Reaching to multiple targets when standing: The spatial organization of feed-forward postural adjustments

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Abstract

We examined the spatial organization of feed-forward postural adjustments produced prior to and during voluntary arm reaching movements executed while standing. We wished to investigate if the activity of postural muscles before and during reaching was directionally tuned and if a strategy of horizontal force constraint could be observed. To this end, 8 human subjects executed self-paced reach-to-point movements upon the random illumination of 1 of 13 light targets placed within a 180º array centered along the mid-line of the body. Analysis was divided into 2 periods: a first corresponding to the 250 ms preceding the onset of the reaching movements (termed pPA period), and a second 250 ms period immediately preceding target attainment (the aPA period). For both periods, EMG activity of the lower limb muscles revealed a clear directional tuning, with groups of muscles being activated for similar directions of reach. Analysis of horizontal ground reaction forces supported the existence of a force constraint strategy only for the pPA period, however, with those in the aPA period being more widely dispersed. We suggest that the strategy adopted for feed-forward pPAs is one where the tuned muscle synergies constrain the forces diagonally away from the centre of mass (CoM) to move it within the support base. However, the need to control for final finger and body position for each target during the aPA phase resulted in a distribution of vectors across reaching directions. Overall, our results would support the idea that end-point limb force during postural tasks depends upon the use of functional muscle synergies, which are used to displace the CoM or decelerate the body at the end of the reach.

Keywords: Feed-forward, EMG, Forces, Human, Reaching, Posture
Introduction

For multi-joint movements executed during standing such as reaching forwards, postural adjustments occurring prior to movement onset shift the CoM within the base of support in order to initiate the movement, and associated postural adjustments overcome the postural disturbances related to movements of the limbs (Bouisset and Zattara 1981; 1987; Commissaris et al. 2001; Friedli et al. 1988; Friedli et al. 1984; Schepens and Drew 2003; Stapley et al. 1998; Stapley et al. 1999). To ensure a controlled transition from one postural configuration to another, these adjustments of posture must be planned by the central nervous system (CNS) in advance, and a feed-forward mode of neural control sends commands to both focal and postural muscles to initiate and stabilize posture. Both the preparatory and associated postural adjustments (pPAs and aPAs, respectively) are considered to be feed-forward in nature as they are produced before feedback from the ongoing movement can influence them (Gahery 1987; Massion 1992). The objective of the present study was to examine the spatial organization of postural muscles and forces produced before and during voluntary reaching movements in multiple directions to gain insights into the nature of their underlying control.

Feedback mediated postural responses to unexpected disturbances of balance have been well characterized. When the surface upon which humans are standing unexpectedly moves, the body is destabilized in the direction opposite to that of the surface displacement. In order to regain balance, humans produce short latency automatic postural responses (APRs) in the supporting limbs that oppose the perturbation and drive the CoM back towards its initial position relative to the support surface (Horak and Nashner 1986). The latency from the initiation of the support
surface movement to the onset of the evoked EMG response is in the order of 80-120 ms in humans (Horak and Macpherson 1996; Nashner 1977; Ting and Macpherson 2004). These compensatory APRs are triggered by somatosensory feedback from the feet and legs (Bloem et al. 2000; Bloem et al. 2002; Horak and Macpherson 1996; Stapley et al. 2002) and unless prior warning of the upcoming perturbation is given (Jacobs and Horak 2007; McChesney et al. 1996), they are produced entirely using a feedback mode of neural control.

Studies in animals and humans have examined feedback-based APRs to unexpected translations of the support surface in multiple directions with the aim of identifying strategies that the CNS may adopt to simplify the control of perturbed stance (Fung et al. 1995; Henry et al. 2001; 1998b; Macpherson 1988a,b; Ting and Macpherson 2004). In the cat, regardless of the direction of horizontal platform translation, force vectors were exerted in one of two main directions at each limb (termed the ‘force constraint strategy’, Macpherson 1988a). Muscle activity displayed a tuning across directions with maximal amplitudes for each muscle arising for one specific direction (Chanaud and Macpherson 1991; Macpherson 1988b). Similar results have also been obtained in standing humans subjected to postural perturbations (Henry et al. 2001; 1998b). Overall, results have supported the hypothesis that force vector production is a high level parameter adopted to reduce the multiple of degrees of freedom associated with complex postural tasks, and that the production of the desired vector is solved at a lower level by the synergic recruitment of muscle groups. More recent studies in the standing cat have elaborated this hypothesis, and have suggested that an internal model of postural force generation coordinates functional muscle synergies rather than biomechanical limb constraints alone (McKay et al. 2007; McKay and Ting 2008). However, the production of a force constraint
strategy is dependent upon the relationship between the muscle synergies produced and the current limb geometry (Torres-Oviedo et al. 2006).

Recent studies have shown that neural commands for feed-forward postural adjustments can be identified in the pontomedullary reticular formation (PMRF) of the brainstem (Schepens and Drew 2006; 2004; Schepens et al. 2008). Neurons in this area discharged either during the $pPA$, the $aPA$ or both during reaching movements in the standing cat (Schepens and Drew 2006; 2004). The activity of this area has also, however, been shown to be implicated in compensatory, or feedback-based, postural control. Microstimulation of peripheral afferents, known to be essential for triggering short latency APRs (Stapley et al. 2002), activate particular subsets of reticulospinal neurons (Drew et al. 1996) and PMRF neurons are activated strongly during postural perturbations in the standing cat (Stapley and Drew 2003; in press). If specific neural sites can modulate postural responses with different underlying modes of control (i.e., feed-forward or feedback), it is plausible to predict that the outward expression of those postural adjustments may show similarities in their organization. The present study aimed, therefore, to investigate if a similar spatial organization of horizontal force and muscle activity to that seen with feedback-based postural responses could be observed for predictive feed-forward postural adjustments in humans, despite their different modes of neural control. To generate directionality, we asked human subjects to reach and point to targets in multiple directions throughout 180° at shoulder height whilst standing. Postural adjustments immediately preceding the onset of the focal limb movement ($pPAs$) and those produced before target attainment ($aPAs$) were recorded and analyzed. We hypothesized that: 1) feed-forward postural adjustments are directionally-tuned to the current goal of the task (initiation or termination of the reaching
movements), and 2) ground reaction forces show directional force constraint, supporting the idea that such a strategy is a high level parameter adopted by the CNS, regardless of the mode (feed-forward or feedback) of neural control.
**Materials and Methods**

**Subjects**

Eight (1 female and 7 male) healthy subjects, without any known neurological, visual or orthopedic disorders, were recruited from the McGill University student population to participate in the present study. Subjects had a mean age of 22.5 ± 4.3 (SD) years, a mean height of 1.74 ± 0.04 (SD) m, and a mean weight of 66.6 ± 5.9 (SD) kg. They were all right-hand dominant. They gave their informed consent to participate and experiments were conducted with the approval of the McGill University research ethics board.

**Experimental apparatus and set-up**

Subjects stood barefoot on 2 tri-axial force plates (model FP4060, Bertec Corp., Columbus, OH, USA) that measured ground reaction force (GRF) and moments in mediolateral (X), anteroposterior (Y) and vertical (Z) axes at 1000 Hz. Stance width (the mediolateral distance between the feet) was taken as the average of each subject’s natural stance distance as measured after 3 trials of walking the length of the laboratory. Foot position was marked for each subject and care was taken that subjects kept their feet in the same position for the duration of the experiments. They were centered in a custom-built 180° light target array, fully adjustable in height and target distance (see Fig. 1A). The array contained a total of 13 light emitting diodes (LEDs) each spaced at 15° intervals. Light targets were 2.5 cm in diameter and consisted of 5V red LEDs encased in modified gaming switches (model 459512, RP Electronics, Burnaby, BC)
that produced a 5V pulse upon contact. The gaming switches were mounted at the ends of lightweight aluminum dowels adjustable in length, affixed to a semi-circular aluminium bar suspended from the ceiling. A chest band worn by all subjects was also equipped with the same switch in order to detect movement onset (see below).

The activity of 16 muscles was recorded using 2 DelSys Bagnoli 8-channel systems (Boston, MA, USA) at 1000 Hz. The following muscles were recorded bilaterally (left and right legs): tibialis anterior (TA\textsubscript{l} and TA\textsubscript{r}, respectively), soleus (Sol\textsubscript{l}, Sol\textsubscript{r}), lateral gastrocnemius (Gas\textsubscript{Ll}, Gas\textsubscript{Lr}), peroneus longus (Per\textsubscript{l}, Per\textsubscript{r}), biceps femoris (BF\textsubscript{l}, BF\textsubscript{r}), rectus femoris (RF\textsubscript{l}, RF\textsubscript{r}) and tensor fascia latae (TFL\textsubscript{l}, TFL\textsubscript{r}). In addition, anterior and posterior deltoid was recorded at the right shoulder. Bilateral kinematic data were collected using a 6 camera MX3 motion capture system (ViconPeak Inc., Lake Forest, CA, USA) sampling at 200 Hz. A total of 36 markers were placed at different locations on the subjects’ whole body as listed in the Plug-in-Gait model (Vicon Peak \textregistered). This model provides an accurate estimate of CoM position when compared to the method of ground reaction force integration (Gutierrez-Farewik et al. 2006). Analog signals from the force plates and EMG system were captured through the Vicon MX3 controller. A customized program written in LabView (National Instruments, Austin, TX, USA) was used to control the illumination of target lights, acquire and synchronize digital signals from the switches (target and chest), and initiate and synchronize data collection with the Vicon system.

**Experimental procedures**
Subjects were centered in the array with their mid-line (xiphoid process) aligned with the 90°
target direction and the 0° and 180° target directions representing, respectively, each subject’s far
right and left side targets (see Fig. 1A). Upon the random illumination of 1 of the 13 target lights,
subjects were asked to point and press the lighted switch. Target lights were placed at a
standardized distance of 130% of the outstretched right arm when holding it in line with each
target. The distance was measured between the subject’s xiphoid process (from where they
initiated pointing movements) and the tip of the right index finger when the arm was extended
towards each target. Subjects were asked to stand straight, maintain neutral scapular retraction
during the measurement, but were permitted to rotate the trunk such that the shoulders were
facing square to the target for leftward targets. This was done in order to measure the distance to
the targets in a postural configuration similar to that adopted during the reaching movements.
During pilot tests, it was found that the target distance of 130% could be attained comfortably by
the subjects using a combined arm and trunk movement, but did not place them at their limits of
stability at target attainment (determined by measuring centre of pressure displacement within
the base of support). Targets were all at right acromion height as measured during quiet stance.
No constraints of accuracy were given to subjects, only that they had to point and press the light
switch at their natural speed, immediately following target illumination.

Subjects began their reaching movements with the index finger of their right hand pressing the
chest switch centered at the xiphoid process of the sternum and their left hand hanging vertically
at the side of the body. They were asked to reach to, press and release the target switch with their
right index finger and hold this body position for 2 s, then return slowly and assume their initial
position. The total acquisition period consisted of a 3 s window. The data collection time line is
illustrated in Fig. 1B. Once the experimenter was satisfied that the subject was standing quietly
data acquisition was begun. After a random period of between .5 s and 1 s, a target illuminated
and subjects initiated their movements. The total acquisition period of 3000 ms was sufficient to
record the postural activity preceding and accompanying the movements. Other than movement
speed (natural speed), no other instructions regarding the strategies to be adopted were given.
Subjects were not encouraged to move as fast as possible (a reaction-time paradigm). Testing
began with an acclimatization period, during which subjects executed 26 trials in random order,
twice to each of the targets. Following the acclimatization period, subjects were required to
execute 15 trials towards each pointing direction, in a pseudo-randomized order, which included
15 catch trials (no target light illuminated) to reduce the possible prediction of the upcoming
target light. Thus, a total of 210 trials per subject was recorded and used in the subsequent
analysis. Generally, subjects performed blocks of approximately 50 trials inter-spaced with 5 min
rest periods to reduce fatigue until the required number of trials at each direction was attained.

\begin{center}
\textit{Figure 1 about here}
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\textbf{Data analysis}
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Kinetic, kinematic and EMG data were recorded and stored on a PC computer for further
analysis using a series of customized programs written in MatLab (The Mathworks, Natick, MA,
USA). Ground reaction forces and moments were low-pass filtered using a digital second-order
Butterworth filter, with a 10Hz cut-off frequency. Raw EMG signals were high-pass filtered at
35Hz, de-meaned, rectified, and low-pass filtered at 100Hz (second-order Butterworth filter).
Individual trials were visually inspected for stability during the quiet stance period (1000 ms prior to target illumination). Any trials that showed significant variation in Fz and/or CoP during the quiet stance phase (0-500 ms following data acquisition onset) were eliminated from further analysis, as were trials in which subjects did not make contact with the target, or used the target as a support. This was evaluated by checking that the centre of pressure (CoP) did not leave the limits of the BoS determined using the kinematic markers on each foot in relation to foot width (included in the Vicon model) and stance distance and whether switch depression was maintained. Following the trial selection criteria, a total of 1437 trials from the 8 subjects were retained for further analysis from a total of 1560 trials.

Focal movement onset and termination were established by chest switch release and target light depression, respectively. The onset of movement using the switch was compared to the first deflection above zero of the tangential velocity of the marker placed on the hand in the Y axis and movement termination was also taken as the moment when hand velocity returned to zero. As no difference greater than 5 ms was found between the onset of motion as determined by the chest switch and the motion capture data (sampling 1 image approximately every 5 ms), movement time was taken as the duration between chest switch release and target depression. Onset of focal movement acted as time zero upon which all preparatory events were based.

To investigate the temporal and spatial organization of feed-forward preparatory postural adjustments prior to movement onset (hereon called the pPA period) and associated postural adjustments produced during the end phase of the reaching movements (the aPA period), the analysis was restricted to 250 ms before chest switch release (pPA) and 250 ms before the end of
the movement (aPA). The choice of the period lengths was based upon well documented changes in anticipatory postural adjustments preceding voluntary movement, or the pPA period (Belenkii et al. 1967; Bouisset and Zattara, 1981; Crenna and Frigo, 1991) and visual inspection of the onset of braking forces and moments exerted under each foot before the end of the movements for a number of trials in each direction (aPA period). Both of these periods were divided into five 50 ms long ‘bins’ chosen to characterize the evolution of the preparation and the termination of reaching movements (e.g., pPA1, pPA2, etc.). EMG amplitudes were calculated as the mean of each 50 ms bin for each period and for each muscle. For each period (pPA and aPA) and muscle, the highest mean response across the 13 reach directions was used to normalize muscle activations, so that values ranged between 0 and 1. Normalized amplitudes were then plotted as muscle tuning curves. Amplitude and direction of the resultant horizontal force were calculated by summing changes in Fx and Fy, according to trigonometric vector addition (Zar 1999). Resultant horizontal plane vectors were plotted in polar coordinates. The torque about the vertical axis at each foot (Tz) was calculated using the following equation:

\[ Tz = Mz - Xp \cdot Fy + Yp \cdot Fx \]

where \( Xp \) and \( Yp \) are the coordinates of the centre of pressure of each foot, \( Mz \) is the moment of the force plate around the vertical (z) axis, and \( Fy \) and \( Fx \) are anterior-posterior and mediolateral forces, respectively.

Statistical analysis
The effect of pointing direction upon movement time was examined using a repeated measures one-way analysis of variance (ANOVA). To determine if a force constraint strategy characterized the horizontal ground reaction forces in each of the periods under study, the angle of the average vector produced in successive 50 ms bins was pooled from all subjects and subjected to circular statistical analysis. Circular statistics refers to a class of techniques developed for the analysis of directional or cyclic data, assuming an arbitrary zero and where 0º and 360º represent the same direction. To determine if pooled vector directions were uniformly distributed or constrained (defined as a significant clustering of the active horizontal force vector, Macpherson 1988a), data were examined for a bimodal distribution using the ‘broken-axis approach’ (Holmquist and Sandberg 1991). This approach tests the null hypothesis that populations of vector direction are uniformly distributed around a circle against the working hypothesis that they are not so. Specifically, it evaluates bi-modality, but does not assume that means of clusters of vectors are separated by 180º. If a bimodal distribution is found, it returns the mean angles of the two modes. Typically, when analyzing circular data sets, to evaluate the degree of dispersion mean vector length (r) is computed. Values may vary between 0 (high dispersion) and 1 (all data concentrated along a single preferred direction). In the broken axis approach, rmax represents the mean vector length (r) where the modality of the data set (k) best fits the data. The value of k specifies the type of modality and no assumption is made that the data is uni- or bimodal. For example, if k=2, the data would be symmetrically bimodal (i.e., 2 clusters separated by 180º). However, when k lies between 1 and 2 the data set would be characterized by an intermediate clustering of a bimodal distribution where clusters are separated by 360º/k (e.g., when k=1.6, modes are separated by angle of 225º). This approach also gives the
mean direction (alpha) of any number of clusters that can be identified. All statistical analyses were custom written and performed in Matlab.
Results

Kinematics of reaching movements during stance

Examples of the general kinematic strategies adopted by subjects when pointing to targets in the array are illustrated in 3D in Figs. 2A-C. Three principle directions of reach are shown for 1 representative subject. For all directions, subjects began from a similar initial quiet stance position with the right finger pressing the chest switch and the left hand by the side of the body regardless of reaching direction. The similarities of the initial CoM positions at movement onset can be seen in Fig. 2D (open colored squares). For movements to 0º, subjects executed a rightward extension of the arm, a clockwise rotation of the torso and a slight rightward displacement of the pelvis (Fig. 2A). For movements to 90º (Fig. 2B) the reaching arm outstretched approximately along the body mid-line, while the torso rotated forwards and slightly downwards. Finally, for far leftward movements (Fig. 2C), the right arm rotated leftwards, crossing the mid-line, with the torso and pelvis also rotating towards the left. For each of the 3 movements shown, the CoM was displaced from its initial position in the approximate direction of the target within the base of support. Ground reaction force vectors during the \( pPA \) period (red vectors) were oriented so that the CoM moved in the direction of each target. At the end of the \( aPA \) period the GRF vector was oriented back towards the CoM (blue vectors) to brake the movement of the body. Although there was some variability (especially between 90º and 120º), trajectories and end CoM positions differed for each reaching direction. This is represented for 5 trials for each direction in Fig 2D. Despite the greater amount of body rotation required by
leftward as opposed to rightward movements, movement times did not significantly increase across the 13 directions. Average movement times for all subjects are shown in Table I.

EMG activity in relation to the forces produced: pPA period

There was a clear modulation of EMG activity and force between 0 and 180º target directions during the pPA and aPA periods. Changes in muscle activity and force for 3 main directions of reaching are shown in Figs. 3A-C, for 1 representative subject. For clarity, the two 250 ms time periods under study have been shaded.

During the pPA period, regardless of pointing direction, the earliest change in EMG activity was typically an inhibition of either the right or left soleus muscles. Postural adjustments for far rightward movements (Fig. 3A) began with an inhibition of Solr followed by an activation of TFLl. This was followed by a leftward and backward push at the left leg and an unloading of Fz under the right foot. The torque about the vertical axis (Tz) showed that the left foot exerted a counter-clockwise (CCW) moment, while the right foot exerted a clockwise (CW) one. Centrally-oriented movements (Fig. 3B) showed a clear bilateral soleus inhibition/tibialis anterior activation and both peroneus muscles activated, which likely assisted the initiation of the forward displacement of the body. The TFLl and RFl also showed anticipatory bursts, as did the BFr. This may have reflected the slightly asymmetric nature of the movement using the right arm and hand reaching to the 90º target. There was very little or no change in Fx under either foot but
instead an increase in Fy (backwards push) and Fz (loading) under the right foot, coupled with a slight forwards push at the left foot. As these movements involved essentially a forward displacement, there was only a slight CW Tz at the left foot. For movements to the far leftward 180° target (Fig. 3C), which required the greatest amount of body rotation, there was significant anticipatory activity in the BF<sub>r</sub>. Additionally, there was a burst in the So<sub>r</sub>. The forces showed that the right (loaded) foot Fx pushed rightwards exhibiting a CW Tz. Interestingly, although unloaded, the left foot also showed a CW Tz.

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**Figure 3 about here**

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**EMG activity in relation to the forces produced: aPA period**

During the aPA period, from 250 ms before to the end of the movements, there were also distinct patterns of muscle activity across the reaching directions, mostly in the extensors. Rightward (0°) movements (Fig. 3A) were characterized by activation of the Gas<sub>Lr</sub>, So<sub>r</sub>, TA<sub>r</sub> and Per<sub>r</sub>. Apart from the slight activation of TFL<sub>r</sub> early in this period, there was little activity in the other muscles. Forces showed that the right foot was loaded, while the horizontal forces stabilized around their original values. The loaded (right) foot exerted a CCW Tz. Reaches to 90° (Fig. 3B) showed bilateral activity in a number of extensor muscles (e.g., gastrocnemius, soleus, biceps femoris and, to a lesser extent, peroneus). The right foot was loaded and pushed forwards (Fy), while Fx forces steadied. The loaded (right) foot exerted a CCW Tz during this period, but which reversed shortly after the hand reached the target (see arrow and asterisk to the right of Movt End). Finally, reaches to 180° (far leftward, Fig. 3C) showed activity in left-side extensors
(GasL and Sol) as well as right side flexors (BFr and TAr). The loaded left foot pushed in a slightly rightward and backward direction exerting a CCW Tz.

**Feed-forward postural adjustments show directional tuning and are synergic**

There was a clear directional tuning of many of the postural muscles recorded during the 2 periods of study (see Fig. 4). In the pPA period, patterns of EMG activity showed that the tibialis anterior and peroneus, as well as the rectus femoris (all bilaterally) were activated principally for pointing to mid-range targets, between approximately 45º and 120º. Other muscles, such as the tensor facia latae, and soleus showed reciprocal patterns of activity between reaches to the left and right. The TFLl activated between 0º and 75º, the TFLr between 105º and 180º, while the Soll displayed inhibition during the pPA period between 45º and 180º and sustained activity for 0º to 30º movements, as did the Solr between 150º and 180º. The gastrocnemius muscles showed no activity in the preparatory period, except for GasLl at the extreme rightward pointing direction (0º). Other muscles, such as the BFr displayed asymmetric patterns of activity, activating between 60º and 180º on the right side, but not on the left.

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*Figure 4 about here*

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In the aPA period reciprocal patterns of activity could also be noted for the extensors soleus and gastrocnemius, left side muscles activating for targets 75-180º and those on the right side from 0-90º. The BFl also activated for 75-180º targets, while other left side muscles remained largely inactive. On the right side, the flexor Perr contracted along with Solr as did the TFlr to a certain
extent. Interestingly, BF\textsubscript{r} showed activity across virtually all reaching directions during this period.

To evaluate the spatial and inter-trial variability characteristics of the muscular patterns described above, tuning curves were generated for each of the 14 postural muscles recorded during 5 successive 50 ms bins. For both pPA and aPA periods, each muscle was activated for a range of pointing directions with many showing directions of maximal recruitment. Typically, during the pPA period (black lines and open circles) in bins 1 and 2 (pPA1 and pPA2, respectively) all muscles were generally inactive or showed a baseline level of activity across directions, hence, for clarity, they are not depicted in Fig. 5. However, in pPA3 (-150 to -100 ms) a directional tuning began to emerge, despite the evident inter-trial variation that existed. During pPA4 and pPA5, the tuning curves show that the muscles worked in groups, with TAr/TAl, Perr/Perl and RFr/RFl activating maximally for targets either side of the central one, TFlr, BF\textsubscript{r} and Sol\textsubscript{r} for leftward targets and TFl\textsubscript{l} and GasL\textsubscript{l} for rightward movements. Clear patterns of tuning were also evident for all bins of the aPA period (grey lines and filled circles) with the patterns emerging from bin 1 onwards (250 to 200 ms before target attainment). Again, for clarity and due to the constancy of tuning across the 5 bins in this period, only bins 3-5 are depicted in Fig. 5. The muscles Sol\textsubscript{r}, GasL\textsubscript{r}, Perr and TFl\textsubscript{r} activated for similar directions, as did GasL\textsubscript{l}, Soll and BF\textsubscript{l}. The BF\textsubscript{r} showed increasing activity from 0-180º.

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*Figure 5 about here*

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This pattern of muscle tuning was very consistent across the 8 subjects tested. This can be seen in Fig. 6. Here, muscles are depicted for the final bin of the $p$PA period (Fig. 6A) and $a$PA period (Fig. 6B) and are grouped according to the directions for which they were recruited to a similar extent. Figure 6C summarizes the recruitment of each of the muscles in the groups identified in the 2 periods in polar coordinates. The spatial pattern of each group represents approximately the outermost limits of the EMG tuning.

Spatial patterns of force differ between preparatory and associated postural adjustments

Horizontal GRFs displayed distinct and opposing patterns for the 2 periods studied. The forces produced during the $p$PA period approached more of a bi-modal distribution with low dispersion of the vector directions, whereas those produced in the $a$PA period, although not unimodal, were more highly dispersed, suggesting that to control final body position for each direction of reaching, a unique vectors of force were produced under each foot.

These trends are illustrated in Fig. 7 for a representative subject. All trials for this subject are plotted as horizontal vectors for each successive bin of 50 ms for each period. In the early phases of the $p$PA period (Fig. 7A, $p$PA1 and $p$PA2) horizontal forces were of very small amplitude and showed a high degree of dispersion in terms of their direction. However, from the bin $p$PA3 onwards, which corresponded approximately to the emergence of EMG tuning described above and shown in Fig. 5, forces, in particular under the loaded foot shared similar directions (e.g., $0^\circ$
to 75° for the left foot and 105° to 180° for the right foot). Clearly constrained directions of force can be seen under the left foot in pPA4 and pPA5, which was loaded for targets 0°-90° pushing outwards and leftwards (see different black-blue colored vectors) and under the right foot, loaded for 105-180° targets, pushing outwards and rightwards (see yellow-orange vectors), although right foot vectors were always slightly more distributed. For clarity in Fig. 7A, the black arrows convey the general direction of the exerted force in the constrained vectors when the limb was loaded limb and grey arrows when it was unloaded. The constraint observed in the horizontal vectors during pPA4 and pPA5 is supported by the circular statistical analysis (see below). Interestingly, the forces produced under the foot that was unloaded during these bins often also showed a constraint of horizontal force under the left foot, but was slightly more dispersed under the right.

During the aPA period, the feet that were loaded for their respective directions of reach during the pPA period now became unloaded and vice versa. In bins pPA4 and pPA5 loaded vectors exerted force backwards and outwards at the foot contra-lateral to the direction of reach (e.g., left foot, pPA5, blue vectors). In comparison, during the aPA period, loaded vectors now pushed outwards and forwards at the limb ipsilateral to the direction of reach (e.g., aPA5, orange-red vectors). Such a low dispersion of vectors seen during the latter stages of the pPA period (especially under the left foot) was not seen during all bins of the aPA period. Horizontal force vectors produced under the loaded or unloaded feet in the aPA period were highly distributed, often throughout a 90° range or greater (see Fig. 7D).

Figure 7 about here
Circular statistical analysis (for an explanation, see Methods) supported this trend of a force constraint strategy during the \( pPA \) but less so during the \( aPA \). The statistical analysis resulting from the broken axis approach is given in Table II for both feet. During the \( pPA \) period, the analysis identified an angular distribution that was significantly different from uniform for progressive bins. The distribution of horizontal force was characterized by a clustering of vectors with \( k \) values that increased during \( pPA4 \) and \( pPA5 \) to \( >1.5 \) for the left foot and 1.35 and 1.42, respectively, at the right foot. This indicated that an asymmetric bimodal distribution existed during those periods. Additionally, \( r_{max} \) values were \( >0.5 \) (e.g. 0.66 and 0.77 for the left foot and 0.55 ad 0.6 for the right foot during bins \( pPA4 \) and \( pPA5 \) respectively) indicating a low degree of dispersion. Such an evolution of significant bimodal clustering was not seen during the \( aPA \) period. Rather, statistical analysis, revealed that the distribution of force vectors was significantly different from uniform with \( r_{max} \) values \( \leq 0.5 \), indicating higher dispersion than in the \( pPA \) period around a single mode.

\[ \text{Figure 8 and Table II about here} \]

The bimodal distribution of force vector direction highlighted by the circular statistics in the \( pPA \) period is also reflected when average vector direction is plotted against each reach direction (Fig. 8A). It can clearly be seen that there was a constraint of force vector direction during \( pPA4 \) and \( pPA5 \), especially under the left foot. This constraint of force vector direction seen in the \( pPA \) period was also accompanied by a modulation of force magnitude with targets at each extremity.
having the largest GRF (Fig. 8B, $p_{PA4}$ and $p_{PA5}$), whereas the $a_{PA}$ period displayed a linearity of GRF vector and reaching direction from bin 2 onwards (Fig. 8C) and a fairly constant magnitude of GRF vector across all directions (see Fig. 8D, all bins).
Discussion

We investigated the organization of feed-forward postural adjustments produced when standing humans reached with their preferred arm to multiple targets placed in a semi-circle throughout 180° with centered respect to their midline. Our objective was to identify spatial tuning of postural muscle activity and a constraint of horizontal GRF, similar to that shown for feedback-based postural responses to unexpected perturbations of balance in humans (Henry et al. 2001) and animals (Macpherson 1988a). The results supported our first hypothesis; that bilateral EMG activity recorded was directionally-tuned and served the current goal of the task (initiating or terminating the movements). However, our second hypothesis; that a generalized force constraint strategy existed for feed-forward postural adjustments, was not completely supported.

The roles of preparatory and associated postural adjustments for reaching during stance

The postural adjustments studied in the two periods likely performed functionally different roles. In the first period (pPA), significant EMG activity emerged approximately between -150 ms to movement onset. The resultant horizontal forces produced under the loaded foot during this period were consistently in the opposite direction to the desired movement direction, the vectors being constrained for a number of reaching directions. Moreover, the moments (Tz) produced indicated that the loaded foot consistently exerted a torque in the opposite direction to the direction of reach (Fig. 3), thus creating a reaction torque that drove the body towards the target. These results would support the notion that the pPA created the necessary conditions for CoM displacement in the direction of the reach, within the base of support (Stapley et al. 1998; Stapley
et al. 1999). This is also supported by the CoM trajectories in Fig. 2D. The pattern of force and torques exerted at the feet reversed during the aPA period, such that the reaction forces opposed the body displacement as the hand reached the target. Perhaps the clearest example of this could be seen under both feet for 180° reaches (Fig. 3C), which required the greatest amount of body rotation. The CCW direction of Tz would have had the effect of slowing and stabilizing CoM position within the support base as the hand neared the target. Such a role of associated postural adjustments has been shown during various arm reaching or lifting tasks (Commissaris 1997; Commissaris et al. 2001; Cordo and Nashner 1982; Krishnamoorthy and Latash 2005; Schepens and Drew 2004; 2003).

Tuned, synergic muscle activity characterizes feed-forward postural adjustments

The activity of the 14 muscles recorded in the pPA and aPA periods showed that each muscle was recruited for a range of directions often with a direction of maximal activation. Muscles were also activated in groups. This grouping across the two periods would support a synergic organization of feed-forward muscular activity. A synergy has been defined as a group of muscles constrained to act in a concerted manner (Macpherson 1991; Sherrington 1961) or ‘activated in synchrony with fixed relative gains and muscle activation patterns with consistent spatial characteristics’ (Torres-Oviedo and Ting 2007). Directionally tuned feed-forward muscle activity has previously been identified during bilateral arm movements performed when standing (Aruin and Latash 1995). When the two arms were moved either forwards or backwards from a central position, groups of muscles were activated in functional groups on the dorsal or ventral side of the body to maintain equilibrium. Direction-specific patterns of feed-forward muscle
activity have also been identified in dorsal muscles in anticipation of perturbations to equilibrium (Latash et al. 1995; Santos and Aruin 2007). The muscle activity identified in the present study also served a range of directions and was maximally tuned to a specific reaching direction in both periods studied. We suggest therefore that the patterns of muscular activation seen in both periods may belong to the same limited number of robust functional muscle synergies, despite the inter-trial variations seen in each subject reflecting different levels of synergy activation. However, APRs are primarily triggered by afferent feedback from the moving surface, whereas in the present study the postural adjustments were produced in anticipation of the upcoming movements. Therefore, similarities in the synergic organization of feedback and feed-forward postural adjustments may support the idea that the CNS adopts functional synergies for both modes of control to produce different motor behaviors (Ting, 2007).

**Clearly constrained force patterns are seen during preparatory but not during associated feed-forward postural adjustments**

A force constraint strategy has been defined as a bimodal clustering of active force vectors where the forces are constrained to act along an approximately diagonal axis directed roughly toward or away from the CoM at a single limb (Macpherson 1988a; Macpherson 1994). Until now, this strategy has been identified in the horizontal forces comprising the feedback-based postural adjustments produced when the surface upon which animals or humans were standing was unexpectedly displaced (Henry et al. 2001; Macpherson 1988a; 1994; Ting and Macpherson 2004). Our results have shown statistically, that a force constraint strategy existed for feed-forward postural adjustments accompanying a pointing task, specifically during the latter stages
of the $p$PA period ($p$PA4 and $p$PA5) during which the objective was to displace the CoM in the direction of the target. During these bins the angular distribution was significantly different from uniform and $r_{max}$ values (quantifying the degree of dispersion, see Methods) supported a low dispersion of vector direction. Our $r_{max}$ values were comparable to, if not greater than, those produced by cats perturbed in the horizontal plane standing at natural stance width (Macpherson 1994). Average values of $k$ during these same periods ($p$PA4 and $p$PA5) were between $>1$ and $<2$, indicating that an asymmetric bimodal distribution existed (less than 180° separation existed between clusters). We conclude, therefore, that a force constraint strategy existed for $p$PA’s. Such an observed $p$PA period force constraint strategy may represent a high-level task variable whereby the CNS groups together the dynamic forces required to execute a number of directions of reaching in order to simplify the complex control of multijoint movement.

It remains, however, that such a low dispersion of force vector was not observed in our study for the forces exerted during the $a$PA period. Values of $r_{max}$ were $<0.5$ (more highly dispersed) and only one single alpha value was identified. This more dispersed force pattern observed during the $a$PA period when compared to the $p$PA period may be explained by the current nature of the task. Task instructions were to maintain final finger position at target position and not to return to the initial position. Thus, the constraints of displacing the CoM from one position to another, as in the $p$PA period, did not apply. Rather, subjects had to maintain their body position and stability at target attainment. Force constraint strategies have been documented to exist mostly when humans or animals are required to actively displace the CoM back towards its initial position following a perturbation (Henry et al. 1998a; 2001; Macpherson 1988a; Ting and Macpherson 2004). In this instance, the force constraint strategy would simplify neural control
mechanisms to coordinate force direction and amplitude during these ‘active’ responses (McKay et al. 2007). During the aPA period of this study, the task was simply to decelerate the body to target position and remain in that position. It did not require a similar ‘active strategy’ of CoM (and body) displacement, but rather a maintenance of posture. Thus, we suggest that the force constraint strategy characterizes feed-forward postural adjustments when the goal is to displace the CoM within the base of support (likened to the active adjustment following a perturbation) but not when task requirements are to precisely control an end posture and finger position during voluntary reach to point movements.

Finally, it may be asked why the force constraint strategy observed during the pPA period was weaker at the right foot than at the left? The right foot, ipsilateral to the reaching arm, showed a less constrained pattern of horizontal force during pPA4 and pPA5. It is possible that the left foot (contralateral to the reaching arm) was primarily responsible for producing the turning moment to targets 0-90°. Indeed, Fig. 3A shows that when loaded, the left foot produced a CCW Tz, while the right foot opposed that torque. The reverse was not true, however for movements to 180°. Here, the left foot (although unloaded) exerted a Tz that was in the same direction as the right to drive the body around to the left. Moreover, at this direction during the aPA period, the right foot consistently opposed the direction of reach, likely to assist the braking of the movement. Thus, we tentatively suggest that the leg contralateral to the arm assists in turning to its contralateral side, whereas the leg ipsilateral to the reaching arm is perhaps more coordinated with the upper limb and establishes a base for the limb’s trajectory during the reaching task. Another possibility is that as all subjects were right-handed, their right leg (and foot) was also their dominant one. If so, it may be that the dominant limb is better adapted to controlling the
limb’s trajectory by producing more dispersed vectors, while the left leg ensures a postural transition at the onset of reaching directions for which it is loaded. A differentiation of trajectory control versus steady-state limb posture has been identified for dominant and non-dominant arms (Duff and Sainberg, 2007). Our further experiments will vary the reaching arm used in an attempt to confirm these hypotheses.

Implications for the neural control of balance: shared control of feed-forward and feedback postural adjustments

This study has shown that EMG tuning characteristics in the pPA period are organized in a similar manner to compensatory postural responses produced via feedback. This raises an important question: To what extent do similar neural pathways control posture during voluntary movements and following unexpected perturbations? It is well known that central commands for feed-forward and feedback postural adjustments originate at supraspinal levels. Commands for APAs arise in different regions of the cortex (Gurfinkel and Elner 1988; Massion et al. 1989; Wiesendanger et al. 1987). In addition, spinal cats have difficulty maintaining equilibrium when the support surface is unexpectedly displaced horizontally (Macpherson and Fung 1999) and do not exhibit the complex patterns of evoked EMG characteristic of APRs in the intact animal (Macpherson et al. 1997). Lesion studies have shown that damage to the brainstem reticulospinal system impairs balance (Gorska et al. 1990; Gorska et al. 1995; Lawrence and Kuypers 1968). In addition, the injection of cholinergic agonists, which excite reticular neurons or noradrenergic agents that block inhibitory neurons to the reticular formation affect feed-forward programming of postural responses accompanying reaching (Luccarini et al. 1990). More recently, it has been
shown that signals in the brainstem pontomedullary reticular formation (PMRF) contribute to feed-forward postural adjustments during reaching with neurons in the PMRF encoding either pPAs or aPAs, or both (Schepens and Drew 2006; 2004). It has also been shown that microstimulation of peripheral afferents, known to be essential for the early triggering of APRs (Stapley et al. 2002), also activate particular subsets of reticulospinal neurons (Drew et al. 1996). Moreover, the activity of RSNs in the same anatomical area of the PMRF as those related to feed-forward postural adjustments (Schepens and Drew 2006; 2004), also contribute to the compensatory postural responses recorded in the limbs following unexpected perturbations (Stapley and Drew, *in press*). Thus, evidence would suggest that an integration of feed-forward and feedback modes of control may occur in the brainstem.

What would be the end result of commands sent from the brainstem to the muscles producing both types of postural adjustments? Recent evidence has shown that, rather than a unique muscle synergy existing for a particular direction of postural perturbation, APRs are organized into a few muscle synergies which represent the general neural strategy that accounts for the spatio-temporal components of the response (Torres-Oviedo and Ting 2007). These muscles synergies, or primitives, may be used to control task level variables such as CoM motion or displacement (Ting and Macpherson 2004) or CoP displacement (Krishnamoorthy et al. 2003). We propose that the similarity in organization of preparatory (feed-forward) postural adjustments and compensatory (feedback) postural adjustments may take place in the PMRF. This structure would then organize the functional muscle synergies required in either mode of control and the outward expression of those synergies, (the active force vectors) required to produce whole body movements or active corrections to balance. The results of this paper do not, however, enable us
to conclude that feed-forward and feedback based postural adjustments share common ‘motor primitives’. Further study is needed therefore, to characterize the muscle synergy organization during feed-forward and feedback postural tasks in the same muscles of the same subject.
Acknowledgements

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Figure legends

Figure 1. Plan view of the target array and the temporal sequence of data collection. A. Subjects stood on 2 force plates, 1 under each foot and were centered in a 180º light target array, adjustable for each subject in height and distance (see Methods). Targets (light emitting diodes, LEDs) were placed at 15º intervals from right to left sides with the position of each LED set to exactly 130% of their outstretched arm length at shoulder height. Fy = anterioposterior force, Fx = mediolateral force and Fz = vertical force. B. Temporal sequence of the data collection period. An auditory tone 500 ms in length sounded to inform subjects of an impending target illumination. A period of 1000 ms preceded the onset of the target light upon which subjects were required to reach and point to the target. The total acquisition period was 3000 ms. A representation of an approximate movement length (movement time, MT) is shown.

Figure 2. 3D kinematic representations of reach to point movements to 3 principal target directions (A. 0º, B. 90º and C. 180º) for 1 subject (S5). Stick figures are shown as if being viewed from the front and slightly to the subject’s left (A) and right (B and C) sides. Body movements are shown at 2 different times: At the onset of finger movement (grey sticks) and at the end of the movement (black sticks) when the finger touched the target. Shown are the following segments bilaterally: foot, shank, thigh, shoulder, upper arm and lower arm. Markers at the level of the 7th cervical and 10th thoracic vertebrae, the clavicle and sternum form a single segment that represents the torso in the sagittal plane. The head is represented by markers placed at 4 locations on the left and right temples and at the same level at the back of the head. Finger trajectory is shown in red. The body centre of mass (CoM) is shown as a grey and black circles (onset and end of the movements, respectively). The ground reaction force vector is represented at the onset of movement in red, and at target attainment in blue. D. Trajectories of the CoM from the onset of the focal movement (open squares) to when the finger touched the target (open circles). Trajectories are represented for 5 trials in each direction and are colour-coded as per the legend across the bottom of the figure.

Figure 3. Electromyographic activity, changes in force and vertical torque (Tz) under each foot for reaching movements to 3 principal directions (A. 0º, B. 90º and C. 180º). Traces are shown for a period of 500 ms preceding movement onset until the end of each movement for one typical trial in subject 5. On each plot, the full grey vertical line indicates the onset of the light target (Light on). The dashed grey line to the left of movement onset (Movt on) indicates the onset of force and Tz changes during the pPA period. The dashed grey line to the right of movement onset (between 500 and 750 ms) indicates the end of the arm movement (Movt end). Forces are shown as forces exerted against the ground. TFlr and TFlL = tensor facia latae muscles (right and left, respectively), RFr and RFl = rectus femoris, BFr and BFl = biceps femoris, GasLr and GasLl = gastrocnemius lateralis, , PerL and PerL = peroneus longus, TAR and TAl = tibialis anterior, Solr and Soll = soleus. Fx = mediolateral force, Fy = anterioposterior force, Fz = vertical force and Tz = torque exerted around the vertical axis. Left =leftwards, back = backwards, load = loading and CCW = counterclockwise. Left and right foot forces are represented by solid and dashed traces, respectively (see legend). Shaded regions represent the 2 periods of 250 ms under study (pPA and aPA). Successive squares underneath the time axes pictorially represent changes in Tz at each foot during the two periods.
**Figure 4.** Representative EMG traces for 14 selected muscles for S5 across the 13 directions of pointing. Muscle activity is shown for a total duration of 500 ms, 250 ms before and after the onset of the pointing movement. Muscle name conventions are as described in Figure 3. The shaded area to the left of time zero on each muscle plot represents the 250 ms preparatory period. Unless shown, muscles have the same scaling for the left leg (top row) as they do for the right leg (bottom row).

**Figure 5.** Muscle tuning curves for the EMG activity of all 14 postural muscles during the final 3 bins of the preparatory and associated periods for the representative subject S5. Differences in tuning and recruitment of the muscle studied can be observed by comparing the activity of the muscles over the 3 $\frac{5}{3}$ equivalent bins (left to right columns). Dots indicate amplitudes from each trial measured and the solid lines the mean responses. Muscle name conventions are as described in Figure 3.

**Figure 6.** Muscle tuning curves in the final bin of the $pPA$ (A) and $aPA$ (B) periods for each of the 8 subjects studied. Muscles have been grouped into the 3 major groups that activated for similar directions of reach. Tuning curves and individual trials are represented as in Figure 5. Schema (C) summarizing the approximate range of directions of reach to which each identified group contributed.

**Figure 7.** Individual resultant horizontal ground reaction force vectors and average values of $Fz$ produced during the $pPA$ period (A, B, respectively) and the $aPA$ period (C, D) for subject 5. Forces are shown for each consecutive bin during each period in successive rows from top to bottom. Black and grey arrows represent the approximate direction of exerted force under the loaded and unloaded feet, respectively. In B and D, bars above the top of the plots marked ‘L’ indicate directions of reach for which $Fz$ under each respective foot was loaded. For reference, the directions of reach used are indicated on the first plot (left foot) for the $pPA_1$ period in Fig. 6A.

**Figure 8.** Average direction and magnitude of horizontal ground reaction force change during each bin of the $pPA$ and $aPA$ periods under both feet.
Table I. *Mean (±1SD) of movement times (in ms) for pointing movements in all 13 directions.*

<table>
<thead>
<tr>
<th>Direction (°)</th>
<th>Movement time (ms)</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>820 ± 185</td>
</tr>
<tr>
<td>15</td>
<td>834 ± 183</td>
</tr>
<tr>
<td>30</td>
<td>881 ± 190</td>
</tr>
<tr>
<td>45</td>
<td>869 ± 216</td>
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<td>60</td>
<td>818 ± 216</td>
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<tr>
<td>75</td>
<td>788 ± 201</td>
</tr>
<tr>
<td>90</td>
<td>792 ± 215</td>
</tr>
<tr>
<td>105</td>
<td>786 ± 211</td>
</tr>
<tr>
<td>120</td>
<td>746 ± 177</td>
</tr>
<tr>
<td>135</td>
<td>772 ± 205</td>
</tr>
<tr>
<td>150</td>
<td>817 ± 193</td>
</tr>
<tr>
<td>165</td>
<td>806 ± 218</td>
</tr>
<tr>
<td>180</td>
<td>836 ± 220</td>
</tr>
</tbody>
</table>
### Table II. Results of the circular statistics conducted on horizontal force vector data from under both feet for the 5 bins and 2 periods studied.

<table>
<thead>
<tr>
<th>Bin</th>
<th>Foot</th>
<th>k</th>
<th>rmax</th>
<th>alpha1</th>
<th>alpha2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>pPA1</td>
<td>Left</td>
<td>1.46</td>
<td>0.39</td>
<td>57.0</td>
<td>303.6</td>
<td>NS</td>
</tr>
<tr>
<td>pPA1</td>
<td>Right</td>
<td>1.00</td>
<td>0.35</td>
<td>110.0</td>
<td>-</td>
<td>NS</td>
</tr>
<tr>
<td>pPA2</td>
<td>Left</td>
<td>1.46</td>
<td>0.38</td>
<td>51.3</td>
<td>297.9</td>
<td>NS</td>
</tr>
<tr>
<td>pPA2</td>
<td>Right</td>
<td>1.00</td>
<td>0.40</td>
<td>112.8</td>
<td>-</td>
<td>&lt; 0.05</td>
</tr>
<tr>
<td>pPA3</td>
<td>Left</td>
<td>1.56</td>
<td>0.42</td>
<td>37.5</td>
<td>268.3</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>pPA3</td>
<td>Right</td>
<td>1.00</td>
<td>0.50</td>
<td>109.0</td>
<td>-</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>pPA4</td>
<td>Left</td>
<td>1.63</td>
<td>0.66</td>
<td>28.9</td>
<td>249.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>pPA4</td>
<td>Right</td>
<td>1.35</td>
<td>0.55</td>
<td>99.4</td>
<td>366.1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>pPA5</td>
<td>Left</td>
<td>1.58</td>
<td>0.77</td>
<td>23.9</td>
<td>251.8</td>
<td>&lt; 0.001</td>
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<tr>
<td>pPA5</td>
<td>Right</td>
<td>1.42</td>
<td>0.60</td>
<td>100.8</td>
<td>354.3</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

### aPA

<table>
<thead>
<tr>
<th>Bin</th>
<th>Foot</th>
<th>k</th>
<th>rmax</th>
<th>alpha1</th>
<th>alpha2</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>aPA1</td>
<td>Left</td>
<td>1.21</td>
<td>0.54</td>
<td>4.33</td>
<td>301.9</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA1</td>
<td>Right</td>
<td>1.00</td>
<td>0.54</td>
<td>149.6</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA2</td>
<td>Left</td>
<td>1.00</td>
<td>0.47</td>
<td>292.9</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA2</td>
<td>Right</td>
<td>1.00</td>
<td>0.51</td>
<td>155.2</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA3</td>
<td>Left</td>
<td>1.00</td>
<td>0.44</td>
<td>285.7</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA3</td>
<td>Right</td>
<td>1.00</td>
<td>0.50</td>
<td>158.9</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA4</td>
<td>Left</td>
<td>1.00</td>
<td>0.44</td>
<td>279.8</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA4</td>
<td>Right</td>
<td>1.00</td>
<td>0.48</td>
<td>162.4</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA5</td>
<td>Left</td>
<td>1.00</td>
<td>0.44</td>
<td>276.5</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>aPA5</td>
<td>Right</td>
<td>1.00</td>
<td>0.43</td>
<td>165.6</td>
<td>-</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>

Results of the broken-axis approach (Holmquist & Sandberg, 1991). \( n = 1437, k \) = degree of modality (1 = unimodal, 2 = bimodal, two clusters separated by 180º), \( r_{\text{max}} \) = mean vector length for which \( k \) best fits data, alpha 1 and alpha 2, = mean angle in degrees of cluster 1 and 2 respectively, identified using the broken-axis algorithm and \( p \) = probability that the distribution of force vector angle is significantly different from uniform. NS = not significantly different from a uniform distribution.
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**Torres-Oviedo G, Macpherson J, and Ting LH.** Muscle synergy organization is robust across a variety of postural perturbations. *Journal of Neurophysiology* 96: 2006.


A. Target array, plan view

B. Data collection
Leonard et al. Figure 2

D. Centre of mass position and trajectory, plan view

- Mvt onset
- Mvt end

Reach direction (°)

0 15 30 45 60 75 90 105 120 135 150 165 180

X - Left

Y - Forward

Y - Back

X - Right

25 mm
A. Preparatory postural adjustments (pPA)

B. Associated postural adjustments (aPA)
A. GRF vectors, pPA
B. Fz, pPA
C. GRF vectors, aPA
D. Fz, aPA

Approx. direction of exerted force (loaded)
Approx. direction of exerted force (unloaded)
A. Direction

Vector Direction (º)

Direction of reach (º)

B. Magnitude

pPA 1

Force (N)

C. Direction

Vector Direction (º)

Direction of reach (º)

D. Magnitude

aPA 1