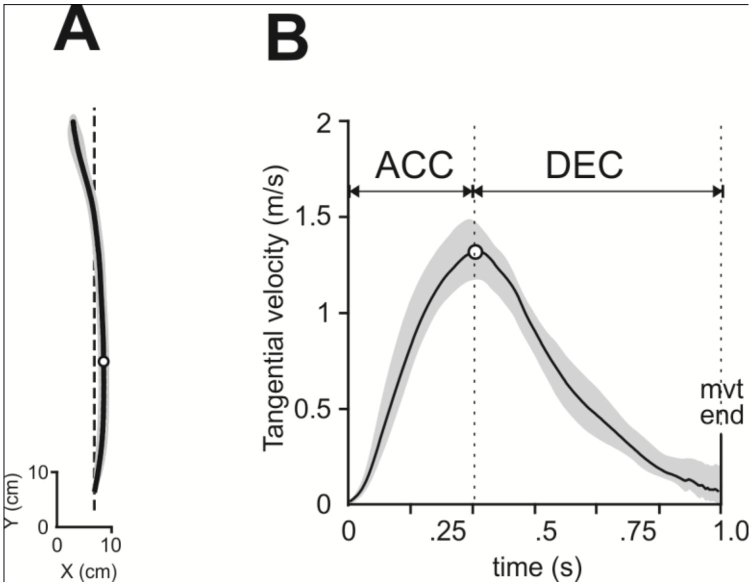

Figure 2.1: Hand path (A) and velocity profile (B) of a typical goal-directed reaching movement. The mean hand velocity profile (± 1 SD) of the corresponding hand path (A) is shown in B. The shape of the velocity curve is often described as "bell-shaped". Peak velocity (○) demarcates the transition from the acceleration phase (ACC) to the deceleration phase (DEC). For this movement, the deceleration phase was, on average, longer than the acceleration phase. The illustrated reaching movement was executed when standing, though its general characteristics can be generalized to reaches executed when seated. (Adapted from Leonard, et al., 2011)

The degree of symmetry of the velocity profile can be affected by various factors such as movement velocity (Jaric, Gottlieb, Latash, & Corcos, 1998; Nagasaki, 1989) and visual conditions (Elliott, Carson, Goodman, & Chua, 1991; Elliott, et al., 1999). Elliott et al. (1991) had subjects perform three-dimensional reaches to small targets either with full vision (target and limb visible) or no vision (of the target or limb), with task instructions prioritizing either movement speed or accuracy. The availability of vision resulted in increased absolute and proportional times spent in deceleration, regardless of whether speed or accuracy were emphasized. Another study by Elliott et al.(1999) found the same effect of vision on deceleration duration. However, whereas the former study found that visual feedback did not have an effect on peak velocity or time to peak velocity, the latter found that the availability of visual feedback resulted in greater and earlier peak velocities. Nonetheless, both these studies demonstrate that the processes underlying goal-directed movements use vision, when available, to modulate the deceleration of the limb for improved movement accuracy. Visual feedback is used even for highly practiced aiming movements resulting in motor learning, which are also characterized by a longer deceleration phase (Elliott, Lyons, & Dyson, 1997).

The use of different target sizes has allowed for the manipulation of accuracy constraints in goal-directing aiming tasks. It has been found that decreasing target size, and thus increasing accuracy demands, results in greater absolute and proportional times spent in deceleration (MacKenzie, et al., 1987; Soechting, 1984). The increased time spent in deceleration is consistent with the current control phase of Woodworth's two-component model, as it would provide greater time to process and use feedback to meet the increased accuracy demands required to bring the limb to the target (Elliott, et al., 2001).

While Elliott and colleagues (1991, 1997, 1999) manipulated the availability of vision to determine its effects on goal-directed movements, the relative importance of vision of the arm compared to vision of the target could not be determined from these experiments. Prablanc et al. (1986) also demonstrated that eliminating vision of the target, at either target onset or 120 ms after the initial saccade to the target, was detrimental to movement accuracy. However, when the target remained visible during the entire movement, subjects had better movement accuracy despite never having visual feedback of the arm. These results led Prablanc et al. (1986), in addition to supporting the idea of feedback-based corrections, to suggest that the controlling mechanism that compares target position and position of the moving limb utilizes visual localization of the target to generate an internal representation of target position and non-visual information about limb position, such as the kinesthetic feedback or efferent copy. This idea will be discussed further in relation to double step reaching paradigms.

2.1.3.2 Early Insights from Double Step Experiments

While the studies outlined above have provided support for the use of vision or other sources of feedback for the online control of reaching, the extent to which these findings can be generalized to real-life situations is limited due to the use of only stationary targets. Double step or online correction paradigms, whereby the target undergoes a discrete change in location to signal movement onset and then a second discrete change in location during movement execution, were first employed to study saccadic eye movements (e.g. Becker & Jürgens, 1979; Levy-Schoen & Blanc-Garin, 1974; Wheeless, Boynton, & Cohen, 1966). Specifically, these double step studies addressed the ability of the oculomotor system to prepare and execute saccadic responses in parallel. The use of double step paradigms in research on goal-directed reaching movements has furthered our understanding of the online control of reaching by using tasks that required the online modification of the outgoing motor response without mechanically and/or cognitively perturbing subjects (Blouin, Teasdale, Bard, & Fleury, 1995).

Since a double step task involves the presentation of two targets, it could be considered a serial reaction time task. Several experiments examining the effect of the interstimulus interval (the time between two stimulus presentations; ISI) on serial reaction time (RT) have found a significantly delayed RT to the second stimulus relative to normal RT when the ISI was below a certain threshold duration (Craik, 1948; Davis, 1956; Telford, 1931; Vince, 1948; Welford, 1952). This delay, known as the psychological refractory period (PRP), is thought to occur due to limitations of the stimulus-response processing system when processing information for both responses concurrently, resulting in sequential processing of stimulus-response requirements (Davis, 1956; Welford, 1952). As a result, if the second stimulus occurs while the system is processing the first stimulus-response pair (i.e. during the RT to the first stimulus), RT to the second stimulus will be delayed until processing of the first stimulus is complete. PRP has been found in a variety of motor tasks, including various combinations of finger key presses (e.g. Davis, 1956; Welford, 1952), tracking of step stimuli (e.g. Vince, 1948), and continuous target tracking (e.g. Craik, 1948).

The principle of sequential processing of stimulus-response requirements formed the basis of early models of the saccadic system; these models predicted that only one saccadic response could be prepared and executed at a time (Robinson, 1973). Later on, however, strong evidence was provided for the parallel programming of sequential goal-directed saccades (Becker & Jürgens, 1979), contradicting these models. In relation to goal-directed aiming movements, the concept of PRP from serial RT studies would predict that in a double step reaching task, a change in target location occurring before reach initiation to the first target would result in a delay of the corresponding adjustment in reach trajectory relative to the normal RT for that target. Just as the double step paradigm provided empirical evidence against discontinuities in processing afferent visual information (i.e. refractory period) by the system generating saccades, its utilization in the study of goal-directed aiming also revealed a lack of PRP in the other movement control systems.

Georgopoulos et al. (1981) conducted one of the earliest studies examining the online control of goal-directed reaching. Primate subjects performed two-dimensional reaching movements of which randomly selected trials had a target that would jump to a location opposite to the starting position (requiring a reversal of movement direction) or adjacent to the original target (requiring an orthogonal change in direction) after a variable delay from target presentation (the ISI). It was shown that the duration and amplitude of the movement to the original target was linearly related to the latency of the change in target location; in other words, the later the change in target location, the longer the movement to the initial target. Examination of velocity profiles confirmed that the initial movement was a fragment of the complete movement to the first target, proportional to the duration for which the original target was presented. This was true across the range of delays used, which corresponded to target jumps both before and during movement. Moreover, even at the shortest ISI, the time of correction was not much longer than the RT to the first target, unlike what would be predicted if an appreciable psychological refractory period was present. Massey et al. (1986) and Soechting and Lacquaniti (1983) confirmed these findings with experiments on human subjects. Furthermore, Soechting and Lacquaniti (1983) determined RT and correction time based on arm EMG activity, which is a more direct indicator of neural corrective mechanisms than arm trajectory alone (used by Georgopoulos et al., 1981), since changes in EMG can be detected earlier and is less affected by inertial and dynamical properties of the arm.

To explain the relative lack of PRP, Georgopoulos et al. (1981) proposed that the nature of the task minimized the demands on information processing by utilizing discrete movements with high stimulus-response compatibility; thus, the control of goal-directed reaching has continuous access to target location information before and during movement and can use this information to allow rapid modifications to motor commands already under execution. Overall, double step studies on saccadic eye movements and goal-directed reaching demonstrate that the CNS is highly efficient for tracking external objects that may unpredictably change location.

2.1.3.3 Signals and Mechanisms for Online Control

2.1.3.3.1 The Source of Visual Cues

The earliest studies of goal-directed reaching, which utilized movements to stationary targets, provided strong support for the ability of the motor system to control aiming movements online and also for the importance of visual feedback for such online control. The adoption of the double step paradigm allowed for a more sophisticated examination of the online control of movement, since successful task completion requires an actual modification of movement trajectory. Pelisson et al. (1986) used such a paradigm. Their particular task required subjects to simultaneously look and reach toward a visual target upon its appearance in the peripheral visual field. On some trials, the target would undergo a displacement to the left or right at peak saccade velocity (immediately before hand movement onset). Pelisson et al.'s (1986) paradigm had key differences from that of classical double step studies (e.g. Georgopoulos, et al., 1981; Massey, 1986;

Soechting & Lacquaniti, 1983). First, whereas classical double step studies displaced the second target by large amplitudes (equal to the initial target displacement in the cases of Georgopoulos et al., 1981 and Massey et al., 1986), Pelisson et al. (1986) displaced the second target by only 10% of the distance between the initial eye fixation and first target. Second, Pelisson et al. (1986) triggered the target jump during the saccade to the initial target such that target displacement was imperceptible to the subject, a phenomenon known as saccadic suppression. Lastly, vision of the limb was extinguished on movement initiation, although the target remained visible. These differences allowed for examination of the roles of conscious perception and of visual feedback of the moving limb in the online control of aiming.

Pelisson et al. (1986) found that subjects were able to correct their reach trajectories in double step trials despite lack of vision of the hand and lack of conscious perception of the target perturbation. Komilis et al. (1993) used a similar task as Pelisson et al. (1986), with the main differences being that target perturbations in the double step trials could be consciously perceived, that there was a direct comparison between conditions with and without visual feedback of the hand during the movement, and also that perturbations were applied either at hand movement onset or at peak hand velocity. In support of Pelisson et al. (1986), they found that visibility of the moving hand did not significantly affect movement time or the ability to correct hand trajectory, although it did allow for slightly better accuracy when the perturbation was applied later in the subject's movement. A more recent double step study by Sarlegna et al. (2003) directly examined the relative contributions of visual information of the hand and of target location to online control of reaches made to targets of different amplitudes. In addition to creating an imperceptible perturbation in target location, the authors created an imperceptible perturbation in perceived hand location by changing the location of the LED light indicating hand position during saccadic suppression (movements were performed in the dark). While subjects were able to correct movement amplitude for perturbations in target location, corrections for perturbations of the indicated hand position either did not occur, in the case when required movement amplitude shortened, or occurred much later, in the case when required movement amplitude was lengthened.

Classical double step studies have investigated the time taken to correct movement trajectory in response to a change in target location. Even when target perturbation preceded arm movement, a distinct correction could be identified based on kinematics (Georgopoulos, et al., 1981; Massey, 1986) or EMG and (Soechting & Lacquaniti, 1983). In contrast, Pelisson et al. (1986) found that kinematic profiles (velocity and acceleration) and movement times did not significantly differ between single step and double step trials, regardless of the direction of target perturbation. Given that subjects were able to correct their trajectories despite lack of conscious perception of the target perturbation, the lack of a distinct inflection point on the velocity or acceleration profiles of double step movements (which would be indicative of a discrete correction) led the authors to suggest that target position information is used early in the movement in a continuous corrective mechanism.

The double step studies by Pelisson et al. (Komilis, et al., 1993; Pelisson, et al., 1986) and Sarlegna et al. (2003) have been influential to our current understanding of the role of vision for the online control of aiming. Taken together, these studies support the existence of a control mechanism that continuously compares observed target location and actual hand location to enable rapid online movement corrections. Although visual feedback of the hand may afford slightly greater accuracy (Komilis, et al., 1993) and/or earlier corrections (Sarlegna, et al., 2003), these findings emphasize the disproportionate contribution of visual information of target position compared to that of hand position. Accordingly, it was proposed that the main driving loop in the corrective mechanism comparing target position relative to hand position is a visuomotor loop: Information about target location is provided to the control system through vision, while information about arm position is provided through proprioception and/or corollary discharges (Komilis, et al., 1993; Pelisson, et al., 1986).

2.1.3.3.2 Knowledge of Limb Position and Updating the Spatial Goal of Movement

The above-mentioned double step studies have shown that subjects are able to update the trajectory of goal-directed reaching movements without visual feedback of the hand. Therefore, one may ask whether knowledge of the position of the moving hand is provided through proprioception, efferent copy, or a combination of the two? Research on deafferented individuals, who do not have somatosensory feedback, allows for an insight into the importance of proprioceptive information. Bard et al. (1999) had a deafferented subject and healthy control subjects perform double step reaching tasks without visual feedback of the arm. Despite not being able to perceive the target jumps, both the control subjects and the deafferented subject were able to successfully correct their arm trajectory in response to the target jump on a majority of trials, with the deafferented subject and controls having comparable success rates (60-85% vs. 52-67%, respectively). Similarly, Blouin et al. (1995) have also suggested that in their experiments, arm corrections in response to unperceived target perturbations occurred without the use of limb proprioceptive cues, since stabilization of the hand at the end of the movement was attained about 200 ms after the end of the primary (uncorrected) submovement, not being significantly different from single step movements. These results support the idea that the corrective mechanism for the online control of arm movement mainly uses the efferent copy to derive information on hand position based on a forward internal model, since it would provide an approximation of hand location to allow for error detection even in the absence of proprioceptive feedback (Bard, et al., 1999; Blouin, et al., 1995).

As it is known that subjects are able to correct their trajectories in response to a change in target location despite lack of conscious perception of the target jump (Gritsenko, et al., 2009; Komilis, et al., 1993; Pelisson, et al., 1986), modification of the motor outflow required for online corrections involves an unconscious updating of the spatial goal of movement (Bard, et al., 1999; Blouin, et al., 1995; Pelisson, et al., 1986; Sarlegna, et al., 2003; Turrell, Bard, Fleury, Teasdale, & Martin, 1998). That an error signal for the online control of reaching can be generated without proprioceptive feedback of the moving arm points to the importance of the efferent copy of corrective saccades in the updating of arm trajectories (Bard, et al., 1999; Blouin, et al., 1995), an idea that has been supported empirically. For double step reaching movements performed with vision completely removed upon movement initiation, corrections that occurred at or before peak velocity were characterized by a longer interval between the target perturbation (applied during saccadic suppression) and hand movement onset (Bard, et al., 1999; Turrell, et al., 1998). When the duration of this interval was longer, the corrective saccade made in response to the induced retinal error was able to update the arm motor program earlier in its execution. Similarly, in a single step reaching task where vision was removed upon movement initiation, hand directional accuracy decreased when foveation of the target was not stabilized before movement initiation (Vercher, et al., 1994). Finally, immobilizing the eyes and head such that the target cannot be foveated decreased the accuracy of the arm movement (Vercher, et al., 1994). Taken together, these results indicate that retinal visual information alone is insufficient for updating the spatial goal of movement; extra-retinal signals, i.e. the efferent copy of saccadic commands allowing for the foveation of the target, are also necessary. Efferent copies of occulomotor commands are thus used in internal (i.e. corollary discharge-based) feedback loops of the ongoing arm movement by providing signals indicating the desired spatial location of the hand which can be compared with hand location estimated from the arm efferent copies (Bard, et al., 1999; Blouin, et al., 1995; Vercher, et al., 1994).

Although evidence from Bard and colleagues (Bard, et al., 1999; Blouin, et al., 1995) supports the role of the arm efferent copy for providing knowledge on limb position in the absence of visual feedback, proprioception may still be important for this function. Support for the role of proprioception is provided by the decreased pointing accuracy by a deafferented subject compared to controls when reaching to targets with the eyes fixated such that the target is not foveated (Blouin, Gauthier, Vercher, & Cole, 1996). It is therefore likely that both extra-retinal visual information and proprioceptive information on the moving limb contribute to the online control of aiming.

Gritsenko et al. (2009) addressed the question of what is the simplest necessary error correction signal for successful online corrections to target displacements during reaching. These authors modeled a two-joint arm controller as the sum of a feedforward motor command and an online correction signal, where the correction signal was superimposed (with a constant gain) on the feedforward command moving the limb to the initial target. The models tested varied according to the signals that the controller used to determine kinematic endpoint error (delayed peripheral arm-state feedback vs. predicted arm state based on a forward internal model) and according to whether the corrective pathways included an inverse dynamic model that transformed the kinematic endpoint error into a dynamically appropriate joint torque error. It was found that only the model that utilized a forward internal model to compensate for peripheral feedback delays and an inverse dynamic model to adjust the outgoing motor command (shown in Fig. 2.2) could approximate the observed kinematics of online corrections of human subjects. These results demonstrate that without the forward and inverse internal models, movement trajectories could not rapidly compensate for target jumps due to feedback delays and the inherent dynamics of the limb. Additionally, their modeling suggests that rapid online corrections resembling those of human motion can be accomplished by superimposing a single error correction signal onto the outgoing feedforward motor command to the original target.

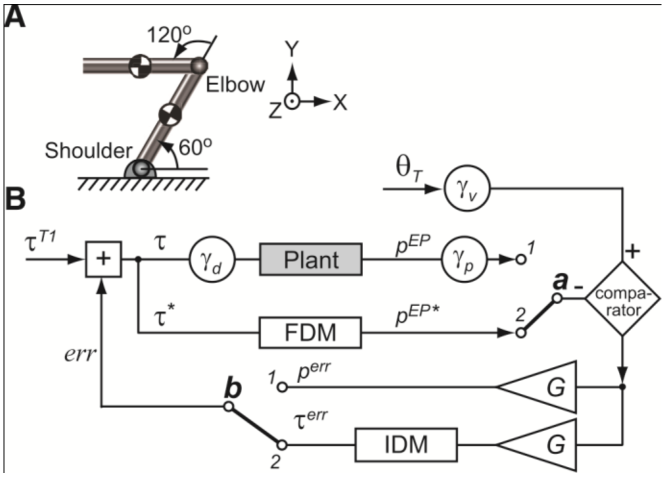

Figure 2.2: : Summary of the model used by Gritsenko et al. (2009) to model a two-joint arm. A. Structure and starting position of the model arm. **B.** Control circuit diagram. The configuration found to produce hand kinematics similar to those observed in human subjects is shown (switches *a* and *b* at 2). Switch *a* determined which arm position signal (sensed position based on peripheral feedback, p^{EP}, delayed by γ_d, vs. estimated position, p^{EP*}, based on a forward internal model, FDM) is used by the system to compare to the target position signal, θ_T. Switch *b* determined whether or not an inverse dynamic model (IDM) transformed the kinematic endpoint error, (p^{err}) into joint torques (τ^{err}) to generate error feedback (*err*). (Adapted from Gritsenko, et al., 2009).

2.1.4 Conscious vs. Unconscious Corrections in Reaching

The finding from double step studies that rapid, unconscious corrections to arm trajectory occurred even without visual reafference of the moving arm highlights the automatic nature of online control of goal-directed reaching. Day and Lyon (2000) investigated the extent to which the processes underlying these automatic adjustments are modifiable by intention. Subjects reached toward a central target which could unpredictably shift 10 cm to the right or left after movement initiation, requiring the subject to either reach to the new target location (reach+ condition) or to the opposite direction of the target shift to a mirror-symmetric location (reach- condition). It was found that even in the reach- condition, the target shift elicited an initial trajectory adjustment toward the new target location, which could not be reversed until at least 160 ms following the target shift. Based on these findings, the authors suggested the presence of an early, highly automatic class of corrections (125-160 ms) and a later class of corrections (>160 ms) that is modifiable by intention. It has been demonstrated that neural substrates for these automatic processes may be located cortically, mainly in the posterior parietal cortex (Desmurget, et al., 1999), or subcortically (Day & Brown, 2001). The automatic corrections observed in studies by Day and Lyon (2000) and others (e.g. Komilis, et al., 1993; Pelisson, et al., 1986; Sarlegna, et al., 2003) indicates how the nervous system is highly evolved to perform movements aimed at visual targets, even overriding conscious and voluntary processes.

2.2 Posture

The postural control system encompasses all the sensorimotor and musculoskeletal components and processes involved in achieving two behavioural goals: postural orientation and postural equilibrium (Horak & Macpherson, 1996; Massion, 1994). Postural orientation refers to the orientation of body segments relative to environmental variables (e.g. earth vertical) and to each other. When the forces acting on the body are balanced so that the body stays in the desired position and postural orientation (static equilibrium), or moves in a controlled way (dynamic equilibrium), postural equilibrium is achieved (Horak & Macpherson, 1996).

Posture has a mechanical antigravity function that maintains a reference posture, i.e. stance, and serves as a reference frame for perception and action in relation to the external world (Massion, 1994). Although posture includes a hierarchy of reflexes, postural reflexes alone cannot account for postural control (Kandel, Schwartz, & Jessel, 2000). The maintenance of postural equilibrium and postural orientation encompasses three main aspects of motor control (Horak & Macpherson, 1996). First, it involves maintaining whole-body stability in a gravito-inertial environment. The behaviour of the postural system in relation to this goal can largely be represented as the control of the position of the centre of mass. Second, posture can refer to the maintenance of body segments in specific configurations in both egocentric and exocentric reference frames. Examples of this include active stabilization of the trunk axis and head axis in the vertical position during locomotion (exocentric reference frame) and maintaining a specific arm configuration to carry a glass of water (egocentric reference frame). Lastly, posture acts to counteract internal perturbations during voluntary movement.

2.2.1 Biomechanical Principles of Stability and Balance

A good understanding of biomechanical principles of postural control is required before a complete understanding of posture and movement can be attained. Common biomechanical concepts in the context of posture include centre of mass (CoM), centre of gravity (CoG), ground reaction force (GRF), centre of pressure (CoP), and base of support (BoS), illustrated in Fig. 2.3. The CoM is the point in space at which the entire mass of the body is balanced and can be determined by the weighted average of the CoM of each body segment in 3D space (Horak & Macpherson, 1996; Winter, 1995). The CoM is closely related to the CoG, which is the vertical projection of the CoM onto the ground (Winter, 1995). The force exerted by the body onto the ground is directly opposed by an equal reaction force from the ground, the GRF, which acts on the body at the point of contact (Enoka, 2008). During quiet stance, the resultant GRF is approximately equal and opposite to the force exerted by gravity on the body. The point of origin of the GRF is the CoP. CoP location is controlled neurally via ankle muscle activity; for example, plantarflexor activity moves CoP anteriorly (Winter, 1995). The difference between CoP and CoG is negatively correlated with horizontal acceleration of the CoM; thus, CoP movement is inversely related to CoG movement (Winter, 1995).

The maintenance of static equilibrium requires the CoG to lie within the base of support (BoS), the region bounded by the points of contact between body segments and the support surface. Consequently, a larger base of support allows for greater excursion of the CoM without loss of equilibrium (Horak & Macpherson, 1996). Other mechanical factors underlying static stability, or the resistance to toppling due to external forces, are the distance from the line of gravity to the edge of the support base; the inverse of the height of the CoM above the base of support; and the weight of the body (Hayes, 1982). Control of the CoM position is thought to be an overriding goal in tasks performed without external support, since it is important for postural equilibrium (Horak & Macpherson, 1996).

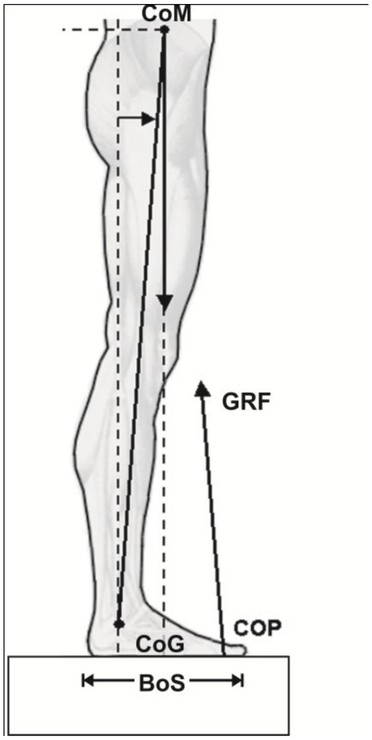

Figure 2.3: Schematic diagram illustrating centre of mass (CoM), centre of gravity (CoG), ground reaction force (GRF), centre of pressure (CoP), and base of support (BoS). (Adapted from Morasso & Sanguineti, 2002).

2.2.2 Modes of Postural Control

Disturbances in postural orientation can be classified as originating from external forces or as internal forces resulting from one's own voluntary movement. Accordingly, the minimization of postural disturbance operates through two mechanisms: feedback control and feedforward control (Horak & Macpherson, 1996; Massion, 1992). Feedback control of posture relies on sensory feedback loops to determine the nature of a perturbation, such as the unexpected movement of the support surface, and trigger the appropriate postural response, known as an automatic postural response. In contrast, postural disturbances resulting from voluntary movements are counteracted by postural adjustments that operate in a feedforward (predictive) manner such that postural equilibrium is maintained throughout the movement. These adjustments are known as anticipatory postural adjustments (APAs) and occur before and during the focal (voluntary) movement. Anticipatory postural adjustments may also serve to generate the mechanical requirements of the focal movement (Lee, Michaels, & Pai, 1990; Stapley, Pozzo, & Grishin, 1998). The feedforward nature of APAs requires the CNS, through learning and adaptation, to anticipate the mechanical effects of the focal movement (Horak & Macpherson, 1996). As with goal-directed reaching, this is thought to be achieved through forward internal models.

2.2.2.1 Feedback Control of Posture

The postural control system receives and integrates multisensory inputs to interpret the body's orientation and dynamic equilibrium (Horak & Macpherson, 1996; Massion, 1994; Mergner & Rosemeier, 1998). The primary sensory inputs important for this purpose are vision, somatosensory information, and vestibular information. These inputs are thought to be compared to an internal representation of the body such that an error between the desired and actual postural orientation and equilibrium is computed to generate the appropriate motor commands for maintaining the required postural variables at the desired levels (Gurfinkel, Levik, Popov, Smetanin, & Shlikov, 1988). These feedback-dependent processes are automatic, stereotyped, and produce postural responses at short latencies (Horak & Nashner, 1986; Nashner, 1977).

A common paradigm for examining feedback control of posture involves the use of support surface perturbations during quiet stance or locomotion, which disrupt postural equilibrium by unexpectedly disturbing the position of the CoM. These perturbations elicit rapid, automatic EMG responses with latencies of 70-100 ms that act to restore postural control (Horak & Nashner, 1986; Nashner, 1977). Though automatic, the response is modified by several factors, including perturbation direction and speed, initial postural orientation, prior experience, central set, the available sensory signals, and the nature of the ongoing task that was disturbed (Horak & Macpherson, 1996; Massion, 1994).

The response to support surface perturbations can be described in terms of different postural strategies, or the high-level plan formulated by the nervous system for achieving the overall goals of maintaining postural equilibrium and orientation (Horak & Nashner, 1986). To reduce the number of degrees of freedom that need to be controlled, the activity of individual muscles are spatially and temporally regulated in functional groups, or muscle synergies (Macpherson, 1988; Torres-Oviedo & Ting, 2010). Muscle synergy is secondary to postural strategy and is highly flexible, such that a given postural strategy could be implemented by several muscle synergies (Macpherson, 1988). A comprehensive understanding of posture thus requires both the examination of postural strategy and the underlying muscle synergy.

2.2.2.2 Feedforward Control of Posture: Anticipatory Postural Adjustments

During voluntary movements, inter-segmental dynamics can disrupt postural orientation and equilibrium since movement of one body segment results in reactive moments that promote unwanted movements in other segments (Horak & Macpherson, 1996; Massion, 1992; Winter, 1995). In the case of shoulder flexion, for example, a flexor moment acting on the upper arm would generate an equal and opposite reactive moment which would cause the trunk to rotate forward if not countered by the hip extensors, which in turn requires a knee flexor moment and an ankle planterflexor moment to keep the lower limb vertical (Eng, Winter, MacKinnon, & Patla, 1992; Winter, 1995). The role of postural adjustments becomes especially important for fast movements, where reactive moments may cause greater disruption to posture (Lee, Buchanan, & Rogers, 1987). Accordingly, postural adjustments accompanying slow movements may be undetectable or more variable (Horak, Esselman, Anderson, & Lynch, 1984). Voluntary movements may also disrupt postural equilibrium by moving the body CoG outside the base of support or changing the base of support to exclude the initial CoG position (Horak & Macpherson, 1996; Massion, 1992). In movements resulting in a change in BoS, such as when raising a leg when standing, postural adjustments preceding the focal movement shift the CoG to fall within the new BoS (Massion, 1992; Mouchnino, Aurenty, Massion, & Pedotti, 1992). As previously mentioned, much of the postural activity accompanying voluntary movements can be explained by the need to control the body's CoM position (Horak & Macpherson, 1996).

The postural adjustments described in the above two examples are classified as anticipatory postural adjustments (APAs). Postural adjustments are termed "anticipatory" because they are produced in a feedforward manner and begin before the disturbance to postural equilibrium and orientation occurs (Massion, 1992). The onset of APAs does not necessarily occur before the onset of the focal movement producing the disturbance, but does occur before the possibility of being influenced by movement feedback (Massion, 1992). Postural adjustments that precede focal movement onset, termed preparatory anticipatory postural adjustments (pAPAs), are distinguished from those that occur during the focal movement, termed associated anticipatory postural adjustments (Schepens & Drew, 2003, 2004; Yakovenko & Drew, 2009). Associated APAs (aAPAs), despite occurring after focal movement onset, are still feedforward in nature since they still occur before there has been sufficient time for feedback to signal a disturbance in posture (Massion, 1992; Schepens & Drew, 2003).

Preparatory anticipatory postural adjustments create conditions permissive to the initiation of movement performed when standing. In some situations, such as self-paced movements performed when standing (Horak, et al., 1984; Lee, et al., 1987; Lee, et al., 1990) and movements of a supporting limb (Mouchnino, et al., 1992; Schepens & Drew, 2003), focal movement initiation does not occur until after pAPA initiation. It has also been suggested that pAPAs actively delay focal movement initiation when the subject is not supported externally (Cordo & Nashner, 1982; Schepens & Drew, 2003). Associated anticipatory postural adjustments ensure successful focal movement execution (Leonard, Brown, & Stapley, 2009; Leonard, et al., 2011; Schepens & Drew, 2003). Both pAPAs and aAPAs can be involved in postural equilibrium maintenance.

Anticipatory postural adjustments occurring before the onset of voluntary arm pointing movements during stance were classically thought to be only responsible for counteracting the expected internal perturbations to postural equilibrium caused by the focal movement (Bouisset & Zattara, 1987; Cordo & Nashner, 1982; Massion, 1992). However, depending on the nature of the arm movement, pAPAs can also initiate the focal movement conducted from a fixed BoS by creating the angular acceleration of body segments needed for focal movement execution. For example, a large backward displacement in CoP occurs before execution of a forward whole-body reaching task, resulting in CoP being posterior to CoM (Leonard, et al., 2009; Stapley, et al., 1998). Because CoP is then positioned behind body CoM, the ground reaction force (GRF) can then create the forward angular moment needed for the task (Stapley, et al., 1998). The involvement of pAPAs in movement initiation is further supported by the finding faster movements are preceded by a greater backwards displacement of CoP, thus increasing the forward angular moment (Stapley, et al., 1998). Similarly, in a bimanual arm pulling task performed at various forces, the duration of ankle torque preceding the focal movement was found to increase with pulling force, allowing subjects to perform the pulling task with a greater impulse (Lee, et al., 1990).

In the global planning of a movement, the APA is, at least in part, integrated with the focal movement it accompanies (Horak & Macpherson, 1996; Massion, 1992; Schepens & Drew, 2003). This is supported by findings that postural adjustments always correctly match the focal movement (Bouisset & Zattara, 1981; Marsden, Merten, & Morton, 1977; Nashner & Forssberg, 1986). Additionally, the relative timing of postural activity and focal activity are maintained in reaction time (RT) tasks (Horak, et al., 1984; Lee, et al., 1987). In self-paced tasks, however, the temporal relationships between postural adjustments and the focal movement are highly variable, with postural adjustments starting significantly before the focal movement instead of simultaneously as in RT tasks (Horak, et al., 1984; Lee, et al., 1987). Schepens and Drew (2003, 2004) showed that pAPA and aAPA onsets were temporally dissociated, yet each were time-locked to specific events: pAPA onset was highly related to the movement “Go” signal, while aAPA onset was highly correlated to focal movement RT. These findings indicate a possibility of independent neural signals for posture and for movement (Fig. 2.4). At the same time, the high correlation between aAPA and focal movement RT provides evidence for the integration of aAPAs in the motor program of the focal movements they accompany (Schepens & Drew, 2003, 2004). What remains uncertain is whether the observation of independence of control of the pAPA and movement (reach and aAPA) is a result of independent, parallel processes in the planning of the global response (Schepens & Drew, 2003). This is a possibility given that, using the same reaching task, Yakovenko and Drew (2009) have recorded pyramidal tract neurons in the motor cortex with activity time-locked to the Go signal and receptive fields in non-reaching limbs. As Schepens and Drew (2003) suggest, it is possible that the response is planned at a global level and that independence of the two components at the execution level is a reflection of variable movement speeds. These studies and others have shown that the boundary between posture and movement is not always well-defined, regardless of whether behavioural (e.g. Schepens & Drew, 2003) or neurophysiological (e.g. Schepens & Drew, 2004; Yakovenko & Drew, 2009) variables are studied.

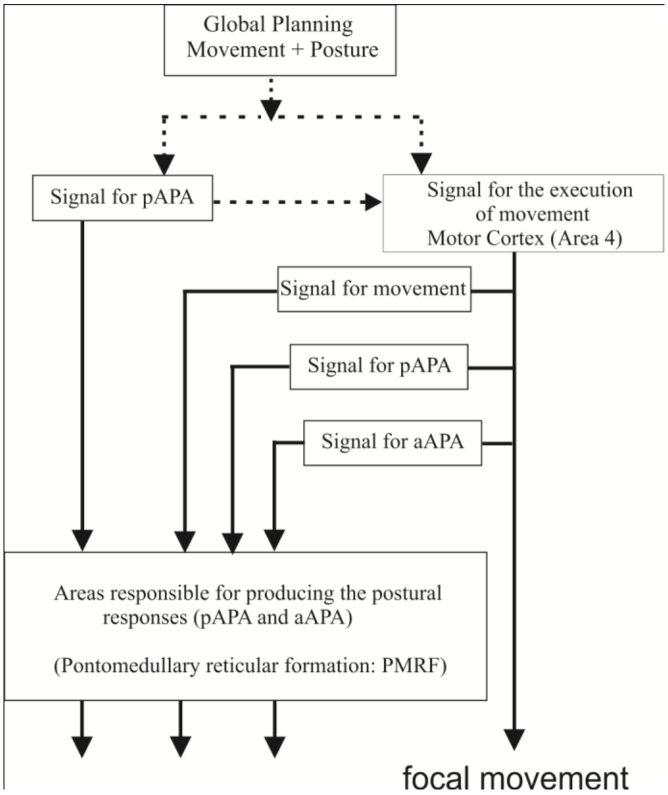

Figure 2.4: Diagram illustrating independent neural signals for posture and movement. There are neural signals for the execution of APAs preceding focal movement (pAPAs) that are independent of the signals for the execution of movement. The neural signals for postural adjustments during the focal movement (aAPAs), however, are part of the signals for the focal movement. Whether or not the pAPAs and movement are *planned* as a single response (dashed lines) is not yet known. (Adapted from Yakovenko & Drew, 2009)

2.3 Online Control of Movement During Stance

Just as goal-directed reaching movements may require online corrections during an unpredictable change in target location, other aspects of motor control, including feedforward postural adjustments, may also require online corrections. Double step reaching paradigms are common for the study of online movement control. Almost all of the experiments on the online control of goal-directed reaching minimized postural equilibrium requirements by having subjects perform movements while seated, sometimes even fixating the head to prevent unwanted head and trunk movements (e.g. Pelisson, et al., 1986; Sarlegna, et al., 2003). While this method was useful for studying the control of arm movement in greater isolation, a better understanding of goal-directed arm movements in real-life situations requires the understanding of how they are affected by the standing configuration, which imposes postural equilibrium constraints due to the decreased BoS and increased height of the CoM.

Since reaching movements performed during stance are accompanied by APAs, it should be expected that online corrections to the reach require corresponding changes to the aAPAs. Corrections in aAPAs have so far been demonstrated in lower leg muscles. Fautrelle et al. (2010) had subjects perform a double step reaching task while standing. Movement corrections in double step trials were determined from EMG traces of arm, leg, and trunk muscles on the right side. The anterior deltoid (DA) and tibialis anterior (TA) muscles consistently showed the earliest corrections, with both muscles having similar latencies of around 100 ms. As movement corrections in double step trials required an increase in movement amplitude, the DA brought the hand toward the new target while the TA brought the body further forward. On average, correction of the DA was earlier than that of the TA. The authors suggested that the similar latencies of DA and TA indicate a lack of hierarchical processing of upper limb over lower limb motor corrections. In contrast, Leonard et al. (2011), who also had subjects perform a double step reaching task during stance, found that online corrections in lower leg muscles (TA, peroneus longus, and soleus) preceded those of arm muscles (DA, posterior deltoid, and biceps brachii). It was suggested that the online corrections in leg (postural) muscles initiated the overall movement correction by accelerating the body toward the new target and created the dynamical conditions necessary for the arm movement correction.

It is possible that discrepancies in the temporal sequence of arm muscle and leg muscle corrections between the two studies resulted from task differences. Unlike Fautrelle et al.'s (2010) task, the movement correction required in Leonard et al.'s (2011) task required primarily a change in movement direction instead of amplitude; thus, the leg muscle corrections recorded in this study primarily acted to rotate the arm and body instead of bringing them further forward. Additionally, the target shifted to 1 of 3 possible locations in Leonard et al.'s (2011) task, whereas it only shifted to one other location in Fautrelle et al.'s (2010) task. As Fautrelle et al. (2010) had suggested, the presence of multiple possible target shift locations would result in longer movement corrections in accordance with Hick's law, which states that RTs increase with the number of response alternatives. It should be noted that a comparison of correction latencies between Fautrelle et al.'s (2010) and Leonard et al.'s (2011) studies is difficult, as Fautrelle et al. (2010) expressed correction latency relative to the time of target shift (which occurred at constant times relative to reach onset) while Leonard et al. (2011) expressed correction latency relative to reach onset (with target shifts having occurred at variable times relative to reach onset). Regardless, the near-simultaneous latencies of DA and TA corrections found by Fautrelle et al. (2010) indicate that the neural signals for online postural correction could not have been a result of sensory feedback signalling the focal movement correction, in agreement with Leonard et al. (2011).

To date, therefore, the studies by Fautrelle et al. (2010) and Leonard et al. (2011) have been the only ones to have used a double step or online correction paradigm for studying reaching during stance. Both studies documented corrections in lower leg muscles accompanying arm movement corrections. However, no studies have directly compared online corrections of reaching movements in seated and standing configurations. Postural stability is decreased when standing compared to when seated, rendering the maintenance of postural equilibrium more demanding on the CNS. *It is therefore hypothesized that the increased equilibrium constraints imposed on the CNS and the need to coordinate a greater number of body segments during stance would affect the online control of goal-directed reaching, resulting in differences in hand movement parameters.*

CHAPTER 3: MATERIALS AND METHODS

3.1 Subjects

Ten right-handed subjects (5 females, 5 males) were recruited from the McGill University student population to participate in the study. Subjects had a mean age of 22.3±2.5 years and measured on average 170.4±7.0 cm and 65.8±12.1 kg in height and weight, respectively. All subjects had normal or corrected vision and were free of any known neurological, orthopedic, or vestibular disorders, and provided their informed consent to participate in this study. The study received ethical approval from the McGill University Research Ethics Board.

3.2 Experimental Apparatus and Set-up

Subjects were positioned in the centre of a custom-built semi-circular light target array with two equidistant height- and distance-adjustable LED targets, one positioned in front of the subject at the midline and the other at 30 degrees of eccentricity to the right (Fig. 3.1). The eccentricity of the second target was identical to the second largest target eccentricity used in a similar study by Leonard et al (2011). Of the three target eccentricities used by Leonard et al (2011), this eccentricity was chosen in order to maximize the size of the aAPA correction while still allowing the target to remain visible if the task was performed while wearing customized goggles (used in a follow-up study). A modified gaming switch (model 459512; RP Electronics, Burnaby, BC), mounted on a chest band worn by subjects and aligned with the subjects xiphoid process, emitted a 5-V signal upon release (0 V emitted when depressed), signalling movement onset. Each target consisted of a 5-V, 5 mm bright white LED (model RL5-W18030; Super Bright LEDs Inc., St. Louis Missouri) encased in a modified gaming switch (model 459512; RP Electronics, Burnaby, BC) that produced a 5-V pulse upon contact, signalling target attainment. The target switch contact surface consisted of a 2.5-cm diameter circle that was opaque except for a central 3-mm hole allowing for light transmission from the LED; thus, the effective target size was 3 mm. Each target was attached to a lightweight aluminum dowel mounted on a semicircular aluminum bar suspended from the ceiling in a way that enabled target height and distance adjustment. The distances of the targets, positioned at the level of the shoulder when standing, were standardized at 130% of the distance between the xiphoid process and tip of the index finger when the subject stood in the centre of the target array with the right arm fully extended toward the target (reach distance). This distance was chosen to elicit a measureable postural adjustment when standing and because previous experiments showed it could be attained comfortably without the CoP of either foot exceeding the perimeter of that foot (Leonard et al., 2009).

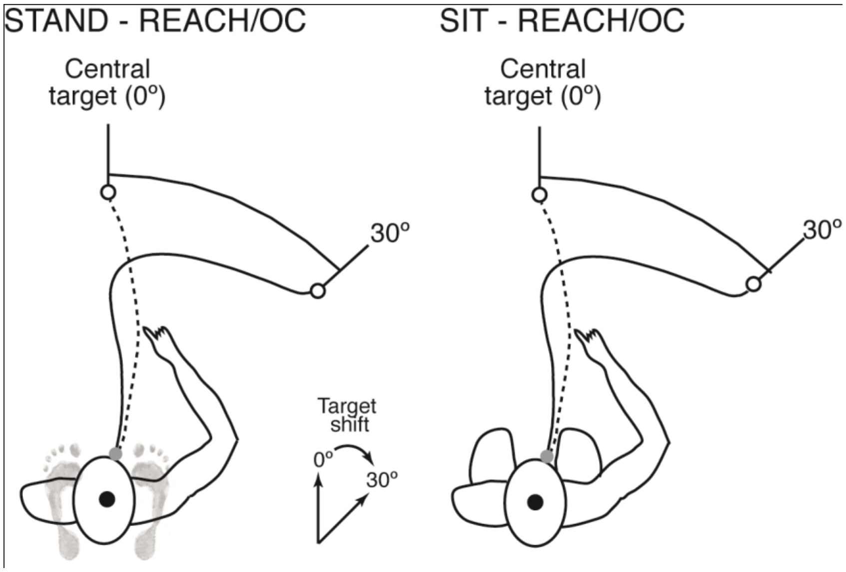

Figure 3.1: Experimental set-up. In the STAND condition (left), subjects stood barefoot on force plates. In the SIT condition (right), subjects sat on a stool with both feet flat on the floor. Trajectories for REACH (dotted lines) and OC (solid lines) trials are shown.

To obtain kinematic data, spherical, reflective kinematic markers were taped to various anatomical landmarks on the subject's body according to the Vicon Plug-in-Gait marker placement (see Fig. A1 in the Appendix). Full-body kinematic data were collected using a six-camera MX3 motion-capture system (Vicon Motion Systems, Los Angeles, CA) sampled at 200 Hz. The MX3 cameras obtain kinematic marker position by emitting infrared light which is then reflected from the markers back to the camera lenses. Surface EMG of the tibialis anterior, soleus, peroneus longus, and external oblique was collected bilaterally in addition to EMG of the right anterior and posterior deltoids, bicep brachii, and triceps brachii, all sampled at 1000 Hz using two DelSys Bagnoli 8-channel systems (Delsys, Bonston, MA), but will not be reported in this thesis. During trials requiring subjects to stand, subjects stood barefoot on two triaxial force plates (model FP4060, Bertec, Columbus OH) that measured ground reaction force and torques in the mediolateral (x), anteroposterior (y), and vertical axes (z) at a sampling rate of 1000 Hz.

The experimental task was studied under two postural conditions: SIT and STAND (Fig. 3.1). In the SIT condition, subjects were seated comfortably on a stool with a vertical rod centered on the back of the seat, against which subjects were instructed to position their lower back at the start of each trial. The subject sat with their bare feet flat on the support surface and knees bent at roughly 90 degrees. To accommodate different subject heights, rectangular blocks were placed underneath the feet and taped to the support surface, providing a stable surface on which to place the feet while ensuring that subjects could attain knee flexion of approximately 90º when seated with the lower leg vertically aligned. This did not affect the position of the trunk and upper body, since seat height remained constant. The subject verified that the effective seat height (i.e. height of the seat relative to the supported feet) could be comfortably maintained before testing began. To standardize initial trunk position across SIT trials, the subject was required to begin each trial with the lower back against the vertical rod. For the SIT and STAND conditions, the feet were positioned according to their preferred mediolateral stance width, which was based on the average distance between the heels measured when subjects had finished walking 5 steps (3 trials). Foot placement was outlined using tape, ensuring constant foot positioning for all trials within each condition. Because the starting position of the trunk was kept constant across both postural conditions, foot placement was more anterior in the SIT condition than in the STAND condition. Target height was set to the height of the acromion in each postural condition, while target distances remained constant for both postural conditions (130% of reach distance).

Within each postural condition, there were two experimental trial types: trials requiring movements to a stationary target (REACH) and trials requiring an online movement correction (OC).

3.3 Data Acquisition

The illumination of target lights and recording of signals from the chest and target switches were controlled using a customized program written in Labview (National

Instruments, Austin, TX). Analog signals from the force plates and EMG system and MX3 camera signals were recorded using Vicon Nexus (Vicon Motion Systems, Los Angeles, CA). Both Labview and Nexus continuously received their respective input signals but did not record them until the experimenter initiated the trial using an external trigger, which consisted of a switch which produced a 5-V signal sent to both data collection softwares. Upon illumination of the central target, which followed a variable foreperiod up to 1000 ms following trial initiation, subjects were cued to initiate a reach to that target. Release of the subject's finger from the chest switch resulted in 5-V pulse that provided a precise, real-time indicator of focal movement onset. The data acquisition duration for each trial was 4000 ms. Data from Labview and Nexus were stored and integrated offline using Matlab software (The MathWorks Inc., Natick, MA).

3.4 Experimental Procedures

Experimental sessions took place at the McGill University Balance and Voluntary Movement Laboratory and were approximately 4 hours in duration, including subject anthropometric measurements, subject preparation with kinematic markers and EMG electrodes, and target array adjustment (actual experimental testing lasted about 2 hours). Ambient lighting was sufficient to allow vision of the target array and background of the laboratory, but minimal to maximize target contrast and illumination and to reduce spurious reflections recorded by the motion capture system.

All trials began with the subject's head and body oriented toward the centre target, with the right index finger pressed against the chest switch and left arm hanging naturally beside the body. Once a subject was standing or sitting still with both feet flat on the support surface, index finger on the chest switch, and head oriented to the centre target, the experimenter initiated the trial. Subjects were instructed to reach to the central target following its illumination. During two-thirds of experimental trials, the central target remained illuminated until the end of the data acquisition period ('REACH' trials). For the remaining one-third of experimental trials, 200 ms following movement initiation (as detected by the voltage change from the chest switch), the LED of the central target was extinguished while the target LED to the right was simultaneously illuminated, indicating a new target location ('OC' trials). Upon detection of the target change, subjects were required to correct arm trajectory to contact the newly illuminated target. Subjects were instructed to move at a natural speed, maintain both feet flat on the support surface for the entire trial (SIT and STAND conditions), and to maintain their final posture (upon target contact) until the end of the trial (i.e. minimum 1 s). Because this research was aimed at understanding online movement control, two measures were taken to ensure that movement corrections were not prepared before the target change due to anticipation. First, REACH and OC trials were randomly presented to prevent the subject from predicting the trial type. Second, the 1:2 ratio of OC trials to REACH trials was selected so that the greater occurrence of REACH trials would decrease the expectation of a target change. A greater number of REACH trials was also necessary as they acted as controls against which OC trials were compared for detection of changes related to the online correction (Leonard et al., 2009). On randomly selected trials, no target was illuminated ('Catch' trials) to ensure that subjects waited for illumination of the central light instead of initiating the movement prematurely based on predicted target illumination time. These trials were not of experimental interest and thus were eliminated from the analysis. To prevent subjects from using the target array for postural support after target contact, subjects were instructed to immediately release the finger from the target after target contact (but to still maintain the same posture until target light extinguishment).

Before data acquisition began, subjects performed practice trials to become familiar with the task and experimental protocol (minimum of 10 trials, maximum of 30 trials, with equal numbers of REACH and OC targets that were randomly presented). These were performed either entirely in the SIT condition or STAND condition, depending on the first postural condition under which trials were executed in the experiment. The SIT and STAND conditions were blocked. To prevent overall effects due to the order of postural conditions, six subjects started the experiment with the STAND condition while the remaining four subjects started with the SIT condition. The first 3 subjects performed 100 trials in each condition (60 REACH, 30 OC, and 10 Catch in randomized order). Subsequent subjects performed 130 trials (80 REACH, 40 OC, and 10 Catch in randomized order) per condition to ensure that a sufficient number of OC trials would meet the inclusion criteria for data analysis. Figure 3.2 outlines the general sequence of events for an experimental session and Table A1 (Appendix) indicates the condition order and number of collected trials for each subject. Subjects were required to take a minimum 30-second break at least every 30 trials to reduce fatigue. Longer or more frequent breaks were permitted upon request.

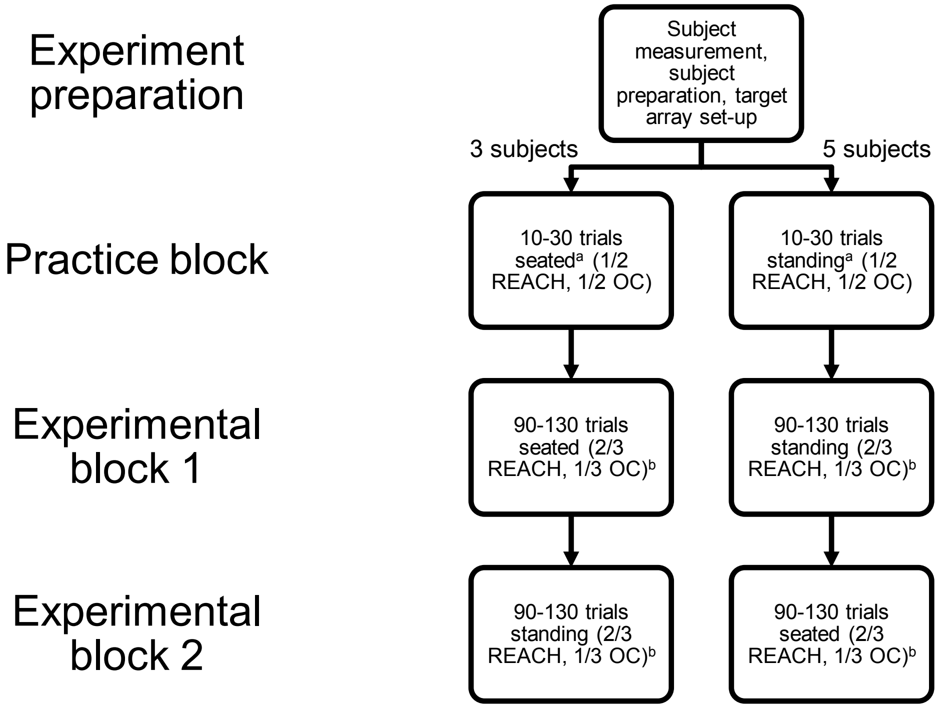

Figure 3.2: Diagram outlining the sequence of events in an experimental session.

[a] Excluded from analysis

[b] Also includes 10 Catch trials

3.5 Data Analysis

Use of the kinematic and analog data first required pre-processing in Vicon Nexus software (Vicon Motion Systems, Los Angeles, CA), which included 3D reconstruction and labelling of recorded kinematic markers. Missing data frames for markers were filled using Vicon IQ software (Vicon Motion Systems, Los Angeles, CA) with either spline interpolation techniques or with the creation of virtual markers (virtual point fixed body). All subsequent data processing steps were performed using custom programs written in Matlab. Data from corresponding Labview and Nexus files for each experimental trial were imported into Matlab and combined into a single file that could be later opened in Matlab as a single structure array.

3.5.1 Inclusion/Exclusion Criteria

Table 3.1 outlines the exclusion criteria for trials along with their rate of occurrence. The experimenter monitored subject movement and target light changes throughout the entire experiment. Occasionally for OC trials, the chest switch would not be fully depressed, resulting in an inappropriately early voltage pulse and thus an early target location change. These trials were identified, either by visual observation of the targets as the light change occurred or posthoc through inspection of chest signals and reach onsets identified through kinematics (Fon), and excluded from analysis (Table 3.1A).

Trials that were initiated before the subject was prepared (i.e. right index finger not on the chest switch, head not facing the centre target) were excluded (Table 3.1B). If the subject returned prematurely to the start position after movement termination (i.e. less than 1 s after target contact; Table 3.1C) or did not release the finger from the target until returning to the start position (Table 3.1D), the trial was also excluded from analysis to ensure that all observations would be made only on the movement towards the target and that posture was maintained without external support.

The velocity profiles of OC trials are characterized by two peaks, one associated with movement of the hand toward the first target, and another associated with reacceleration of the hand toward the new target (Fig 2.1B; Leonard et al., 2011). Because we were only interested in looking at *online* corrections for OC trials, in order to have successful task completion in an OC trial, hand tangential velocity had to remain above 3% of the peak value of that trial until the end of the movement. Throughout the experiment, the experimenter also took note of OC trials where the subject did not successfully correct movement before the finger arrived at the centre target. OC trials without successful reach correction were excluded from analysis (Table 3.1E).

Although the positioning of the MX3 cameras was optimized (within the limitations of the laboratory space) to capture all kinematic markers during this experiment, the nature of the movement, presence of experimental equipment (e.g. target array, stool), and limited number of cameras caused some markers to occasionally not appear in the reconstructed 3D video in some or all video frames of a trial. Vicon IQ software allowed for the estimation of the 3D position of markers that disappeared in the 3D video by either spline interpolation (based on that marker's position during video frames before and after the missing frames) or virtual marker techniques (based the positions of three markers on the same body segment during the virtual marker video frames). If one or more kinematic markers in a trial had missing frames of 3D data that could not be accurately estimated using either of these techniques, the trial was excluded from analysis (Table 3.1F).

Data from one subject was excluded from analysis due to an insufficient number of trials meeting the inclusion criteria. Specifically, on over half of the OC trials, he was unable to successfully correct his movement before reaching the first target. Another subject's data was excluded due to hardware problems during the experimental session that rendered the timing of Labview signals inaccurate. Posthoc analysis revealed that the sampling frequency of the Labview signals was significantly lower than the programmed 1000 Hz, indicating the likelihood that the target change in OC trials also deviated from 200 ms. Results presented in this thesis are for the remaining 8 subjects (5 females, 3 males; Table 3.2).

Table 3.1: Trials excluded from analysis. Values indicate the number of trials that were excluded by subject and criterion.

Exclusion Criterion	Subject (total trials)	S01 (100)	S02 (100)	S03 (100)	S04 (130)	S05 (130)	S06 (130)	S07 (130)	S08 (130)
A. Incorrect target change latency in OC trial	SIT	1	0	2	3	1	0	9	0
	STAND	2	1	0	2	1	0	4	0
B. Subject unprepared at trial start	SIT R	0	1	0	0	2	0	1	1
	SIT C	0	0	0	0	0	0	0	0
	STAND R	0	0	0	0	2	0	0	0
	STAND C	0	0	0	0	0	0	0	0
C. Subject returned to start position too early	SIT R	0	1	0	5	1	0	2	1
	SIT C	0	2	0	0	2	0	0	1
	STAND R	0	0	0	3	1	0	1	2
	STAND C	0	1	0	0	0	0	0	0
D. Target contact duration too long	SIT R	0	0	0	0	0	0	0	0
	SIT C	0	0	0	0	0	0	0	0
	STAND R	0	0	0	0	0	0	11	0
	STAND C	0	0	0	0	0	0	6	0
E. Unsuccessful online correction in OC trials	SIT	0	0	4	3	0	1	0	1
	STAND	4	1	11	2	0	5	0	0
F. Incomplete kinematic data	SIT R	0	1	1	2	6	3	5	0
	SIT C	0	0	0	0	1	0	0	0
	STAND R	0	1	1	2	0	2	0	2
	STAND C	0	0	0	0	0	0	0	1

Table 3.2: Characteristics of subjects included in the data analyses.

Subject ID	Sex	Age (years)	Height (cm)	Weight (kg)	Reach distance (cm)		Target distance (cm)	
					Centre	Right	Centre	Right
S01	M	21	177.5	73.0	64.0	70.0	83.2	91.0
S02	M	28	174.5	61.0	67.0	74.0	87.1	96.2
S03	F	20	157.5	55.9	58.5	65.0	76.1	84.5
S04	F	24	166.0	47.8	68.5	70.0	89.1	91.0
S05	M	24	168.5	64.8	64.0	69.0	83.5	90.0
S06	F	20	166.0	79.2	65.5	73.5	85.2	95.6
S07	F	20	173.0	65.6	62.0	72.5	80.6	94.3
S08	F	21	167.0	62.9	59.5	69.0	77.4	89.7
Mean (SD)		22.3 (2.9)	168.8 (6.2)	63.8 (9.7)	63.6 (3.5)	70.4 (2.9)	82.8 (4.5)	91.5 (3.8)

Reach distance: Distance from the xiphoid process to the tip of the right index finger when the arm was extended (neutral scapula protraction, chest facing the target) toward the target (at shoulder height).
Target distance: Distance from the xiphoid process to the target at the beginning of each trial (130% of reach distance).

3.5.2 Hand-Related Variables

Kinematic data from a marker placed on the head of the second metacarpal (RFIN) were used to quantify kinematic variables for the reaching hand. The RFIN position data were first low-pass filtered using a digital second-order Butterworth filter with a cut-off frequency of 20 Hz. Position data along the x (anteroposterior) and y (mediolateral) dimensions were combined to obtain hand position in the horizontal plane. Tangential velocity of the hand was then determined by differentiating the x-y position data. Velocity profiles of REACH trials (no online correction) were bell-shaped, characterized by a single velocity peak (PeakVel), whereas OC trials (with an online correction) were characterized by two velocity peaks (PeakVel1 and PeakVel2, see Fig 3.3, right panel). All temporal events used for analysis were verified on a trial-by-trial basis by visual inspection of the described velocity profile and 2D spatial trajectory.

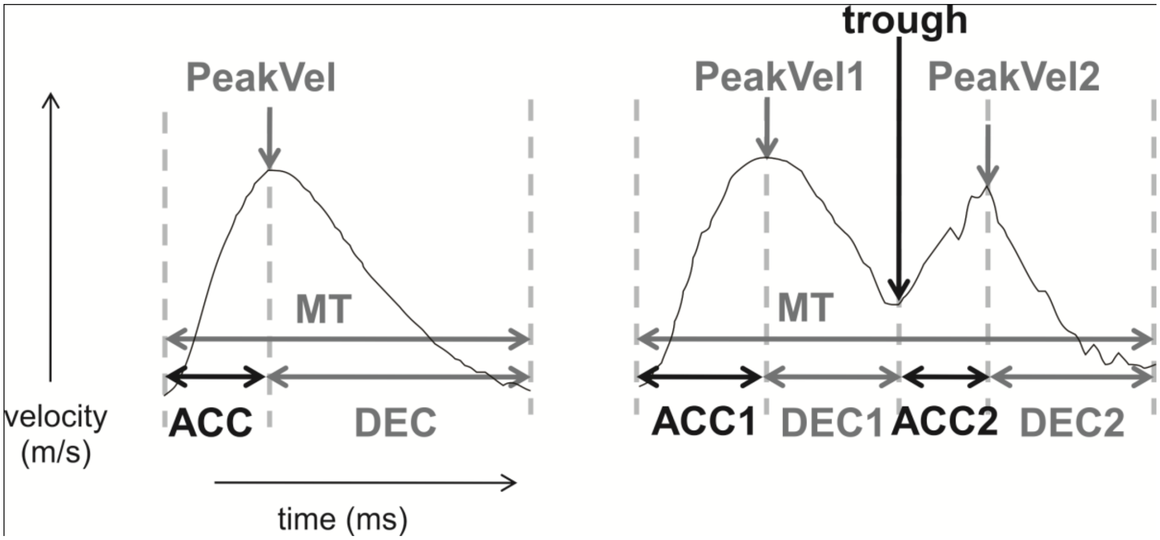

Figure 3.3: Typical velocity curves of a REACH trial (left) and a OC trial (right). The following variables were identified by visual inspection of the tangential velocity curves on a trial-by-trial basis: Acceleration phase duration (ACC, ACC1, and ACC2), deceleration phase duration (DEC, DEC1, DEC2), movement time (MT), velocity peak latency (PeakVel, PeakVel1, PeakVel2), and inter-peak trough latency (trough).

3.5.2.1 Movement Onset and Movement End

Reach onset (Fon) was identified as the point at which tangential hand velocity surpassed 3% of the peak velocity for that trial. This threshold has previously been used to successfully determine movement start and end based on hand kinematics (Leonard et al., 2009; Shabbott & Sainburg, 2009). All other temporal events are reported in relation to Fon. Because the reaching hand was held against the sternum at the start of each trial, visual inspection of the RFIN and sternum marker (STRN) velocity profiles ensured that the identified onset of movement coincided with a marked deviation of tangential velocity of the hand from that of the sternum, such that reach onset was not prematurely detected due to forward chest movement alone. This method of reach onset determination was preferred over reach onset detected by the chest switch in posthoc analyses because it is sensitive the subject's movement velocity, whereas movement onset detected by the chest switch was necessary for triggering the target light change because it was available in real time. Reach end (Fend) was determined as the time at which hand velocity dropped below 3% of the peak velocity for that trial. Movement time (MT) was the time elapsed from Fon to Fend (MT = Fend – Fon).

3.5.2.2 Acceleration and Deceleration Duration

Periods of acceleration and deceleration were determined based on the tangential velocity profiles (described above). For REACH trials, the acceleration period of each trial (ACC) begins at Fon and ends at PeakVel, whereas the deceleration period (DEC) begins at PeakVel and ends at Fend (Jaric, et al., 1998; MacKenzie, et al., 1987). OC trials are characterized by two acceleration (ACC1 and ACC2) and two deceleration (DEC1 and DEC2) periods. ACC1 begins at Fon and ends at PeakVel1, where DEC1 begins. The trough between PeakVel1 and PeakVel2 demarcates the end of DEC1 and the beginning of ACC2. Finally, PeakVel2 demarcates the end of ACC2 and the onset of DEC2, which ends at Fend. These variables are shown in Figure 3.3.

3.5.2.3 Focal Movement Correction

For the purposes of this study, reach correction in OC trials ('Fcorrect') was defined as the reacceleration of the hand towards the second target. Steps were taken to determine the latency of reach correction in OC trials. First, for a given subject and postural condition, the mean velocity and mean velocity ±1 standard deviation of all REACH trials were plotted. For each OC trial, the velocity profile was plotted against this mean profile and an algorithm detected the time at which the velocity deviated from one standard deviation of the mean REACH velocity profile (Fig. 3.4). Each trial was visually inspected to ensure that Fcorrect was appropriately determined. The latency of Fcorrect relative to Fon is reported throughout the document as absolute values and as percentages of MT.

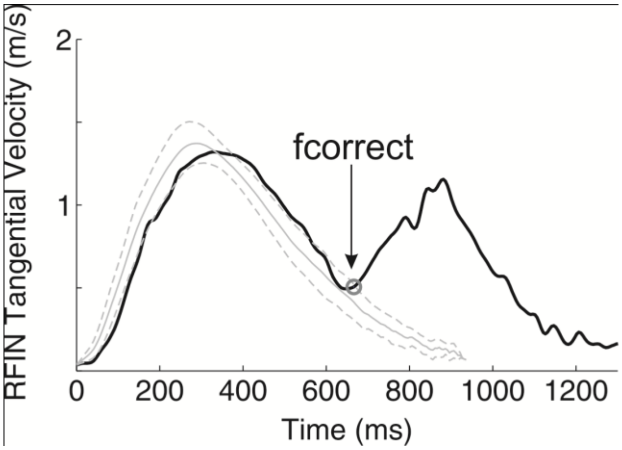

Figure 3.4: Identification of Fcorrect. For each subject and postural condition, Fcorrect for OC trials was identified by comparing the tangential velocity profile of each trial (black) to that of the mean±1 SD of all REACH trials (grey). The correction was tagged when the trial velocity went above 1 SD of the mean of REACH trials (○).

3.5.2.4 Symmetry Ratio

Symmetry Ratio (SR) was determined for REACH trials as a ratio between ACC and DEC (i.e. SR = ACC/DEC). An SR equal to one indicates that equal time is spent in acceleration as in deceleration, while a SR of less than one indicates that greater time is spent in deceleration than in acceleration. This variable was not calculated for OC trials because, unlike REACH trials, they have more than one acceleration-deceleration cycle.

3.5.3 Whole-Body Kinematic Strategy

Of particular interest to this study was the whole-body kinematic strategy underlying reaching under each postural condition. Posthoc viewings of the 3D videos of sample trials in each postural condition revealed notable differences in pelvis and trunk movement (see Results). Based on these observations, the following kinematic variables were analysed: pelvis translation in the anteroposterior (y) and mediolateral (x) directions, pelvis obliquity, pelvis rotation, and trunk rotation. Angular kinematics were calculated by the Plug-in-Gait model accompanying Vicon Nexus software.

3.5.3.1 Pelvis Translation

Subjects had kinematic markers attached to the skin overlying the left and right anterior superior iliac spines (LASI and RASI, respectively) and left and right posterior superior iliac spines (LPSI and RPSI, respectively) of the pelvic bones. The average 3D position of these four markers (AvgHip) was calculated at each video frame for each trial. For each trial, AvgHip displacement was quantified from Fon to Fend along the x dimension and from Fon to Fon+500ms along the y dimension.

3.5.3.2 Pelvis Obliquity and Pelvis Rotation

Pelvis obliquity and rotation, provided by the Plug-in-Gait model, are absolute angles referenced to laboratory coordinates. The origin of the pelvic coordinate system is at the midpoint between LASI and RASI. Pelvis rotation is calculated about the vertical (z) axis of the pelvic coordinate system, which is perpendicular to the line joining LASI and RASI markers (pelvis mediolateral (x) axis). Pelvis obliquity is defined as rotation about the pelvis anteroposterior (y) axis, which is perpendicular to the pelvis vertical and mediolateral axes. These angles are illustrated in Figure 4.5. The change in pelvis obliquity and pelvis rotation from Fon to Fend was quantified for each trial.

3.5.3.3 Trunk Rotation

Markers were placed on the spinous process of C7 vertebra (C7), spinous process of T10 vertebra (T10), suprasternal notch of the sternum (CLAV), and xiphoid process of the sternum (STRN). As for the pelvis angles, trunk rotation is an absolute angle referenced to laboratory coordinates. It is defined as rotation of the trunk anteroposterior (y) axis about the trunk vertical (z) axis. The direction of the former axis is parallel to a line joining the C7-T10 midpoint and CLAV- STRN midpoint, while the latter axis runs through the CLAV marker in a direction parallel to the line joining the C7-CLAV midpoint and T10-STRN midpoint. The change in trunk rotation from Fon to Fend was quantified for each trial.

3.5.3.4 Right Elbow Flexion-Extension

Elbow flexion-extension angle (Fig. 4.5) is a relative angle calculated between the longitudinal axes of the humerus and radius. These axes were defined by the shoulder joint centre (SJC), elbow joint centre (EJC), and wrist joint centre (WJC). Joint centre locations were calculated by the Plug-in-Gait model based on subject anthropometric measurements and on markers placed on the suprasternal notch (CLAV), acromion of the scapula (RSHO), lateral epicondyle of the humerus (RELB), and markers on both ends of a 10-cm rod placed on the dorsal side of the wrist joint (RWRA and RWRB).

3.5.3.5 Right Shoulder Adduction-Abduction

The shoulder adduction-abduction angle is a relative angle between the long axis of the humerus and mediolateral (x) axis of the trunk (perpendicular to the trunk anteroposterior axis, as described above). Due to the shoulder joint permitting circumduction of the humerus, the axis of this angle is not constant relative to the trunk. In other words, the rotational axis is influenced by shoulder flexion-extension. Figure 4.5 illustrates a plan view of right shoulder adduction (however, the plane of this angle is variable and not necessarily always in the horizontal plane).

3.5.3.6 Right Shoulder Flexion-Extension

Shoulder flexion-extension angle is a relative angle calculated between the anteroposterior (y) axis of the trunk and long axis of the humerus about an axis parallel with the trunk mediolateral axis. Unlike for the shoulder adduction-abduction angle, the Plug-in-Gait model defines the axis of this angle as fixed relative to the trunk mediolateral axis.

It should be noted that while right shoulder flexion-extension and adduction-adduction are quantified separately, they are not independent and the actual shoulder movement consists of concurrent changes in these angles.

3.6 Statistical Analyses

Within each trial type (REACH and OC), two-sample t-tests and tests for equality of two variances were performed to test for significant effects of postural condition on the dependent variables. If the test for equality of two variances revealed significant differences in variances ($p \leq 0.05$), then separate variances were used in the corresponding t-test. Otherwise, pooled variances were used. All statistical analyses were performed in MYSTAT 12 (Systat Software, Chicago, IL)

CHAPTER 4: RESULTS

4.1 Whole-Body Kinematic Strategies for Reaching Movements in Different Postural Conditions

Typical movement strategies displayed by subjects in the 4 conditions are shown in Fig. 4.1 The figure represents the sagittal plane positions of the recorded markers for one typical subject (S02). In the STAND conditions (left side), both REACH and OC movements were characterised by a slight forward lean of the trunk as the arm was outstretched. There was typically little or no movement of the lower limbs. Similar forward lean movements of the trunk can also be seen in the two SIT conditions (right side of figure). However, the pelvis markers typically shifted upwards and forwards in these conditions for REACH and OC conditions. Figure 4.1E further illustrates typical movement strategies by showing the changes in thorax rotation, pelvis rotation and obliquity, shoulder joint angles, and elbow joint angles during sample trials of the same representative subject.

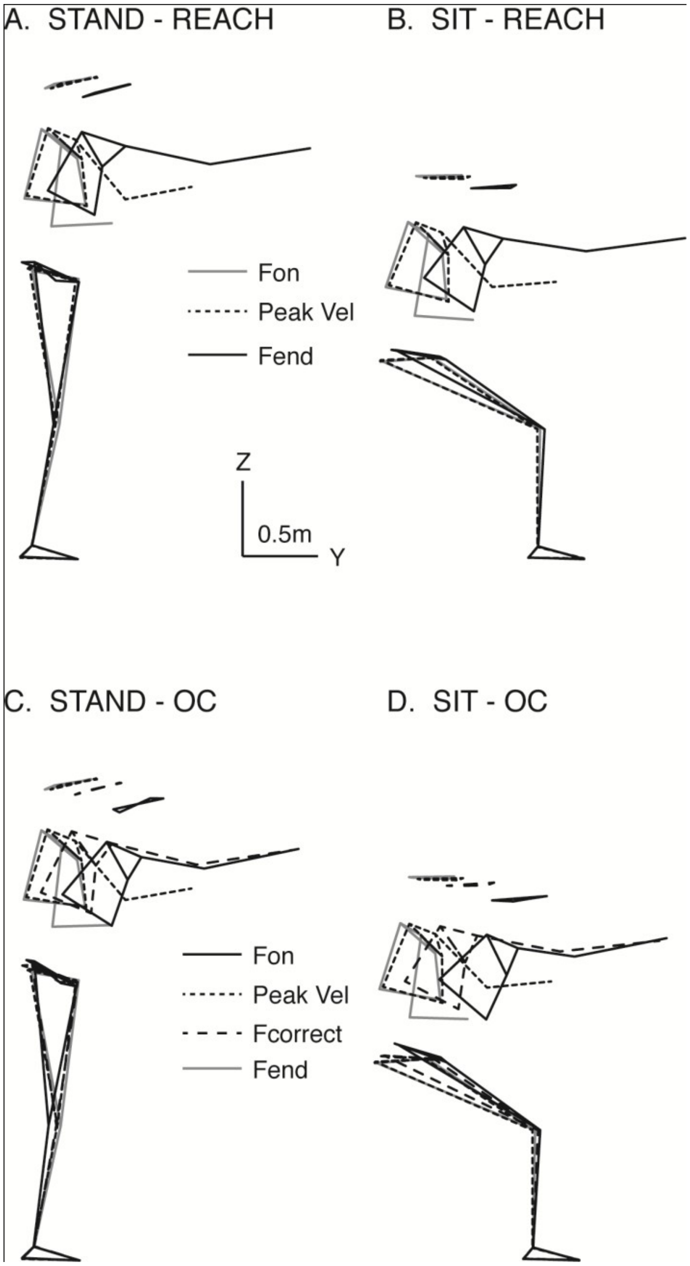

Figure 4.1A-D: Sagittal plane view of a representative subject's average position at various times during the movements. A-D: STAND-REACH, SIT-REACH, STAND-OC and SIT-OC conditions, respectively. For the OC conditions, a total of 4 stick positions are shown corresponding to movement onset (Fon), peak velocity, Fcorrect, and movement end (Fend). Positions for REACH conditions are shown for Fon, peak velocity, and Fend only.

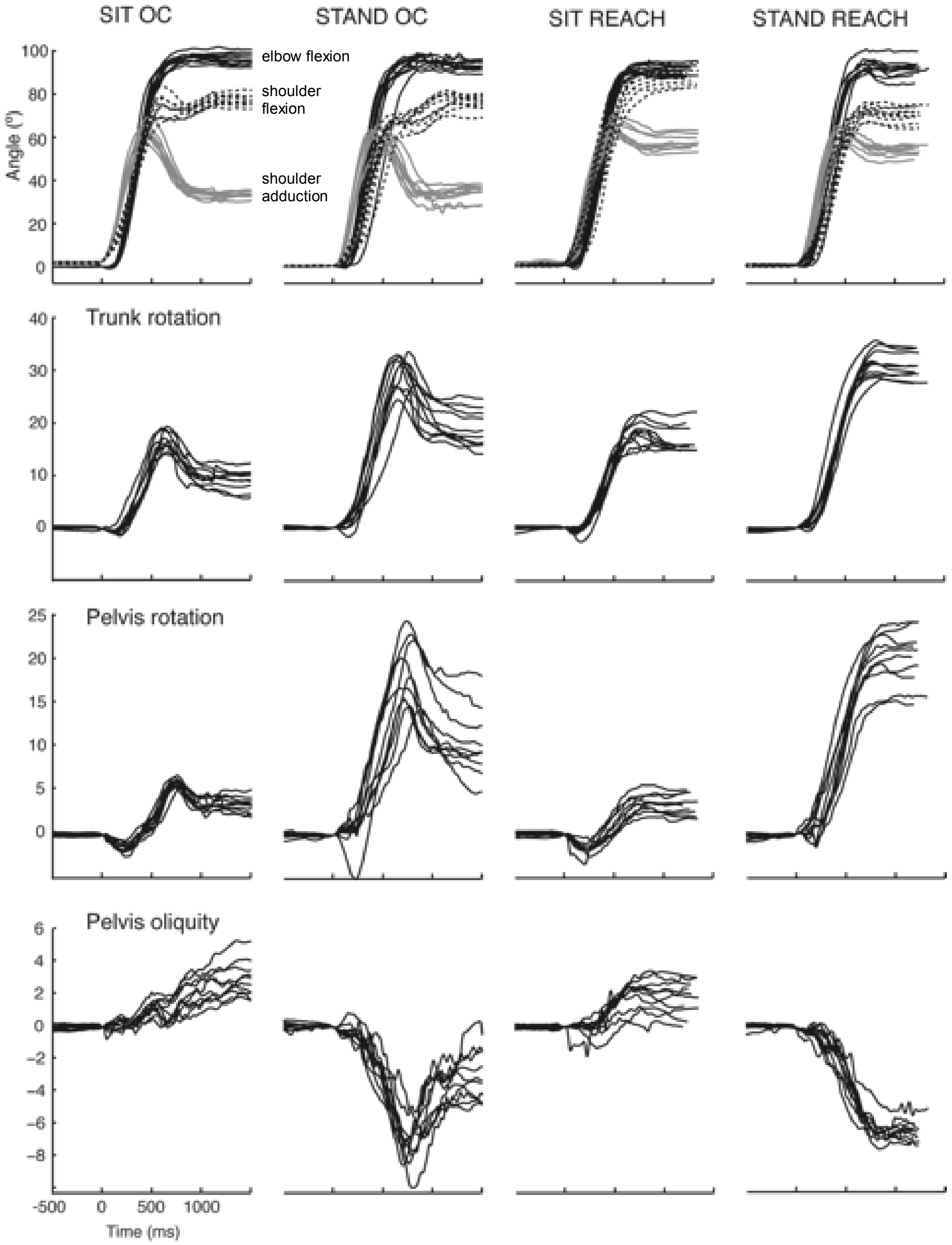

Figure 4.1E: Changes in thorax rotation, pelvis rotation and obliquity, shoulder adduction, shoulder flexion, and elbow extension during sample trials for a representative subject (same subject as in Fig. 4.1A-D). Trials were plotted from Fon-500ms to Fend+500ms. All values indicate angular displacement with respect to the angle at Fon (time=0). A positive rotational displacement (trunk and pelvis) indicates counterclockwise rotation, while a positive change in pelvis obliquity indicates that the right side is displaced upwards relative to the left side. Mean subject MTs ±1SD for SIT OC, STAND OC, SIT REACH, AND STAND REACH:1129±55, 1141±71, 770±49, and 737±51 ms, respectively.

4.1.1 Trunk and Pelvis Displacements

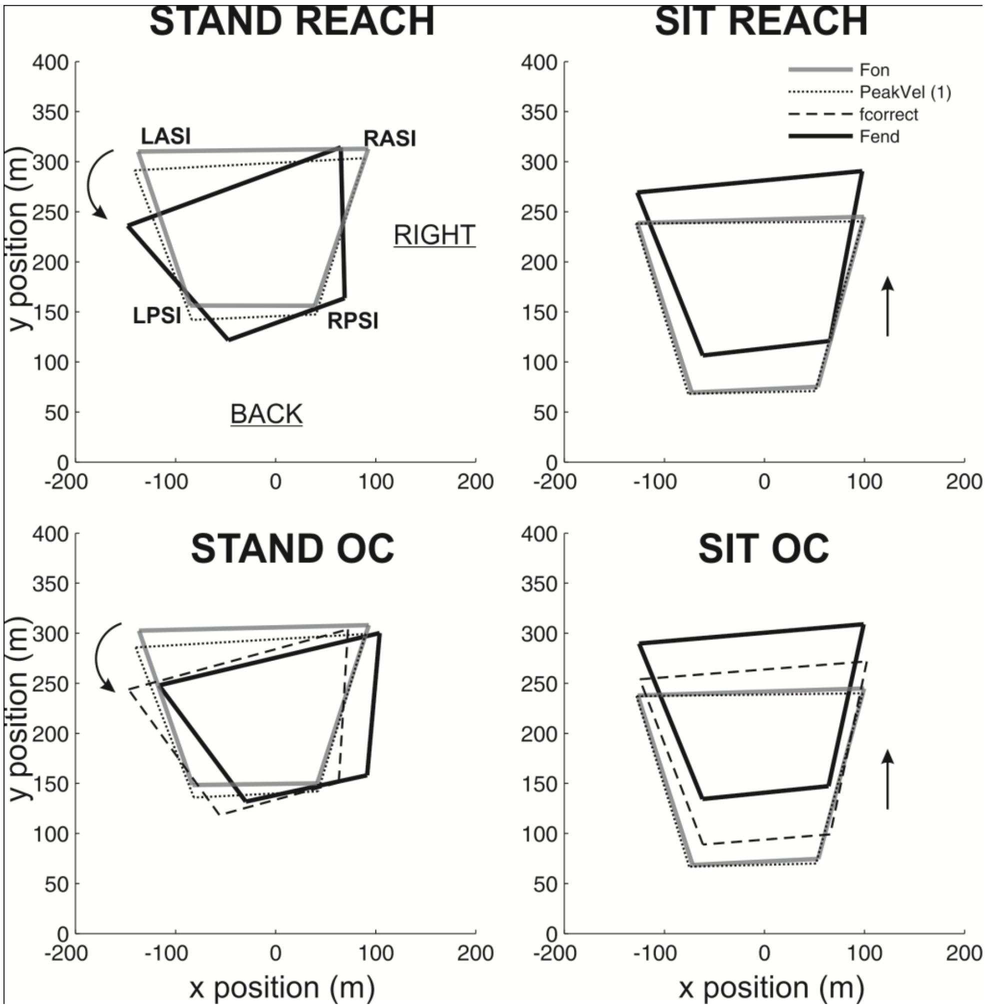

Figure 4.2: Plan view of the average position of the pelvis markers for a representative subject. Kinematic markers were placed on the left and right anterior superior iliac spines (LASI and RASI, respectively) and left and right posterior superior iliac spines (LPSI and RPSI, respectively). *Top:* REACH trials. *Bottom:* OC trials. *Left:* STAND trials. *Right:* SIT trials.

Movements in all conditions and trial types involved counterclockwise rotations of the trunk and pelvis (see averages of 1 subject in Figs.4.1E and 4.2). This was typical of all subjects. Movement corrections in OC trials were characterized by a reversal in rotation direction in these body segments to shift the upper limb to the right, toward the new target, but the pelvis and trunk angles at Fend were still displaced in the counterclockwise direction relative to their position at Fon (see Fig. 4.1 E, 2nd and 3rd rows and Fig. 4.2, left panels). REACH and OC movements in the STAND condition exhibited greater mean trunk rotation and pelvis rotation from Fon to Fend (Fig. 4.5). The change in pelvis obliquity from Fon to Fend was also affected by postural condition: In the STAND condition, the pelvis tilted such that left side was displaced upwards relative to the right side, whereas in the SIT condition, the opposite occurred. This is illustrated in Fig. 4.1E (bottom row) and Fig. 4.5, where pelvis tilt values for the SIT condition are positive while those for the STAND condition are negative.

On average, the pelvis moved to the right except in SIT REACH trials, which had negligible mean AvgHip x-displacements (Fig. 4.3). The greatest effect of posture on pelvis mediolateral (x) displacement was observed in OC trials; when standing, the pelvis moved on average almost 3 cm further to the right than when seated, bringing the body closer to the target on the right.

Visual inspection of average pelvis anteroposterior (y) trajectories revealed that in STAND trials, the pelvis initially moved backwards in the majority of trials, sometimes reversing its direction later on in the movement. This trend was not observed in SIT trials, for which movement in the y-dimension was primarily forward due to the pelvis tilting forwards (see Figs. 4.1, 4.2, and 4.4). These differences were consistent across REACH and OC trials. Quantification of the average pelvis y-displacements from Fon to Fend did not reveal the initial backwards displacements seen in STAND reaches, since it was often reversed later in the movement. Consequently, pelvis translation along the y-dimension was determined from Fon to Fon+500ms for each trial. This interval was selected on the basis that the reversal of pelvis movement direction along the y-dimension, if present, occurred around 500 ms in STAND trials (Fig. 4.4). Comparisons of the means indicated that 500 ms following Fon, the direction of pelvis anteroposterior y-displacement was forward in SIT trials whereas in STAND trials it was backwards (Fig. 4.3).

A t-test for independent samples showed that the effects of postural condition in REACH trials were significant for mean trunk rotation, $t(748.1)=19.1$, $p<.001$ ($24.8\pm7.1^\circ$ vs. $18.4\pm3.3^\circ$); pelvis rotation, $t(586.5)=29.2$, $p<.001$ ($12.0\pm6.3^\circ$ vs. $3.8\pm1.4^\circ$); and pelvis obliquity, t(636.5)=-11.8, p<.001 (-4.3±2.1º vs. 0.1±1.5º). In other words, reaches to a stationary target executed from the standing position exhibited significantly greater trunk rotation and pelvis rotation, as well as pelvis obliquity in the opposite direction. The same trend was also recorded for OC trials; differences in mean trunk rotation, pelvis rotation, and pelvis obliquity between postural conditions were significant, t(340.1)=8.8, p<.001 (14.4±6.2º vs. 10.5±3.14º); t(304.1)=13.6, p<.001 (6.9±4.9º vs. 2.2±2.0º); t(492.0)=21.2, p<.001 (-1.7±2.0º vs. 2.1±2.0º), respectively. Pelvis translations in the mediolateral (x) dimension were significantly greater in the STAND condition in both REACH and OC trials, t(636.5)=-11.8, p<.001 (0.01±0.02m vs. 0.00±0.00m) and t(294.6)=-23.3, p<.001 (0.03±0.02m vs. 0.01±0.01m), respectively. A significant effect of posture on average anteroposterior (y) pelvis displacements was also found in REACH and OC trials, t(803.5)= 30.1, p<.001 (-0.01±0.02m vs. 0.01±0.01m) and t(355.9)= 19.1, p<.001 (-0.01±0.02m vs. 0.01±0.01m), respectively.

Therefore, in summary, whole body kinematics revealed significant differences in pelvis and trunk movements between seated and standing reaches.

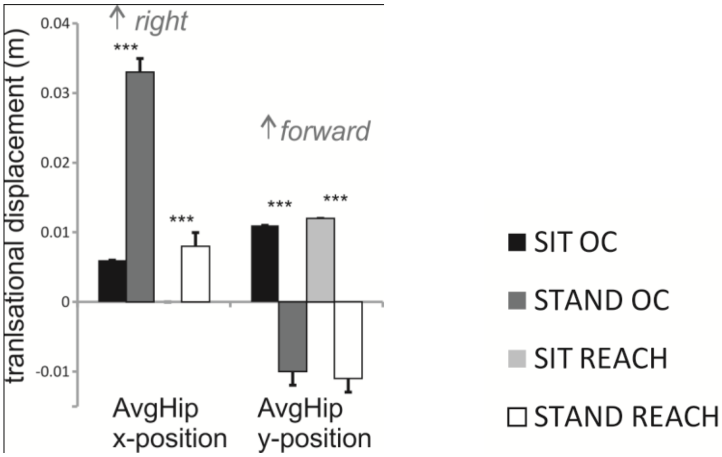

Figure 4.3: Mean AvgHip translational displacement across subjects. Displacements along the x-axis were calculated as the difference in x-position from Fon to Fend, while displacements along the y-axis were calculated as the difference in y-position from Fon to Fon+500ms. Positive values indicate rightward or forward displacements for x and y axes, respectively. Significant differences from the t-tests examining the effect of posture (SIT vs. STAND) are indicated as follows: *p<.05; **p<.01; ***p<.001. Error bars indicate the 95% confidence interval (CI).

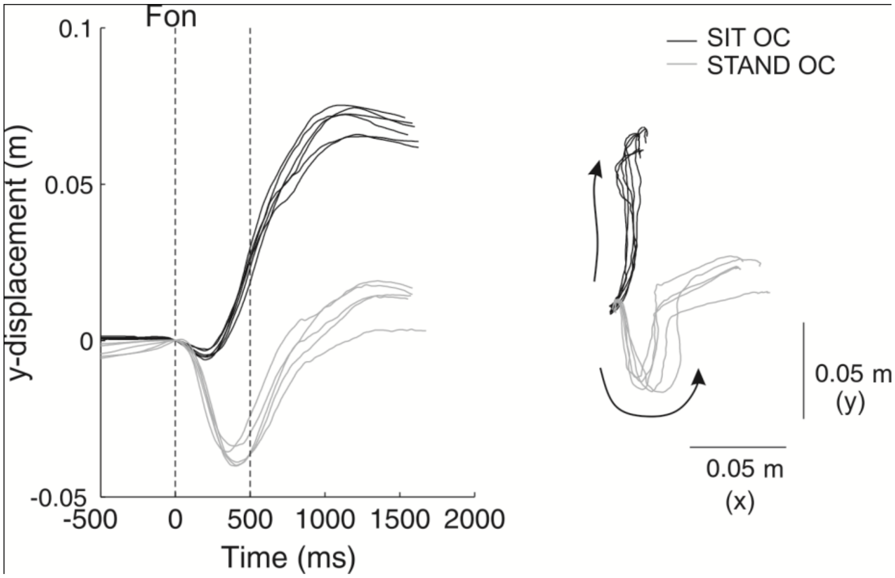

Figure 4.4: AvgHip y-position of sample OC trials (Fon-500ms to Fend+500ms) from one representative subject. *Left:* Average anteroposterior pelvis displacement vs. time. In STAND trials (grey), average pelvis anteroposterior movement was initially backwards before reversing directions about 500 ms after Fon. However, there was little backward pelvis anteroposterior movement in SIT trials (black). The same trends were observed for REACH trials (not shown). For the purposes of analysis, average pelvis anteroposterior displacements were calculated as the change in y-position from Fon to Fon+500ms (demarcated by the dotted lines). *Right:* Spatial trajectory of AvgHip.

4.1.2 Right Upper Limb

Before each trial, subjects stood with the right index finger on a switch located on the xiphoid process of the sternum. The reaching task involved elbow extension, shoulder adduction, and shoulder flexion of the right upper limb in all four conditions. In OC trials, the movement correction required after the change in target position consisted primarily of shoulder abduction but the final shoulder angle remained more adducted than the starting position. Fig. 4.1E (top row) illustrates the changes in shoulder and elbow angles for sample trials of one subject.

Elbow extension was greater in the STAND condition than in SIT condition for REACH and OC trials, t(1063)=7.5, p<.001 (94.5±5.7 vs. 92.0±5.2º) and t(492)=3.7, p<.001 (101.7±4.9º vs. 100.1±4.5º), respectively. For REACH trials, mean shoulder adduction was significantly greater in the SIT condition than in the STAND condition, t(1053.9)=7.2, p<.001 (75.0±12.3º vs. 69.3±13.5º), but not significantly different between

OC trials in the two postural conditions (see Fig. 4.5). Given that the shoulder adduction-abduction angle was calculated relative to the trunk, and that the trunk rotated such that the right shoulder was more forward than the left shoulder during the reach, this may have been attributed to the increased trunk rotation observed in STAND trials. There was no significant effect of postural condition on shoulder flexion-extension angular displacement.

An additional noteworthy observation is that, compared to OC trials, REACH trials not only showed greater mean shoulder adduction (~72° vs. ~57°), but also less mean shoulder flexion (~70° vs ~78°). While it is possible that these observations are due to an inverse relationship between shoulder flexion angle and shoulder adduction angle, they can also be explained by differences in trunk movement between REACH and OC trials: Since shoulder flexion is measured with respect to the trunk anteroposterior axis, which varies with trunk flexion, greater trunk flexion would result in a greater shoulder flexion angle if the absolute humerus orientation remained constant. Indeed, for all subjects, trunk flexion was shown to be greater in OC trials than for REACH trials (data not shown). Fig. 4.1 of a representative subject provides evidence of greater trunk flexion in OC trials (C-D) compared to REACH trials (A-B).

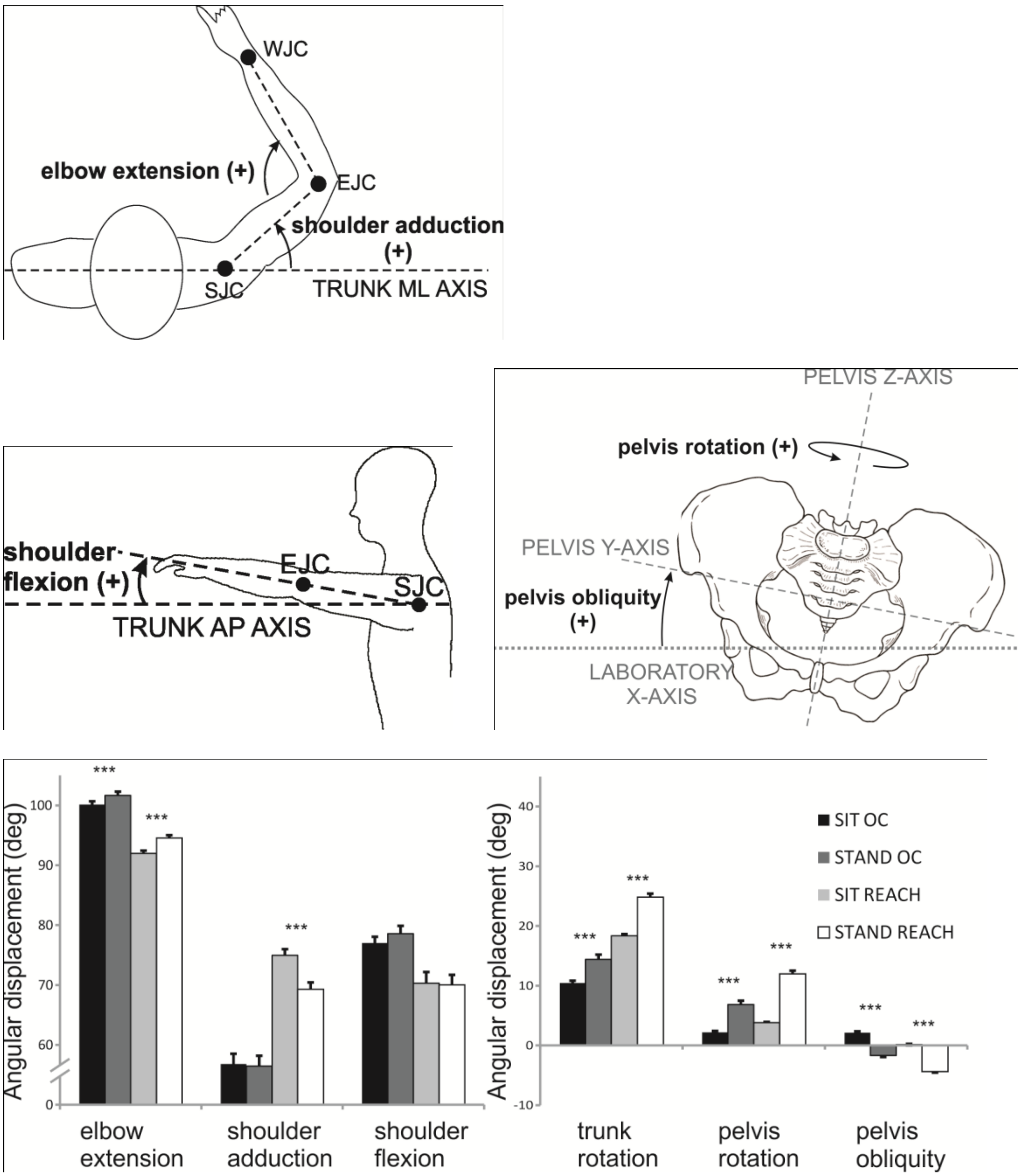

Figure 4.5: Mean angular displacements from Fon to Fend across subjects. A positive rotational displacement (trunk and pelvis) indicates counterclockwise rotation, while a positive change in pelvis obliquity indicates that the right side is displaced upwards relative to the left side. Significant differences from the t-tests examining the effect of posture (SIT vs. STAND) are indicated as follows: *p<.05; **p<.01; ***p<.001. Error bars indicate the 95% CI. *Abbreviations:* WJC, wrist joint centre; EJC, elbow joint centre; SJC, shoulder joint centre; AP, anteroposterior; ML, mediolateral.

Tables A6 and A7 in the Appendix summarize the results of the two-sample t-tests and equality of variance tests performed on whole-body kinematic variables. Means and standard deviations of these variables are presented in Table A5 and Figure 4.5.

4.2 Arm Movement Endpoint Kinematics in the Different Postural Conditions and Trial Types

Figure 4.6 displays the spatial trajectory and velocity profile of select trials for the same subject shown in Figs. 4.1 and 4.2. For each trial type, SIT and STAND hand kinematics appear to be very similar. The main difference that can be seen between SIT and STAND conditions is that in OC trials, the troughs in the velocity profiles (approximate time when reaccelerations began) are slightly deeper (lower velocity) in STAND OC than in SIT OC trials.

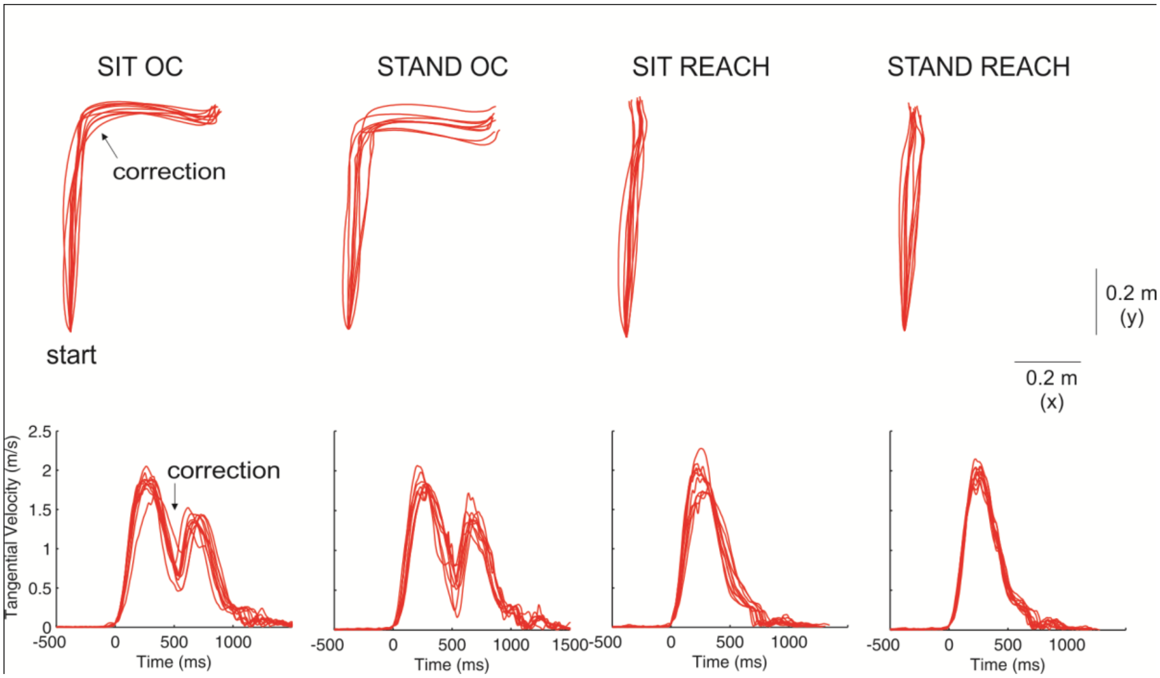

Figure 4.6: Sample spatial trajectories (top) and velocity profiles (bottom) of the reaching hand for one representative subject (same subject as in Figs. 4.1 and 4.2). Trials were plotted from Fon-500ms to Fend+500ms. Trials are aligned at Fon. The arrows indicate approximately when movement correction occured in OC trials (‘Fcorrect’), defined as the reacceleration of the hand towards the second target

4.2.1 REACH Trials

On average, STAND REACH movements had longer ACC, larger SR, and greater PeakVel magnitude than SIT REACH movements (344.9±93.6 ms vs. 331.0±81.6 ms; 0.543±0.130 vs. 0.508±0.121; and 1.507±0.341 m/s vs. 1.457±0.323 m/s, respectively; see Fig. 4.7). Two-sample t-tests revealed that these differences were significant, t(1045.44)=-2.6, p=.010; t(1049)=-4.5, p<.001; and t(1060)=-2.8, p=.006, respectively. The effect of postural configuration on DEC and MT did not reach significance.

4.2.2 OC trials

In OC trials, velocity trough magnitude was greater in the SIT condition than in the STAND condition (0.556±0.211 m/s vs. 0.509±0.236 m/s, respectively; see Fig. 4.7). This difference was statistically significant, t(497)=2.3, p=0.020. There was no effect, however, of postural condition on the remaining variables (ACC1, ACC2, DEC1, DEC2, MT, Fcorrect, SymRatio, PeakVel1 magnitude, and PeakVel2 magnitude).

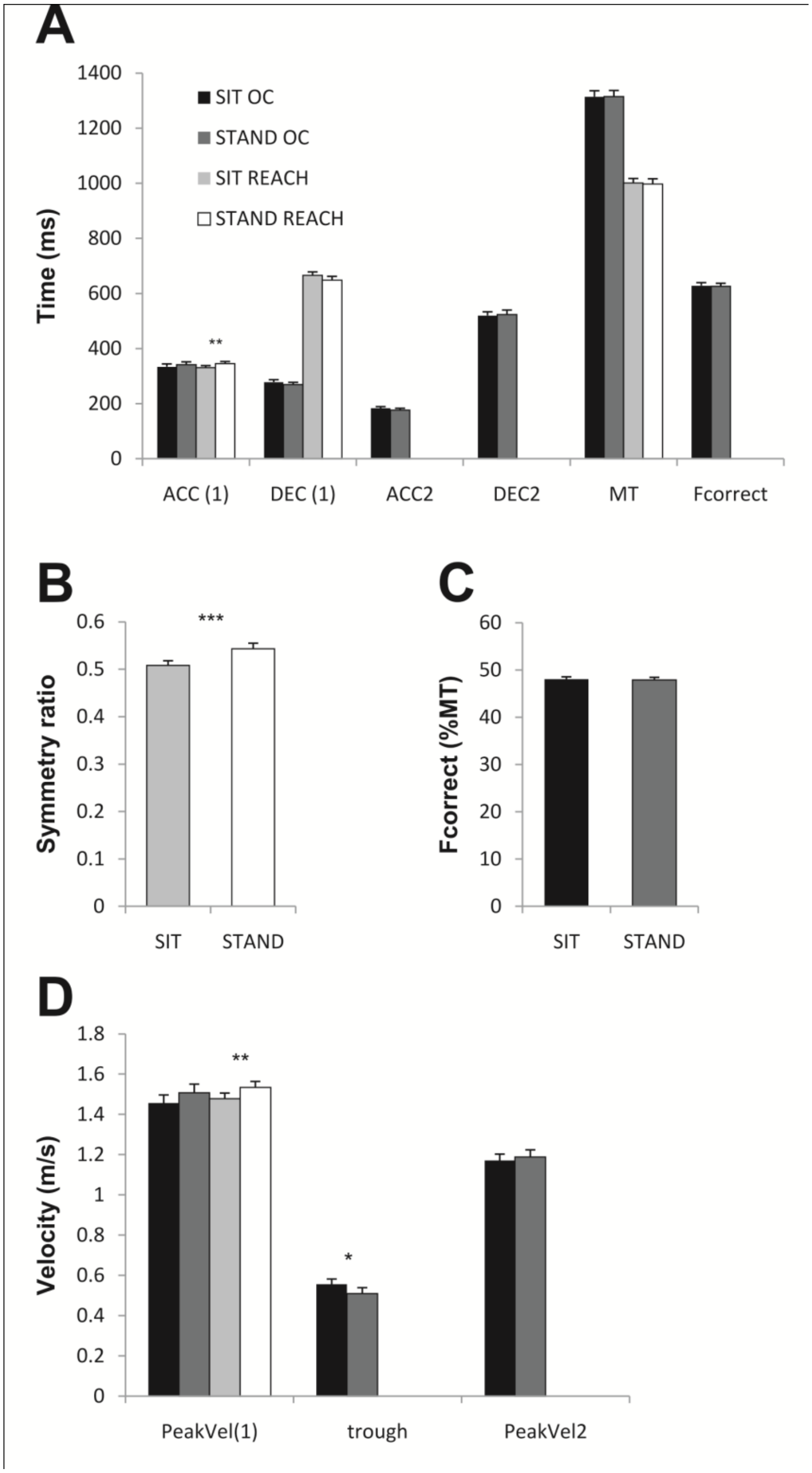

Figure 4.7: Means of hand kinematic variables across subjects. Significant differences from the t-tests examining the effect of posture (SIT vs. STAND) are indicated as follows: *p<.05; **p<.01; ***p<.001. Error bars indicate the 95% CI.

In summary, therefore, results showed that endpoint kinematics of the reaching arm were generally unaffected by whether the movement was executed in a seated or standing position. This was true for movements to a stationary target and for movements requiring an online correction. The only significant effects were a slightly longer mean acceleration phase (REACH trials), higher mean SR (REACH trials), greater mean peak velocity (REACH trials), and deeper mean velocity trough (OC trials) during reaching when standing. The rest of the measured hand kinematic variables remained unchanged by postural configuration in the two trial types (REACH and OC). Tables A3 and A4 summarize the results of the two-sample t-tests and equality of variance tests performed on movement endpoint kinematic variables. Means and standard deviations of these variables are presented in Table A2 and Figure 4.7.

CHAPTER 5: DISCUSSION

The present study aimed to determine the effects of postural configuration (sitting vs. standing) on the control of goal-directed reaching. Results showed that kinematics of the reaching hand were generally unaffected by postural configuration (SIT vs. STAND). However, during REACH trials, the STAND condition had greater ACC, SR, and PeakVel magnitude, while in OC trials, the SIT condition had greater velocity trough magnitude. Whole-body kinematic strategies, however, did show marked and significant differences between the two postural conditions.

Compared to reaches performed when seated, subjects had greater change in pelvis obliquity, pelvis rotation, trunk rotation, and elbow extension from Fon to Fend during reaches performed when standing. Translational movement of the pelvis also differed between the two postural conditions: In the STAND condition, the pelvis initially moved backwards, unlike in the SIT condition, and had greater rightward translation. These differences were true for both REACH and OC trials. For REACH trials, shoulder adduction from Fon to Fend was smaller during the STAND condition. These kinematic differences clearly show that the equilibrium constraints associated with standing required distinct differences in movement strategies to achieve a similar end result in both REACH and OC conditions. With this in mind, the results support the notion that equilibrium constraints do not affect reach-to-point and online correction movements due to marked whole-body compensatory strategies.

5.1 Putting the Results into Perspective: A Comparison with Previous Studies of Seated and Standing Reaches

There were several methodological differences between the reaching task used in the present study compared to those of previous studies on goal-directed arm reaching. Many studies minimized movements in segments other than the reaching arm by 1) using target distances within arm's length (Day & Lyon, 2000; Elliott, et al., 1991; Georgopoulos, et al., 1981; MacKenzie, et al., 1987; Pelisson, et al., 1986; Prablanc, et al., 1986; Vercher, et al., 1994) and 2) by stabilizing the head, for example with a bite-bar (e.g. Komilis, et al., 1993; Pelisson, et al., 1986; Prablanc, et al., 1986; Sainburg, et al., 2003) or chin rest (Gritsenko, et al., 2009). In the present study, however, attainment of the targets (placed beyond reach) required movement of the trunk and pelvis; the only movement restriction was that the feet remained flat on the support surface. In the SIT condition, contact between the seat of the chair and gluteal region was maintained. Additionally, unlike some studies of goal-directed reaching in which task instructions emphasized RT/movement speed and/or accuracy (Elliott, et al., 1991; Fautrelle, et al., 2010; MacKenzie, et al., 1987; Prablanc, et al., 1986; Sarlegna, et al., 2003), subjects in the present study were simply told to reach toward and press the target.

Movement times for goal-directed reaching movements reported in the literature vary greatly. When considering goal-directed reaching studies using comparable reaching distances, reported movement times to stationary targets ranged from 285 ms to 980 ms (Elliott, et al., 1991; Fautrelle, et al., 2010; Leonard, et al., 2011; Pelisson, et al., 1986; Prablanc, et al., 1986). The mean MT in the present study (1157 ms across conditions and trial types) is comparable to that found by Leonard et al. (2011), who used a very similar reaching paradigm and reported a mean MT of 1058 ms across trial types. The literature also reveals large variability in peak velocity. For example, Gritsenko et al. (2009) reported a mean peak velocity of 0.75 m/s for movements executed at the subjects' preferred speeds while Fautrelle et al. (2010) found peak velocities of 2.9-3.5 m/s during movements for which task instructions emphasized speed. Given that reach distance used in the present study was much greater than those used in the above-mentioned studies and that task instructions of the present study did not emphasize movement speed, it is not surprising that relatively greater mean MT (1157 ms) and lower mean peak velocity (1.49 m/s) were recorded.

Mean symmetry ratio was found to be 0.5, indicating that subjects spent about twice as much time in the deceleration phase than in the acceleration phase of the reaching movement (a ratio of 1 would mean equal durations of the 2 phases). This value is intermediate between those found by Elliott et al. (1991) when either speed or accuracy was emphasized (0.64 and 0.33, respectively), thus suggesting in the present study that both movement accuracy and speed may have been taken into consideration by the subjects. Although focal movement accuracy was not quantified, subjects successfully made contact with the surface of the target switch (a 2.5-cm diameter circle) during all trials.

In the present study, a shift in target position in OC trials was triggered 200 ms following the release of the right finger from the chest switch. Because the change in target location in the present study was very large and was not triggered by an eye saccade, the double step reaching paradigm used differed from studies which previously looked at online corrections to unperceived target shifts (i.e. Bard, et al., 1999; Komilis, et al., 1993; Pelisson, et al., 1986; Sarlegna, et al., 2003; Turrell, et al., 1998). Indeed, in the above-mentioned studies, the visual angles by which the targets were displaced were only 5-10º and were triggered during saccadic suppression. Regardless, it has been demonstrated that movement correction latencies to an unexpected target shift do not appear to be affected by whether or not the target shift is perceived (Gritsenko, et al., 2009; Komilis, et al., 1993) or by the amplitude of the target shift (Gritsenko, et al., 2009).

Based on hand kinematics, the average time for subjects to correct hand trajectory in response to the target shift (triggered 200 ms following movement onset) was 427 ms. The mean latency of Fcorrect corresponded to 48% of the trial MT and was similar to the latency reported by Leonard et al. (2011; 47% of MT). The mean correction time with respect to the target shift is much longer than values reported in studies of online reaching corrections, which ranged from 125 to 320 ms based on hand kinematics (Day & Lyon, 2000; Fautrelle, et al., 2010; Georgopoulos, et al., 1981; Gritsenko, et al., 2009; Sarlegna, et al., 2003). This is likely due to several methodological differences. First, task instructions in the present study did not emphasize movement speed, which meant that it was not essential for subjects to correct movements as fast as possible. Second, movement corrections in the present study involved corrections of body segments other than the reaching arm (e.g. trunk and pelvis), which served to change the direction of movement. Consequently, corrections involved the control of a greater number of body segments and the overcoming of a greater amount of inertia. The double step task used by Fautrelle et al. (2010) also required trunk flexion and leg muscle corrections, but their task involved corrections in movement amplitude instead of movement direction, unlike in the present study and in Leonard et al.'s (2011) study.

Additionally, in the study by Fautrelle et al. (2010), the muscle activity responsible for initiating a correction of arm trajectory was the anterior deltoid, an agonist in the movement toward the initial target. In Leonard et al.'s (2011) task, however, arm corrections were characterized by activation of muscles that were antagonists in the initial motor program (posterior deltoid and triceps brachii), followed by inhibition of the agonist (anterior deltoid). It is therefore possible that a change in hand movement direction would require greater processing time than a change in hand movement amplitude. This is supported by Brebner's (1968) suggestion that because corrections involving a change in movement direction require the initiation of new muscle patterns, the central processing of these corrections are delayed, unlike corrections that increase the amplitude of an ongoing movement in the same direction.

Another explanation for the discrepancies in correction latencies between the present study and previous double step reaching studies is the operationalization of the focal movement correction (Fcorrect). In many cases, the hand velocity in OC trials dropped below the mean velocity of REACH trials (but remained above the 3% peak velocity threshold used to identify movement end) before reacceleration to the second target, indicating that before the initial target was attained, movement of the hand to the initial target was interrupted due to the change in desired end position. As Fcorrect was defined only as the reacceleration of the hand towards the second target, it likely overestimated the true time of hand movement correction (see also Georgopoulos, et al., 1981, p. 740). Fcorrect may have also been overestimated since it was determined based on comparisons of velocity profiles instead of acceleration profiles (unlike in Fautrelle et al. (2010)), from which kinematic changes would be detected sooner.

5.2 Equilibrium constraints have no effect on the endpoint kinematics of goal-directed reaching

When seated with the feet flat on the floor, the mobility of the lower body is restricted by contact of the gluteal region with the seat of the chair. The function of the increased pelvis and trunk movement in the STAND condition relative to the SIT condition was not necessarily only for the maintenance of equilibrium in a less stable postural orientation, but may have resulted in part from the greater number degrees of freedom (DFs) available in the standing configuration. It has been shown that APAs create the dynamical conditions necessary for executing reaching movements (Stapley, et al., 1998) as well as online movement corrections (Leonard, et al., 2011). Thus, it is likely that movements of non-focal segments observed in the present study served these purposes. For example, counterclockwise rotation of the trunk and pelvis would position the reaching (right) hand in a more optimal (forward) position for contacting the target. Also, rightward translation of the pelvis during OC trials would bring the body closer to the final target (see Figs. 4.3 and 4.4).

Despite the differences in whole-body kinematic strategy, endpoint kinematics of the focal movement (i.e. the reaching hand) were largely unaffected in both REACH and OC trials. Although the STAND condition had significantly greater ACC, SR, and PeakVel magnitude in REACH trials and smaller velocity trough magnitude in OC trials when data across subjects were pooled (see Fig. 4.7 and Tables A2-A3 in the Appendix), these effects were not consistent when data were analyzed on a subject-by-subject basis. Nonetheless, as the task involved movement of the trunk and pelvis to bring the hand to the target, the greater mean ACC, SR, and PeakVel magnitude in the STAND condition could have been due to the greater total inertia of the moving segments, resulting in greater forward momentum during the acceleration phase and delaying the effect of forces involved in decelerating the body as the hand neared the target.

There was also no effect of postural condition on MT in the present study. Moreover, there was no effect of postural condition on Fcorrect. Spatial parameters of focal movement endpoint kinematics (e.g. spatial variability and position at various time points) were not quantified. However, for each subject, the trajectories of the reaching hand were compared between the two postural conditions, with no noticeable, consistent differences revealed across subjects (see Fig 4.6). These findings provide further evidence for the efficiency of the neural processes underlying the online control of goal-directed reaching.

This is not the first study to report invariance of reaching endpoint kinematics despite different whole-body kinematics. Kaminski et al. (1995) showed that the extent of trunk and scapular motions in seated reaching movements did not affect the variability or smoothness of hand trajectory, nor did it affect the coupling of the elbow and shoulder joints in the deceleration phase of movement. Similarly, Ma and Feldman (1995) found that hand kinematics in seated goal-directed reaching movements were unaffected by simultaneous trunk movement in the sagittal plane, regardless of whether the direction of trunk movement coincided with or opposed the direction the arm. Finally, Robert et al. (2007) showed that during a step and reach task, changes in the equilibrium-related APAs induced by the placement of asymmetrical loads on the head (which changed the CoM) did not affect the spatial or temporal parameters of the hand movement.

Therefore, the redundancy in the DFs in the body, even when seated, allow for compensatory strategies that maintain constant endpoint kinematics despite potentially disruptive movements of non-focal segments such as the trunk (Kaminski, et al., 1995; Ma & Feldman, 1995). In this experiment, the increased pelvis and trunk motion in the STAND condition relative to the SIT condition was likely compensated by increased elbow extension (REACH and OC trials) and decreased shoulder adduction (OC trials), and perhaps compensation in other DFs that were not analyzed. Signals responsible for compensatory arm movements that maintain consistent hand-in-space trajectory across different body kinematics have been suggested to be based on vestibular information about head motion and gaze direction (Robert, et al., 2007). Since vestibular (Blouin, Guillaud, Bresciani, Guerraz, & Simoneau, 2010) and visual signals (Day & Lyon, 2000; Pelisson, et al., 1986) can trigger rapid arm corrections that are independent of cognitive processes, it remains possible that these signals enabled consistent hand kinematics across different body kinematics by triggering rapid, automatic compensatory movements. However, it is beyond the scope of the present study to investigate the possible signals involved in the coordination between focal and non-focal body segments.

The basis for comparing reaches when seated and when standing was that during stance, the maintenance of postural equilibrium is more demanding on the CNS due to decreased postural stability, requiring the coordination of postural segments with focal segments (i.e. involving more degrees of freedom). Indeed, Fautrelle et al. (2010) and Leonard et al. (2011) showed that online corrections in hand movements were accompanied by online corrections of aAPAs (specifically, in lower leg muscles) during a double step reaching task performed when standing. One possible reason that hand kinematics were generally unaffected by postural condition is that APAs (i.e. muscle activity in non-focal segments) and online corrections of aAPAs were still present in the SIT condition, as suggested by previous research on seated reaches. APAs are present in seated arm movements (Moore & Brunt, 1991) and have the same functions as the APAs of standing arm movements, serving to counteract reactional forces from the focal movement as well as maintain postural equilibrium (Chabran, Maton, Ribreau, & Fourment, 2001; van der Fits, Klip, van Eykern, & Hadders-Algra, 1998). The placement of targets beyond reach also necessitated forward trunk movement in both postural conditions to bring the hand to the target (Kaminski, et al., 1995). Furthermore, movement patterns of the trunk and pelvis during the reach also had components involved in the online correction, as shown by differences in whole-body kinematics between OC and REACH trials (see Figs. 4.2 and 4.5). It is therefore possible that the postural demands on the CNS did not differ enough between the SIT and STAND conditions to impact the focal movement. This is further supported by the suggestion that the muscle synergies underlying APAs for a given focal movement are predetermined, and that the only gain is modified according to gravitational effects (Chabran, et al., 2001).

5.3 Posture and Movement are Controlled in Parallel

For the purposes of this paper, “posture” refers to the control of body segments other than the reaching arm, while “focal movement” refers to movement of the arm involved in attaining the target. This dichotomy is a convention generally adopted in the literature for the sake of convenience. It should be noted that in practice, however, there is no clear separation between posture and movement, since body segments other than the reaching arm contribute to bringing the hand to the target (Leonard, et al., 2009; Schepens & Drew, 2003; Stapley, et al., 1998).

Results from the present study provide indirect support for a parallel mode of coordination of posture and movement, in which independent neural signals exist for controlling posture and movement (Massion, 1992). Although posture differed between standing and seated reaches, endpoint kinematics of the focal movement were generally consistent for reaches to a stationary target and for reaches requiring an online correction. Robert et al. (2007) also found invariant hand kinematics across different body motions. They suggested that the compensatory strategies allowing for this phenomenon were mediated by feedback signals from the vestibular and visual systems. Another explanation could be that posture and movement are planned globally as a single response, but that the execution of the two components are independent of each other, as suggested by Schepens and Drew (2003). In this way, the compensatory forces that keep the hand trajectory constant across different postural responses may be preprogrammed during the planning of the overall movement. It is not within the scope of the present study, however, to determine the source or nature of neural signals involved in the coordination of posture and movement. However, due to the fact that the arm components remained unchanged across the two postural configurations, it is likely that they may be subserved by separate neural commands.

5.4 Methodological Considerations and Limitations

Movements examined in the present study were executed at subjects' preferred speeds. Consequently, there was considerable inter-subject variability in movement velocity (individual mean peak velocities ranged from 1.25 to 2.10 m/s), which could have led to type II errors in the analysis of focal movement parameters. However, subject-by-subject analyses of these variables did not reveal reliable effects of postural condition (results not shown), contradicting this possibility. That task instructions did not emphasize RT or MT limits the applicability of these results to situations where movement speed is important. For arm raising movements, the optimal foreperiod duration (leading to the fastest RT) has been shown to be higher when movements are executed while standing than while seated (Cuisinier, Olivier, & Nougier, 2005, 2007). Also, RT at the optimal foreperiod is higher for standing movements (Cuisinier, et al., 2007). These findings suggest that the motor preparation required for movement is more complex when standing than when seated. Thus, it is possible that postural condition would have affected focal movement parameters if subjects had been told to move as fast as possible. Another limitation of the present study is that since the accuracy of the reaching movements was not determined, the presence or absence of systematic variations in accuracy could not be inferred.

The paradigm used in the present study had only two target locations. While the occurrence of target shifts was unpredictable, the new target location in the case of a target shift was not. In real-life situations, the location of a moving target is not always predictable. A better understanding of the effects of posture on online movement corrections may require the use of multiple target shift locations in seated and standing reaches.

CHAPTER 6: CONCLUSIONS

This study provided insights into differences or similarities in goal-directed reaching movements performed during standing and sitting. Results did not support the hypothesis that the increased equilibrium constraints associated with maintaining a standing posture affect the online control of goal-directed reaching. On the contrary, the temporal parameters of the reaching hand were generally unaffected by postural configuration during reaches to a stationary target and during reaches to a target that changed position following movement initiation. Instead, postural configuration altered the kinematic strategy of postural body segments (trunk and pelvis) and proximal segments of the reaching arm (shoulder and elbow). That the endpoint kinematics of the focal movement remained constant across different postural orientations and whole-body kinematics highlights the efficacy of the neural processes underlying goal-directed arm reaching and its online control mechanisms.

6.1 Implications and Directions of Future Research

Results from the present study provide a basis for further research of goal-directed reaching tasks performed when standing, particularly using online correction paradigms. Most of what is known about the online control of goal-directed arm reaching has been achieved using seated reaching tasks. Greater real-world applicability of the knowledge acquired from research on goal-directed reaching requires an understanding of how these processes are affected by postural constraints, as many reaches are made during stance. Although arm movements in different body positions have been used to study anticipatory postural adjustments (van der Fits, et al., 1998) and motor preparation (Cuisinier, et al., 2005), no previous study has directly compared the characteristics of reaching movements under seated and standing postures. From our results, it appears that in healthy young subjects, endpoint kinematics of goal-directed reaching movements executed when standing are comparable to those executed when seated. Consequently, our results suggest that experiments can use goal-directed reaching and online correction tasks executed while standing without greatly impacting the endpoint kinematics.

The corrective loops involved in the online control of seated goal-directed reaching movements have been found to mainly rely on visual information about target location (Prablanc, et al., 1986; Turrell, et al., 1998; Vercher, et al., 1994) and hand location information based on forward internal modeling (Bard, et al., 1999; Blouin, et al., 1995; Desmurget & Grafton, 2000; Gritsenko, et al., 2009). The signals contributing to corrective loops involved in the online control of reaching and the associated APAs during stance remain to be investigated. Insight into this question would require standing double step reaching paradigms whereby relevant sensory signals (i.e. visual/somatosensory information of the limb/target) are selectively manipulated.

Finally, it has been shown that postural muscle activity in healthy subjects is adjusted in a feedforward manner with respect to online corrections of focal arm movement (Fautrelle, et al., 2010; Leonard, et al., 2011). For populations at greater risk of falling, such as the elderly or populations with neuromuscular deficits (e.g. stroke survivors), online corrections during reaches executed from standing positions may be less efficient or more likely result in a loss of equilibrium if the CNS is unable to adjust posture to meet the dynamical requirements of the focal online correction. Even in a seated double step reaching task, older adults have been shown to correct movements less frequently and at longer latencies than younger adults (Sarlegna, 2006). Thus, a greater understanding of the sensorimotor signals required for the online control of reaching executed from the standing position could be useful for identifying effective therapeutic practices for postural control.

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APPENDIX

Table A1: Condition order and number of trials for each subject.

Subject	Condition Order	Trials Per Postural Condition
S01	STAND, SIT	100 (60 REACH, 30 OC, 10 Catch)
S02	STAND, SIT	100 (60 REACH, 30 OC, 10 Catch)
S03	SIT, STAND	100 (60 REACH, 30 OC, 10 Catch)
S04	SIT, STAND	130 (80 REACH, 40 OC, 10 Catch)
S05	STAND, SIT	130 (80 REACH, 40 OC, 10 Catch)
S06	SIT, STAND	130 (80 REACH, 40 OC, 10 Catch)
S07	STAND, SIT	130 (80 REACH, 40 OC, 10 Catch)
S08	STAND, SIT	130 (80 REACH, 40 OC, 10 Catch)

Table A2: Means and SDs of hand kinematic variables

	OC		REACH	
	SIT	STAND	SIT	STAND
ACC or ACC1 (ms)	333.9 (83.4)	341.3 (81.7)	331.0 (81.6)	344.9 (93.6)
DEC or DEC1 (ms)	278.3 (69.7)	270.0 (60.9)	666.1 (139.2)	648.6 (156.2)
ACC2 (ms)	183.0 (48.7)	176.5 (51.5)	--	--
DEC2 (ms)	519.3 (114.3)	523.9 (122.8)	--	--
MT (ms)	1313.9 (179.4)	1314.4 (176.2)	1001.3 (188.0)	997.4 (223.2)
Fcorrect (ms)	628.1 (90.3)	626.0 (85.3)	--	--
Fcorrect (%MT)	48.0 (4.3)	47.9 (4.6)	--	--
SymRatio	--	--	0.508 (0.121)	0.543 (0.130)
PeakVel(1) magnitude (m/s)	1.457 (0.323)	1.507 (0.341)	1.478 (0.317)	1.534 (0.343)
trough magnitude (m/s)	0.556 (0.211)	0.509 (0.236)	--	--
PeakVel2 magnitude (m/s)	1.171 (0.257)	1.188 (0.268)	--	--

Table A3: Summary of results of the t-tests performed on hand kinematic variables.

*p<.05; **p<.01; ***p<.001

Variable	df	t	p
ACC(1)			
OC	492.00	-.994	.321
REACH	1045.44	-2.595	.010**
DEC(1)			
OC	486.98	1.477	.140
REACH	1060.00	1.924	.055
ACC2			
OC	489.00	1.422	.150
REACH	--	--	--
DEC2			
OC	490.00	-.432	.666
REACH	--	--	--
MT			
OC	501.00	-.033	.974
REACH	1055.29	.315	.753
Fcorrect (ms)			
OC	500.00	.267	.790
REACH	--	--	--
Fcorrect (%MT)			
OC	500.00	.427	.670
REACH	--	--	--
SymRatio			
OC	--	--	--
REACH	1049.00	-4.490	<.001***
PeakVel(1) magnitude			
OC	492.00	-1.693	.091
REACH	1060.00	-2.766	.006**
trough magnitude			
OC	497.00	2.342	.020*
REACH	--	--	--
PeakVel2 magnitude			
OC	489.00	-.697	.486
REACH	--	--	--

D

Table A4: Summary of results of the Equality of Two Variances tests performed on hand kinematic variables.

*p<.05; **p<.01; ***p<.001

Variable	df	F	p
ACC(1)			
OC	256.236	1.044	.737
REACH	525.535	.759	.002**
DEC(1)			
OC	253.236	1.308	.037*
REACH	525.535	.794	.008
ACC2			
OC	255.234	.894	.382
REACH	--	--	--
DEC2			
OC	256.234	.867	.264
REACH	--	--	--
MT			
OC	259.242	1.036	.780
REACH	538.544	.709	<.001***
Fcorrect (ms)			
OC	259.241	1.121	.369
REACH	--	--	--
Fcorrect (%MT)			
OC	259.241	.878	.303
REACH	--	--	--
SymRatio			
OC	--	--	--
REACH	516.533	.877	.135
PeakVel(1) magnitude			
OC	256.236	.894	.377
REACH	525.535	.857	.077
trough magnitude			
OC	256.241	.802	.082
REACH	--	--	--
PeakVel2 magnitude			
OC	255.234	.917	.495
REACH	--	--	--

Table A5: Means and SDs of whole-body kinematic variables

	OC		REACH	
	SIT	STAND	SIT	STAND
Elbow flexion-extension angle	100.13 (4.47)	101.68 (4.88)	92.00 (5.23)	94.54 (5.73)
Shoulder adduction-abduction angle	56.82 (13.96)	56.46 (13.60)	74.95 (12.25)	69.29 (13.48)
Shoulder flexion-extension angle	77.03 (8.49)	78.59 (10.13)	70.30 (22.09)	70.01 (19.87)
Trunk rotation	10.45 (3.14)	14.42 (6.23)	18.37 (3.26)	24.82 (7.09)
Pelvis rotation	2.19 (2.00)	6.87 (4.92)	3.81 (1.42)	11.98 (6.29)
Pelvis obliquity	2.13 (1.95)	-1.68 (2.03)	0.14 (1.47)	-4.34 (2.10)
Pelvis x-displacement	0.01 (0.01)	0.03 (0.02)	0.00 (0.00)	0.01 (0.02)
Pelvis y-displacement	0.01 (0.01)	-0.01 (0.02)	0.01 (0.01)	-0.01 (0.02)

Table A6: Summary of results of the t-tests performed on whole-body kinematic variables.

Variable	df	t	p
Elbow flexion-extension angle			
OC	492.00	3.669	<.001***
REACH	1063.00	7.509	<.001***
Shoulder adduction-abduction angle			
OC	492.00	.293	.770
REACH	1053.86	7.165	<.001***
Shoulder flexion-extension angle			
OC	460.27	-1.849	.065
REACH	1050.83	.224	.823
Trunk rotation			
OC	340.30	8.804	<.001***
REACH	748.08	19.106	<.001***
Pelvis rotation			
OC	304.08	13.635	<.001***
REACH	586. 50	29.248	<.001***
Pelvis obliquity			
OC	492.00	21.242	<.001***
REACH	953.66	40.566	<.001***
Pelvis x-displacement			
OC	294.58	-23.344	<.001***
REACH	636.55	-11.828	<.001***
Pelvis y-displacement			
OC	355.89	19.092	<.001***
REACH	803.48	30.063	<.001***

*p<.05; **p<.01; ***p<.001

Table A7: Summary of results of the Equality of Two Variances tests performed on whole-body kinematic variables.

Variable	df	F	p
Elbow flexion-extension angle			
OC	257.24	.836	.161
REACH	531.53	.847	.056
Shoulder adduction-abduction angle			
OC	257.24	1.053	.686
REACH	531.53	.826	.028*
Shoulder flexion-extension angle			
OC	257.24	.703	.006**
REACH	531.53	1.237	.015*
Trunk rotation			
OC	257.24	.255	<.001***
REACH	531.53	.212	<.001***
Pelvis rotation			
OC	257.24	.163	<.001***
REACH	531.53	.051	<.001***
Pelvis obliquity			
OC	257.24	.921	.521
REACH	531.53	.492	<.001***
Pelvis x-displacement			
OC	259.24	.117	<.001***
REACH	532.54	.093	<.001***
Pelvis y-displacement			
OC	259.24	.264	<.001***
REACH	532.54	.264	<.001***

*p<.05; **p<.01; ***p<.001

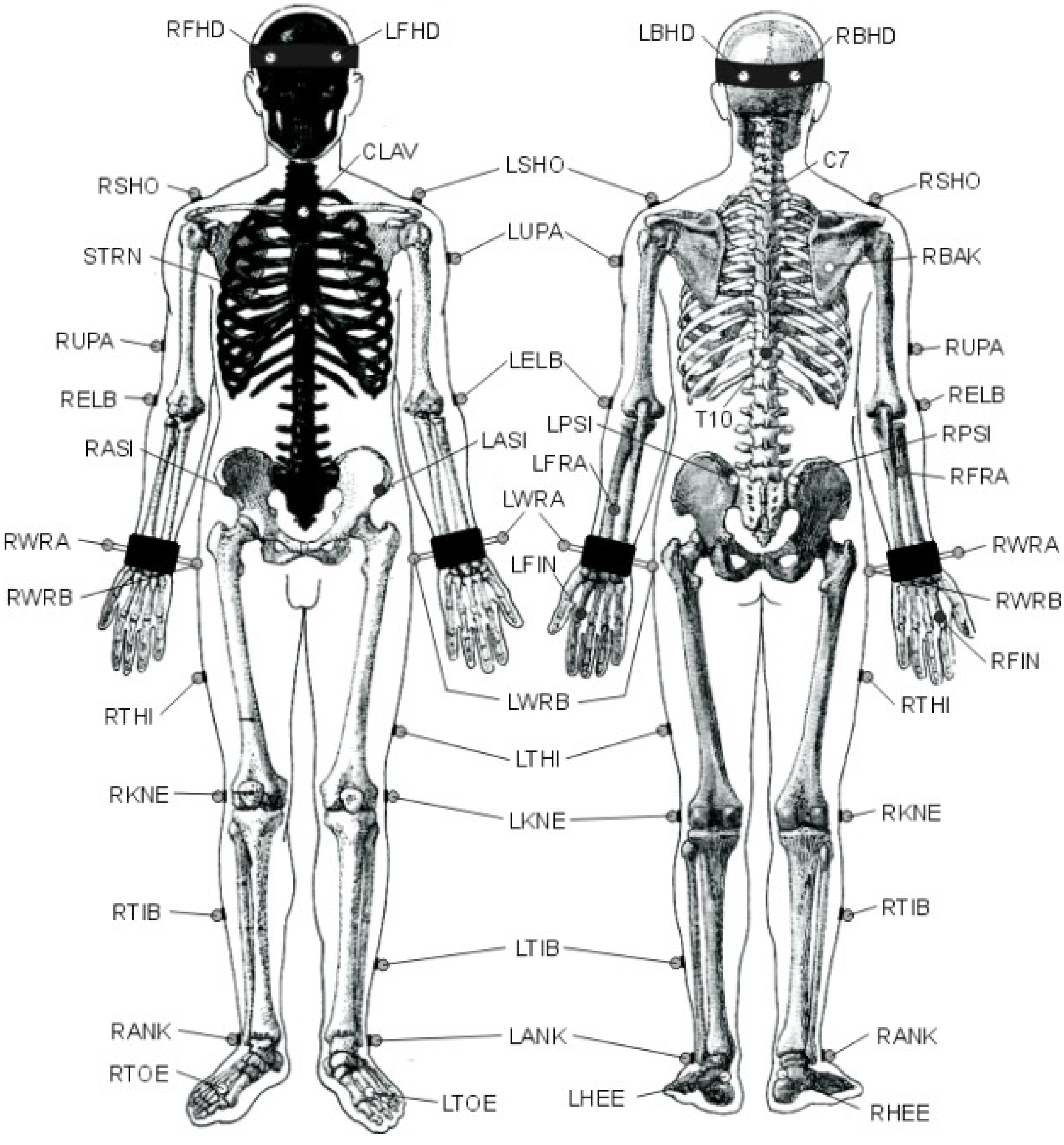

Figure A1: Plug-in-Gait marker placement