Reaching to Multiple Targets When Standing: The Spatial Organization of Feedforward Postural Adjustments

Julia A. Leonard, Ryan H. Brown, and Paul J. Stapley

Balance and Voluntary Movement Laboratory, Department of Kinesiology and Physical Education, McGill University, Montreal, Quebec, Canada

Submitted 9 October 2008; accepted in final form 4 February 2009

Leonard JA, Brown RH, Stapley PJ. Reaching to multiple targets when standing: the spatial organization of feedforward postural adjustments. J Neurophysiol 101: 2120–2133, 2009. First published February 11, 2009; doi:10.1152/jn.91135.2008. We examined the spatial organization of feedforward postural adjustments produced prior to and during voluntary arm reaching movements executed while standing. We sought to investigate whether the activity of postural muscles before and during reaching was directionally tuned and whether a strategy of horizontal force constraint could be observed. To this end, eight human subjects executed self-paced reach-to-point movements on the random illumination of one of 13 light targets placed within a 180° array centered along the midline of the body. Analysis was divided into two 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, electromyographic 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 feedforward pPAs is one where the tuned muscle synergies constrain the forces diagonally away from the center 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 endpoint limb force during postural tasks depends on the use of functional muscle synergies, which are used to displace the CoM or decelerate the body at the end of the reach.

INTRODUCTION

For multijoint movements executed during standing such as reaching forward, postural adjustments occurring prior to movement onset shift the center of mass (CoM) within the base of support (BoS) 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. 1984, 1988; Schepens and Drew 2003; Stapley et al. 1998, 1999). To ensure a controlled transition from one postural configuration to another, these adjustments of posture must be planned by the CNS in advance and a feedforward 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 feedforward in nature because 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 on which humans are standing unexpectedly moves, the body is destabilized in the direction opposite to that of the surface displacement. To regain balance, humans produce short-latency automatic postural responses (APRs) in the supporting limbs that oppose the perturbation and drive the CoM back toward 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 electromyographic (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, 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. 1998b, 2001; 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. 1998b, 2001). 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 production of the desired vector is solved at a lower level by the synergic recruitment of muscle groups.

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.
FEEDFORWARD POSTURAL ADJUSTMENTS IN HUMANS

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 and Ting 2008; McKay et al. 2007). However, the production of a force constraint strategy is dependent on 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 feedforward postural adjustments can be identified in the pontomedullary reticular formation (PMRF) of the brain stem (Scheppens and Drew 2004, 2006; Scheppens et al. 2008). Neurons in this area discharged either during the pPA, the aPA, or both during reaching movements in the standing cat (Scheppens and Drew 2004, 2006). The activity of this area, however, has also 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 (RSNs) (Drew et al. 1996) and PMRF neurons are activated strongly during postural perturbations in the standing cat (Stapley and Drew 2003, 2008). If specific neural sites can modulate postural responses with different underlying modes of control (i.e., feedforward or feedback), it is plausible to predict that the outward expression of those postural adjustments may show similarities in their organization. The present study thus aimed to investigate whether a similar spatial organization of horizontal force and muscle activity to that seen with feedback-based postural responses could be observed for predictive feedforward 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 while 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) feedforward 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 (feedforward or feedback) of neural control.

METHODS

Subjects

Eight (one female, seven 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 setup

Subjects stood barefoot on two triaxial force plates (model FP4060; Bertec, Columbus, OH) that measured ground reaction force (GRF) and moments in mediolateral (x), anteroposterior (y), and vertical (z) axes at 1,000 Hz. Stance width (the mediolateral distance between the feet) was taken as the average of each subject’s natural stance distance as measured after three 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 5-V red LEDs encased in modified gaming switches (model 459512; RP Electronics, Burnaby, BC, Canada) that produced a 5-V pulse on contact. The gaming switches were mounted at the ends of lightweight aluminum dowels, adjustable in length, affixed to a semicircular aluminum bar suspended from the ceiling. A chest band worn by all subjects was also equipped with the same switch to detect movement onset (see following text).

The activity of 16 muscles was recorded using two DelSys Bagnoli eight-channel systems (Boston, MA) at 1,000 Hz. The following muscles were recorded bilaterally (left and right legs): tibialis anterior (TA), anterior tibialis (A; TA and TA, respectively), soleus (Sol), lateral gastrocnemius (GasL; GasL), peroneus longus (Per, Perr), biceps femoris (BF), biceps femoris (BF), rectus femoris (RF), rectus femoris (RF), and tensor fascia latae (TFL, TFLr). In addition, anterior and posterior deltoid was recorded at the right shoulder. Bilateral kinematic data were collected using a six-camera system that consisted of 12 cameras (model CyberDragon 459512; RP Electronics, Burnaby, BC, Canada) that produced a 5-V pulse on contact. The gaming switches were mounted at the ends of lightweight aluminum dowels, adjustable in length, affixed to a semicircular aluminum bar suspended from the ceiling. A chest band worn by all subjects was also equipped with the same switch to detect movement onset (see following text).

FIG. 1. Plan view of the target array and the temporal sequence of data collection. A: subjects stood on 2 force plates, one under each foot, and were centered in a 180° light target array, adjustable for each subject in height and distance (see METHODS). Targets (light-emitting diodes [LEDs]) were placed at 15° 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, anteroposterior 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 1,000 ms preceded the onset of the target light on which subjects were required to reach and point to the target. The total acquisition period was 3,000 ms. A representation of an approximate movement length (movement time [MT]) is shown.
MX3 motion-capture system (Vicon Peak, Lake Forest, CA) sampling at 200 Hz. In all, 39 markers were placed at different locations on the subjects’ whole body as listed in the Plug-in-Gait model (Vicon Peak). This model provides an accurate estimate of CoM position when compared with the method of GRF 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) 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 midline (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). On the random illumination of one 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 toward each target. Subjects were asked to stand straight and 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 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 center-of-pressure [CoP] displacement within the BoS). 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 2 s, then return slowly to 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 0.5 and 1 s, a target illuminated and subjects initiated their movements. The total acquisition period of 3,000 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 toward each pointing direction, in a pseudorandomized 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 about 50 trials interspersed with 5-min rest periods to reduce fatigue until the required number of trials at each direction was attained.

**Data analysis**

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). GRFs and moments were low-pass filtered using a digital second-order Butterworth filter, with a 10-Hz cutoff frequency. Raw EMG signals were high-pass filtered at 35 Hz, demeaned, and rectified, and low-pass filtered at 100 Hz (second-order Butterworth filter). Individual trials were visually inspected for stability during the quiet stance period (1,000 ms prior to target illumination). Any trials that showed significant variation in vertical force ($F_z$) 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 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, 1,437 trials in all from the eight subjects were retained for further analysis from a total of 1,560 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 with 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. Because no difference $>5$ ms was found between the onset of motion as determined by the chest switch and the motion capture data (sampling one 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 0 on which all preparatory events were based.

To investigate the temporal and spatial organization of feedforward preparatory postural adjustments prior to movement onset (hereafter 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 on 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 $F_x$ and $F_y$, 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 ($T_z$) was calculated using the following equation

$$T_z = M_z - (Xp \cdot F_y) + (Yp \cdot F_x)$$

where $Xp$ and $Yp$ are the coordinates of the center of pressure of each foot, $M_z$ is the moment of the force plate around the vertical (z) axis, and $F_y$ and $F_x$ are anteroposterior and mediolateral forces, respectively.
Statistical analysis

The effect of pointing direction on movement time was examined using a repeated-measures one-way ANOVA. To determine whether 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 0 and 360° represent the same direction. To determine whether 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 bimodality, but does not assume that means of clusters of vectors are separated by 180°. 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, $r_{\text{max}}$ 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 are uni- or bimodal. For example, if $k = 2$, the data would be symmetrically bimodal (i.e., two clusters separated by 180°). 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 $360°/k$ (e.g., when $k = 1.6$, modes are separated by an angle of 225°). 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 three dimensions in Fig. 2, A–C. Three principal directions of reach are shown for one representative subject. For all direc-
tions, 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 0°, 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 90° (Fig. 2B) the reaching arm outstretched approximately along the body midline, whereas the torso rotated forward and slightly downward. Finally, for far leftward movements (Fig. 2C), the right arm rotated leftward, crossing the midline, with the torso and pelvis also rotating toward the left. For each of the three movements shown, the CoM was displaced from its initial position in the approximate direction of the target within the BoS. 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 toward the CoM (blue vectors) to brake the movement of the body. Although there was some variability (especially between 90 and 120°), trajectories and end CoM positions differed for each reaching direction. This is represented for five 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 1.

**EMG activity in relation to the forces produced**

**pPA period.** There was a clear modulation of EMG activity and force between 0 and 180° target directions during the pPA and aPA periods. Changes in muscle activity and force for three main directions of reaching are shown in Fig. 3, A–C, for one 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 TFLr. This was followed by a leftward and backward push at the left leg and an unloading of Frz under the right foot. The torque about the vertical axis (Trz) showed that the left foot exerted a counterclockwise (CCW) moment, whereas 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 TFLr and RFr 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 90° target. There was very little or no change in Fx under either foot but instead an increase in Fy (backward push) and Frz (loading) under the right foot, coupled with a slight forward push at the left foot. Because these movements involved essentially a forward displacement, there was only a slight CW Trz 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 BFr. Additionally, there was a burst in the Solr. The forces showed that the right (loaded) foot Frz pushed rightward, exhibiting a CW Trz. Interestingly, although unloaded, the left foot also showed a CW Trz.

**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 GasLr, Soll, Tar, and Perr. Apart from the slight activation of TFLr early in this period, there was little activity in the other muscles. Forces showed that the right foot was loaded, whereas the horizontal forces stabilized around their original values. The loaded (right) foot exerted a CCW Trz. 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 forward (Fy), whereas Frx forces steadied. The loaded (right) foot exerted a CCW Trz 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 (GasLl and Soll) as well as right-side flexors (BFr and Tar). The loaded left foot pushed in a slightly rightward and backward direction exerting a CCW Trz.

**Feedforward postural adjustments show directional tuning and are synergic**

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

---

**TABLE 1.** *Mean (±SD) of movement times for pointing movements in all 13 directions*

<table>
<thead>
<tr>
<th>Direction, deg</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>
</tr>
<tr>
<td>60</td>
<td>818 ± 216</td>
</tr>
<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>
In the aPA period reciprocal patterns of activity could also be noted for the extensors soleus and gastrocnemius, left-side muscles activating for 75–180° targets and those on the right side from 0 to 90°. The BF also activated for 75–180° targets, whereas other left-side muscles remained largely inactive. On the right side, the plantar-flexor Per contracted along with Sol as did the TFL to a certain extent. Interestingly, BF showed activity across virtually all reaching directions during this period.

To evaluate the spatial and intertrial variability characteristics of the muscular patterns described earlier, tuning curves were generated for each of the 14 postural muscles recorded during five 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; thus 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 intertrial variation that existed. During pPA4 and pPA5, the tuning curves show that the muscles worked in groups, with TA/TA, Per/Per, and RF/RF activating maximally for targets on either side of the central one, TFLr, BF, and Solr for leftward targets and TFLl and GasLl for rightward movements. Clear patterns of tuning were also evident for all bins of the aPA period (gray lines).
FIG. 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 Fig. 3. The shaded area to the left of time 0 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).
and filled circles) with the patterns emerging from bin 1 onward (250 to 200 ms before target attainment). Again, for clarity and due to the constancy of tuning across the five bins in this period, only bins 3–5 are depicted in Fig. 5. The muscles Solr, GasLr, Perr, and TFLr activated for similar directions, as did GasLl, Soll, and BFl. The BFr showed increasing activity from 0 to 180°.

This pattern of muscle tuning was very consistent across the eight subjects tested. This can be seen in Fig. 6. Here, muscles are depicted for the final bin of the pPA period (Fig. 6A) and the aPA 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 two 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 two periods studied. The forces produced during the pPA period approached more of a bimodal distribution with low dispersion of the vector directions, whereas those produced in the aPA period, although not unimodal, were more highly dispersed, suggesting that to control final body position for each direction of reaching, 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 pPA period (Fig. 7A, pPA1 and pPA2) horizontal forces were of very small amplitude and showed a high degree of dispersion in terms of their direction. However, from the bin pPA3 onward, which corresponded approximately to the emergence of EMG tuning described earlier and shown in Fig. 5, forces—in particular under the loaded foot—shared similar directions (e.g., 0 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 outward and leftward (see different black-blue colored vectors) and under the right foot, loaded for 105–180° targets, pushing outward and rightward (see yellow-orange vectors), although right foot vectors were always slightly more dispersed. 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 and gray arrows when it was unloaded. The constraint observed in the horizontal vectors during pPA4 and pPA5 is supported by the circular statistical analysis (see following text). 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 backward and outward at the foot contralateral to the direction of reach (e.g., left foot, pPA5, blue vectors). In comparison, during the aPA period, loaded vectors now pushed outward and forward 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 (see Fig. 7D).

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 2 for both feet. During the pPA period, the analysis identified an angular distribution that was significantly different from uni-
form 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, \( r_{\text{max}} \) values were \( >0.5 \) (e.g., 0.66 and 0.77 for the left foot and 0.55 and 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 \( r_{\text{max}} \) values \( \leq 0.5 \), indicating higher dispersion than that in the \( pPA \) period around a single mode.

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, \( pPA4 \) and \( pPA5 \)), whereas the \( aPA \) period displayed a linearity of GRF vector and reaching direction from bin 2 onward (Fig. 8C) and a fairly constant magnitude of GRF vector across all directions (see Fig. 8D, all bins).
DISCUSSION

We investigated the organization of feedforward postural adjustments produced when standing humans reached with their preferred arm to multiple targets placed in a semicircle 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 feedforward postural adjustments—was not completely supported.

![Diagram](image_url)

FIG. 7. Individual resultant horizontal ground reaction force vectors and average values of \( F_z \) produced during the pPA period (A and B, respectively) and the aPA period (C and D) for subject 5. Forces are shown for each consecutive bin during each period in successive rows from top to bottom. Black and gray 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 \( F_z \) under each respective foot was loaded. For reference, the directions of reach used are indicated on the first plot (left foot) for the pPA1 period in Fig. 6A.
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 feedforward 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 feedforward muscle activity has previously been identified during bilateral arm movements performed when standing (Aruin and Latash 1995). When the two arms were moved either forward or backward 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 feedforward muscle activity have also been identified in dorsal muscles in anticipation of perturbations to equilibrium (Latash et al. 1995; Santos and Aruin 2008). 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 therefore suggest that the patterns of muscular activation seen in both periods may belong to the same limited number of robust functional muscle synergies, despite the intertrial 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 feedforward postural adjustments may support the idea that the CNS adopts functional synergies for both modes of control to produce different motor behaviors (Ting 2007).

**Tuned, synergic muscle activity characterizes feedforward postural adjustments**

Roles of preparatory and associated postural adjustments for reaching 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 toward 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, 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 2003, 2004).

**Clearly constrained force patterns are seen during preparatory but not during associated feedforward 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, 1994). Until now, this strategy has been identified in the horizontal forces comprising the feedback-based postural adjustments produced when the surface on which animals or humans were standing was unexpectedly displaced (Henry et al. 2001; Macpherson 1988a, 1994; Ting and Macpherson 2004). Our results have statistically shown that a force constraint strategy existed for feedforward postural adjustments accompanying a pointing task, specifically during the latter stages of the pPA period (pPA4 and pPA5) 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 (quantify-
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 (pPA4 and pPA5) were between $>1$ and $<2$, indicating that an asymmetric bimodal distribution existed ($<180^\circ$ separation existed between clusters). We thus conclude that a force constraint strategy existed for pPAs. Such an observed pPA 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 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 aPA 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 aPA period when compared with the pPA 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 pPA 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 toward 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 feedforward 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 that 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 $T_z$, whereas the right foot opposed that torque. The reverse was not true, however, for movements to 180°. Here, the left foot (although unloaded) exerted a $T_z$ 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 because 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, whereas 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 nondominant 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 feedforward and feedback postural adjustments**

This study has shown that EMG tuning characteristics in the $pPA$ period are organized in a manner similar to that of 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 feedforward and feedback postural adjustments originate at supraspinal levels. Commands for $aPAs$ arise in different regions of the cortex (Gurfinkel and Elnor 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 $aPAs$ in the intact animal (Macpherson et al. 1997). Lesion studies have shown that damage to the brain stem reticulospinal system impairs balance (Gorska et al. 1990, 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 feedforward programming of postural responses accompanying reaching (Luccarini et al. 1990). More recently, it has been shown that signals in the brain stem pontomedullary reticular formation (PMRF) contribute to feedforward postural adjustments during reaching with neurons in the PMRF encoding either $pPAs$ or $aPAs$, or both (Schepens and Drew 2004, 2006). 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 (RSNs) (Drew et al. 1996). Moreover, the activity of RSNs in the same anatomical area of the PMRF as those related to feedforward postural adjustments (Schepens and Drew 2004, 2006) also contribute to the compensatory postural responses recorded in the limbs following unexpected perturbations (Stapley and Drew 2008). Thus evidence would suggest that an integration of feedforward and feedback modes of control may occur in the brain stem.

What would be the end result of commands sent from the brain stem 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 that represent the general neural strategy that accounts for the spatiotemporal 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 (feedforward) 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 study do not, however, enable us to conclude that feedforward- and feedback-based postural adjustments share common “motor primitives.” Further study is thus needed to characterize the muscle synergy organization during feedforward and feedback postural tasks in the same muscles of the same subject.

**Acknowledgments**

We thank J. J. Loh for expert technical assistance and Drs. Jane Macpherson and Trevor Drew for helpful discussions about earlier versions of this work.

**Grants**

This study was supported by Canadian Foundation for Innovation/New Opportunities Fund Grant 10613 and a Natural Sciences and Engineering Research Council Individual Discovery grant to P. J. Stapley.

**References**


