Postural adjustments for online corrections of arm movements in standing humans

Julia A. Leonard, Valeriya Gritsenko, Ryan Ouckama, and Paul J. Stapley

In standing humans, postural adjustments for online corrections of arm movements are predictive or rely on feedback from the moving limb. To answer this question, we measured online corrections in arm and leg muscles during pointing movements while standing. Nine healthy right-handed subjects reached with their dominant arm to a visual target in front of them and aligned with their midline. In some trials, the position of the target would switch from the central target to one of the other targets located 15°, 30°, or 45° to the right of the central (midline) target. For each target correction, we measured the time at which arm kinematics, ground reaction forces, and arm and leg muscle electromyogram significantly changed in response to the target displacement. Results show that postural adjustments in the left leg preceded kinematic corrections in the limb. The corrective postural muscle activity in the left leg consistently preceded the corrective reaching muscle activity in the right arm. Our results demonstrate that corrections of arm movements in response to target displacement during stance are preceded by postural adjustments in the leg contralateral to the direction of target shift. Furthermore, postural adjustments preceded both the hand trajectory correction and the arm muscle activity responsible for it, which suggests that the central nervous system does not depend on feedback from the moving arm to modify body posture during voluntary movement. Instead, postural adjustments lead the online correction in the arm the same way they lead the initiation of voluntary arm movements. This suggests that forward models for voluntary movements executed during stance incorporate commands for posture that are produced on the basis of the required task demands.

posture; reaching; visuomotor control; prediction

When standing humans reach out to point at or grasp an object, the central nervous system (CNS) must resolve two major task constraints: the production of the correct hand and arm trajectory toward the target and the necessary associated postural adjustments (aPAs) in the supporting limbs and trunk for the maintenance of equilibrium. Using prior knowledge of the dynamics of the moving arm and the internal disturbances that arm movements inflict upon the body, the CNS can anticipate the impending disturbance and correctly program the aPAs accordingly. However, what happens when the final position of a visual target unexpectedly changes after the onset of a planned voluntary movement that is executed while standing? In this situation, the CNS must correct online the arm trajectory toward the new target and modify the required postural adjustments. The objective of this study is to investigate how posture is modified with respect to arm movements during visual perturbations of the reaching goal.

The online control mechanisms for arm movements have been extensively investigated during experiments with seated subjects. These studies have shown that modifications of hand trajectory in response to target displacements occur at short latencies of 100 to 150 ms (Day and Lyon 2000; Goodale et al. 1986; Paulignan et al. 1990; Pélisson et al. 1986; Prablanc and Martin 1992; Soechting and Lacquaniti 1983; Zelaznik et al. 1983). Other studies have shown that visuomotor corrections are automatic and occur without voluntary intervention (Day and Lyon 2000; Gritsenko et al. 2009). Because of the inherent delays associated with the use of sensory feedback, the short latencies of online correction support the notion that the CNS adopts predictive mechanisms to execute rapid arm movements to visual targets. Such a prediction involves the formulation of an initial plan of the movement using a feedforward mode of control, but also a continuous estimation of the actual state of the system compared with the desired one, which is achieved using rapid, internal feedback loops (Bhushan and Shadmehr 1999; Desmurget and Grafton 2000; Mehta and Schaal 2002; for reviews, see Sabes 2000; Shadmehr and Krakauer 2008). This efference copy-based state estimation ensures that motor commands can be modulated at short latencies, and online, automatic corrections of movement can be made without detriment to the resulting movement (Nijhof 2003; Saunders and Knill 2003).

Anticipatory modulation of muscular activity in the supporting limbs that precedes the onset of voluntary movements during stance also suggests that a degree of prediction of the future state of the body occurs in advance of an impending disturbance to posture (Davidson and Wolpert 2005). The characteristics of aPAs occurring before the onset of movement depend on the prior knowledge of arm and body dynamics (Bouisset and Zattara 1981; 1987). In these paradigms (e.g., arm raising), however, a postural disturbance can be predicted in advance and need not be modified online during the execution of the movement, as the end goal matches that for which the postural adjustments were initially programmed. Indeed, during reaching to fixed targets in multiple directions when standing, feedforward postural adjustments follow a consistent spatial pattern both before and during the movements (Aruin and Latah 1995; Leonard et al. 2009). What happens, however, when postural adjustments for reaching, programmed
based on an initial state and an expected outcome, must be modified because of an unexpected change in the visual position of the final goal? Does the CNS still adopt a predictive mode of control, or does it correct arm trajectory before posture, which is then updated on the basis of the feedback obtained from the arm correction?

We attempted to investigate these questions by inducing unexpected shifts in the visual location of the target after the onset of reaching movements during stance. All targets were placed at a distance such that subjects could point to them and retain their center of mass (CoM) within the support base, without the need for a corrective step. Thus subjects were aware that they could complete the corrections and not become unstable to the extent that they would lose balance. Therefore, two mechanisms of postural control were possible: 1) postural adjustments occur after the arm movement corrections for the visual perturbations, and the feedback from the change in arm and body configuration is used to update the necessary postural adjustments; or 2) postural adjustments are predictive and precede online corrections of arm movement. This may indicate that, rather than acting to reduce the disturbance induced by the upcoming arm correction, the postural control system participates in the movement component of the action. We hypothesized that, because a change in the trajectory of the arm in response to an unexpected shift in target position could potentially destabilize one’s balance, the CNS predicts the postural adjustments necessary to execute smooth online corrections of arm movements. In other words, when the target shift occurs, leg muscle activity is updated and precedes the necessary changes in ground reaction force (GRF) in advance of changes in arm muscle activity or trajectory toward the new target. We show that this is indeed what occurs for online corrections of arm movements during stance.

METHODS

Subjects. Nine right-handed subjects (5 females, 4 males) were recruited from the McGill University student population to participate in the study. Subjects had a mean age of 22.9 ± 3.1 (SD) yr and measured on average 1.68 ± 0.1 m and 62.4 ± 9.6 kg in height and weight, respectively. All subjects were free of any known neurological, visual, or orthopedic disorders, and provided their informed consent to participate in this study. The study had ethical approval from the McGill University Research Ethics Board.

Experimental apparatus and setup. Subjects stood barefoot on two triaxial force plates (model FP4060; Bertec, Columbus, OH) that recorded GRFs and moments in the mediolateral (x), anteroposterior (y), and vertical (z) axes at 1,000 Hz. Each subject stood with their feet positioned according to their preferred mediolateral stance width, which was based on the average distance between the two heels calculated immediately after three trials of walking 15 m across the laboratory. This preferred stance configuration was recorded and marked on the force plates, and subjects maintained it throughout the experiments.

The experimental apparatus consisted of four target lights arranged about a semicircular radius separated by 15° (see Fig. 1A). The apparatus was fully adjustable to each subject’s reach distance and height. Light targets were 2.5 cm in diameter and consisted of a 5-V red LED encased in a modified gaming switch (model 459512; RP Electronics, Burnaby, BC, Canada) that produced a 5-V pulse upon contact. Targets were mounted on lightweight aluminum dowels, adjustable in length, affixed to a semicircular aluminum bar suspended from the ceiling. Subjects wore a chest band with the same switch that

![Fig. 1. Experimental setup and data collection schema. A: subjects standing on 2 force plates reached to a central target, aligned with their xiphoid process. Unperturbed reach trials were interspersed with online correction (corr) trials involving unexpected illuminations of 1 of 3 other targets placed successively at 15° increments to the right of center. fx, shear force; fz, vertical force; fv, anterior posterior force; +ve, positive B: explanation of the changes in voltage related to the sequence of light changes. When the signal rose to 5 V each light was illuminated. L1, light one; L2, light 2; chest, chest switch attached around the subject’s sternum that acted as a signal from which L2 illumination could be triggered; movt, movement. C: histogram showing the distribution of L2 onset as a percentage of mean reach peak velocity. Trials from all corr conditions have been pooled (n = 652). rFin, right finger.](http://jn.physiology.org/)

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enabled the detection of movement onset upon its release. Targets were situated at a distance corresponding to 130% of each subject’s reach length measured to each respective target. Previous experiments adopted this distance, which was attained comfortably without the center of pressure of either foot leaving foot length or width (Leonard et al. 2009). Any trials where this occurred were rejected from further analysis. The choice of 130% was especially important, as we sought to evoke postural adjustments for online corrections readily distinguishable above those produced for ongoing (initial) reaches to the central target. Reach length (100%) was measured as the distance between the xiphoid process (where the finger tip was held at the start of each trial) to the tip of their outstretched finger when the arm was extended in the direction of each of the targets (neutral scapula retraction).

The muscle activity of 16 leg, trunk, and arm muscles was sampled at 1,000 Hz using two DelSys Bagnoli 8-channel systems (Delsys, Boston, MA). For all subjects, the activity of the following leg muscles was recorded bilaterally: tibialis anterior (ITA and rITA), soleus (ISol, rSol), peroneus longus (IPer, rPer), rectus femoris (IRF, rIRF), biceps femoris (BF, rBF) and tensor facia latae (ITFL, rITFL). Additionally, recordings of muscle activity of the reaching arm (right) included anterior and posterior deltoid (rADel and rPDel, respectively), long head of the triceps (rTric) and the long head of the bicep muscle (rBic). Bilateral kinematics were collected using a six-camera MX3 motion-capture system (Vicon Peak, Lake Forest, CA) sampled at 200 Hz. A custom-written program using LabVIEW (National Instruments, Austin, TX) controlled the illumination of the target lights and acquired and synchronized signals from the chest and target switches. Synchronization with the analog signals obtained from the force plates and electromyogram (EMG) system was done using the Vicon controller.

Experimental procedures. Subjects began each trial standing with the head forward in the direction of the central (90°) target, which was aligned along the midline of the body (see Fig. 1A). Before each trial, they depressed the chest switch attached at the xiphoid process with their right index finger. The left arm was held in a relaxed downward pointing position at the side of the body. The study comprised two principal types of trials: regular reaches (“reach”) trials to the central (90°) target and trials that required corrections of arm trajectory toward three other targets at different times after a reach was initiated (online corrections, or “corr” trials).

Subjects were asked to stand quietly before each trial began. Once the experimenter was satisfied that the subject was stable, he/she initiated data collection, and, after a variable delay, the central target light (90° or L1) would illuminate. Subjects were instructed to reach and press the illuminated light at their natural speed (reach trials, dashed trajectory, Fig. 1A), remaining in that position until told to return (approx. 2 s). For some trials, the target light would shift from L1 to any one of the other three targets, 75° (corr75), 60° (corr60), or 45° (corr45) at different times after the onset of the initial reach movement. All reach and corr trials were randomly presented as well as trials when subjects were prepared but with no light illuminated. For the corr trials, subjects were instructed to correct arm trajectory when they detected the light change and point to the newly illuminated target. The target shift could occur after a variable delay from when they detected the light change and point to the newly illuminated target. The target shift could occur after a variable delay from the onset of the initial finger (reach) movement. N = number of trials; corr, correction; Fcorrect, online correction of focal movement, deviation of a corr trajectory from the mean of all regular reaches.

Table 1. Breakdown of total number of trials collected and retained after trial selection procedures

<table>
<thead>
<tr>
<th>Condition</th>
<th>N Collected</th>
<th>N Retained</th>
<th>Movement Time, ms</th>
<th>L2 onset, ms</th>
<th>Fcorrect, ms</th>
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</thead>
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<td>reach</td>
<td>477</td>
<td>228</td>
<td>877.6 (176.3)</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>corr75</td>
<td>168</td>
<td>158</td>
<td>1090.7 (141.4)</td>
<td>360.1 (127.4)</td>
<td>567.7 (103.8)</td>
</tr>
<tr>
<td>corr60</td>
<td>161</td>
<td>148</td>
<td>1237.7 (137.8)</td>
<td>348.5 (76.9)</td>
<td>563.5 (87.6)</td>
</tr>
<tr>
<td>corr45</td>
<td>139</td>
<td>118</td>
<td>1318.8 (269.0)</td>
<td>340.1 (91.4)</td>
<td>566.5 (90.1)</td>
</tr>
</tbody>
</table>

Average (±SD) movement time, light 2 (L2) onset, and time to correction of finger trajectory (the latter 2 for the applicable conditions) for all experimental conditions tested. For L2 onset and Fcorrect, latencies were calculated relative to the onset of the initial finger (reach) movement. N = number of trials; corr, correction; Fcorrect, online correction of focal movement, deviation of a corr trajectory from the mean of all regular reaches.

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Trials were aligned to movement onset, which was determined on a trial-by-trial basis to be the time at which the tangential velocity (derivative of $x$ and $y$ velocity) of the right finger marker surpassed a value of 3% of the peak velocity in that trial. Movement end was also established as when velocity reduced below the 3% threshold in that trial. We, and others, have previously used this threshold value to successfully determine movement onset and end (Leonard et al. 2009; Shabbott and Sainburg 2009). Correction (corr) trials were also eliminated if 1) they showed tangential velocity profiles that did not illustrate a pronounced “trough” indicating that a significant reacceleration occurred; in other words, in these trials, the subject may have hesitated sufficiently to execute a reach directly to a corr target; or 2) the trough between the first and second peaks of tangential velocity (see Fig. 3B) descended below the 3% initial peak-velocity threshold, indicating that subjects moved too fast and reached the central target before correcting to the corr target.

Once these trial-rejection procedures were implemented, a number of essential measures were determined on the basis of each subject’s average trajectories. These included the deviation of a corr trajectory from the mean of all regular reaches, or the online correction of focal movement (Fcorrect), the times at which particular EMG traces during corr trials significantly deviated from an average of reach trials (EMGcorrect), and times at which forces in the three axes significantly deviated from the average force exerted for reach trials (GRFcorrect). Fcorrect was detected on a trial-by-trial basis for all corr trials using the tangential velocity of the marker placed on the right index finger with respect to the original target. First, the mean ± 1SD of all reach trial $x$–$y$ trajectories was computed for a subject (see dashed trajectory and shaded area, respectively on Fig. 2A). Second, the tangential velocity of each corr trial was compared with the mean tangential velocity of all reach trials, and an algorithm calculated the time at which the reacceleration of the finger for the corr trials (corresponding to the online correction) exceeded 1SD of the mean reach trials. This is shown in Fig. 2B (Fcorrect), occurring for this particular trial at 460 ms, 169 ms after the change in the target light (L2). Similar methods were used to calculate EMGcorrect and GRFcorrect, but corrections were detected using a threshold of mean ± 2SDs, rather than 1SD for Fcorrect (kinematics). Mean ± 2SDs was...
found to be more robust for detecting EMGcorrect and GRFcorrect than mean ± 1SD. An illustration of the calculation of these variables is given in the relevant section of RESULTS (see below). After a stable initial posture, ability to detect significant EMG corrections in arm or leg muscles and other corr-trial rejection procedures were implemented; a total of 652 trials were retained and used for further analysis for the nine subjects after the unstable trials were eliminated as well as those in which the algorithm for EMG or force corrections could not detect a significant change with respect to regular reaches. Table 1 lists the total number of trials collected and retained in each reaching condition.

A custom-written algorithm detected the time at which the EMG activity of the muscles identified as participating in the corrections in corr trials exceeded that produced for reach trials, and values for each corr trial were verified on a trial-by-trial basis. For example, Fig. 2C illustrates Sol activity for the same corr45 trial as in Fig. 2, A and B (finger trajectory), and shows how the EMG activity of this muscle increases well above the mean + 2SD of the reach trials, and well before the correction of the arm trajectory (Fcorrect). EMGcorrect was computed for a total of the three leg muscles in the left leg as well as the three identified in the right arm (lSol, lPerl, lTA, rADel, rPDel, and rTric) and additionally rBic. A similar algorithm was used to detect when shear force (Fx) and Fz also increased above the force produced during a regular reach (Fig. 2D).

Statistical analysis. To detect significant differences in total MTs and Fcorrect values between reach and corr conditions, a one-way ANOVA was used, with experimental condition as the single factor. The statistical comparison between EMG correction times of arm and leg muscles was done using ANOVA with four factors. First, for each individual trial, the EMGcorrect values of each postural leg muscle were subtracted from the EMGcorrect values of each arm muscle. Positive differences indicate that leg muscles change after the target jump before arm muscles. Values (EMGcorrect of leg muscles minus arm muscle EMGcorrect) were sorted for trials in which the target jump occurred during the acceleration or deceleration phases of the initial reach movement. This was done to investigate whether the leg/arm muscle corrections were influenced by the extra time and feedback that may have been available when target jumps occurred in the acceleration phase. Then ANOVA was applied to these differences to determine the main effects of the following factors: target (corr75, corr60, and corr45), postural muscle (lSol, lPerl, and lTA), subject (9 subjects), and phase (acceleration or deceleration of the arm during the target jump). Post hoc comparisons were performed with Sidak-Bonferroni correction for α (Abdi 2007). Further post hoc comparisons were done using linear regressions between the EMG correction times for arm muscles deemed as contributing to the online kinematic corrections and Fcorrect values, as well as between postural and arm-muscle EMG correction times. For each type of linear regression, we report slope (m, the amount of increase in y that accompanies one unit of increase in x) and the y-intercept, the point conventionally chosen to define y coordinates when x = 0. Thus, for the relationship between leg- and arm-muscle correction times, we sought to investigate what latency the arm muscle corrected at when the postural muscle was 0 (or vice versa).

RESULTS

Unperturbed reaching and characteristics of online corrections. Trials executed to the central 90° target (reach) typically showed an early phase, up to peak velocity, during which the trajectory curved slightly rightward from the midline. This is illustrated by the average trajectory (± 1SD of the mean) for one representative subject in Fig. 3A. The acceleration phase was followed by a longer deceleration phase, during which the trajectory curved inward toward the target. Trials that required online corrections of trajectory showed significant deviations...
(Fcorrect) from the reach trajectory, represented by filled circles on average trajectories to each of the three targets. This deviation became more accentuated as corrections were required further toward the right target (45°). However, subjects were able to successfully correct their trajectory, attain the targets, and remain balanced.

The curvilinear velocity of the right finger marker enabled a very clear identification of the online correction of the pointing movements (Fcorrect, filled circles). Average velocity profiles for reach, corr75, corr60, and corr45 are shown in Fig. 3B for subject S2 (corresponding to the average trajectories, Fig. 3A). Typically, at Fcorrect, the finger reaccelerated and displayed a second peak in velocity before the arm decelerated to the target (movement end). The online correction of trajectory (Fcorrect) occurred at, on average, 178.1 ± 58.3 ms (corr75), 187.6 ± 58.4 ms (corr60), and 191 ± 48.1 ms (corr45) after L2 onset (values shown on Fig. 2B for subject S2 are absolute values after the onset of the movement). MTs and Fcorrect values for all corr conditions are given in Table 1. MTs increased between each of the four conditions from 815.5 ms (reach) to 1294.6 ms (corr45), and there was a significant main effect of condition between reach, corr75, corr60, and corr45 [F(3,772) = 492, P = 0.00]. However, there was no significant difference between the Fcorrect times to any of the three conditions that required online corrections (corr75, corr60, and corr45), indicating that, when the whole range of perturbations was considered, the online corrections were constant with respect to the onset of the initial reaching movement and L2 onset. Table 1 lists averages (± 1SD) of MT, times to L2 onset, and Fcorrect for all conditions.

Corrective forces and EMG activity accompanying online corrections of arm movements. Typical EMGs and GRFs produced for both a reach and corr45 are shown in Fig. 4. Four arm muscles are shown on the same time scale as six bilateral lower limb muscles and the corresponding Fx, Fy, and Fz forces. During a typical reach (Fig. 4A), the arm movement was initiated by the activation of the rADel, and also bilateral anticipatory TA activity and Sol inhibition in the legs. The effect of this postural muscle activity at the beginning of the movements was to produce a backward-directed Fy and a loading (Fz) of the right foot to induce a forward sway of the body to the target. Toward the end of the movement, the PDel and, to a lesser extent, the Tric and Bic muscles, became active. This activation of arm muscles to brake the arm movement at the target was accompanied by associated postural adjustments in the extensor muscles of the legs, represented in Fig. 4A by bilateral Sol muscle activity, starting ~500 ms after movement onset. Forces showed that during this phase of the movement both feet exerted force forward (Fy), and the right foot Fz was loaded. This pattern of EMG and force activity preceding and during the reach movements was the same as that described previously (Leonard et al. 2009).

Movements necessitating online corrections of finger trajectory evoked specific adjustments of both arm- and leg-muscle activity preceding Fcorrect. The adjustments in the postural muscles were recorded principally in the muscles of the left limb during the period between L2 onset and Fcorrect (shaded areas of EMG traces in gray bar, Fig. 4B) and produced distinct changes in Fx and Fz components of GRF under the left foot, compared with reach trials (see vertical arrows). The most significant adjustments in arm-muscle activity were evident in the rADel, rPDel, and rTric. In the postural muscles, significant activations between L2 onset and Fcorrect occurred in the lSol, lTA, and lPerl. During approximately the same period of reach trials, no such postural or arm muscle activity could be seen (see Fig. 4A, approximate area of Fcorrect). The postural adjustments from L2 to Fcorrect recorded during online corrections led to an increase in leftward-directed shear force (Fx), and a reloading of Fz also under the left foot. Analysis of the times to correction of arm and leg muscles corresponding to the online correction of movement and their relationship was therefore principally limited to this subset of left-side postural muscles (lSol, lTA, and lPerl) and the three right arm muscles (rADel, rPDel, and rTric).

Arm-muscle activity responsible for corrections of finger trajectory. Of the right arm muscles recorded, which were related to the online correction of finger trajectory. Figure 5 shows linear correlations calculated between the latency of onset of Fcorrect and EMGcorrect of each of the recorded arm muscles (rPDel, rTric, rADel, and rBic). Of these four muscles, it can be seen that three (rPDel, rTric, and rADel) showed highly significant correlations between the onset of the corrective muscle activity of the arm and the correction of curvilinear finger trajectory (Fcorrect). The corrective muscle activity in these three muscles preceded Fcorrect by average values of ~104.5 ms (rPDel), ~101.8 ms (rTric), and ~30.4 ms (rADel), as determined by the intercept of the regression lines. Therefore, on the basis of this, we sought to determine whether the left-leg postural activity that evoked changes in shear (Fx) and vertical force (Fz) that reoriented the body toward the new target during online corrections did or did not precede the corrective arm-muscle activity in each of the three right arm muscles that were correlated to Fcorrect (rPDel, rTric, and rADel).

Corrective postural adjustments in leg muscles lead arm-muscle corrections during online corrections of arm trajectory to unexpected shifts of target position. Most of the EMGcorrect times in the postural leg muscles identified as participating in the online corrections during corr trials (lSol, lPerl, and lTA) were shorter than those in the reaching arm muscles related to Fcorrect (rPDel, rADel, and rTric; Fig. 5). The average GRFcorrect values for Fx preceded Fcorrect by ~80–85 ms (corr45: −84.8 ms ± 40.6; corr60: −79.7 ms ± 85.5; corr75: −85.9 ms ± 69.6). Thus it was likely that the postural activity occurred before the changes in GRF and corrections of arm muscular activity (see Fig. 4) and kinematics (Fcorrect). ANOVA found a significant main effect of the subject factor (F = 26.23, P < 0.001) but nonsignificant main effects of target (F = 0.49, P = 0.61), phase (F = 1.61, P = 0.20), and postural muscle (F = 2.34, P = 0.10) factors. Post hoc multiple comparisons show that the EMGcorrect times in the postural muscles were significantly shorter than those in the reaching muscles for the corr60 target (Fig. 6A). However, this effect is significant for the lSol and lPerl muscles, but not for the lTA muscle (Fig. 6B). Furthermore, the differences between postural and reaching EMGcorrect times are even stronger for the corr45 target, in which the visual perturbation was the largest and the intertrial variability of the EMGcorrect times was the lowest (Fig. 6B). However, the variability of differences between the postural and reaching EMGcorrect times was large across subjects, with two of nine subjects showing shorter EMGcorrect times for the arm muscles (Fig. 6C). Lastly, the
differences between postural and reaching EMGcorrect times did not vary between the acceleration and deceleration phases of the reach (Fig. 6D).

Each of the EMGcorrect times in the postural muscles was linearly correlated with the EMGcorrect times in the reaching muscles. All EMGcorrect times were calculated with respect to the onset of the initial reach movement across the entire range of L2 light onset latencies (Fig. 1C). Figure 7 shows an example of nine linear regressions between postural and reaching muscles (data for all corr

trials were pooled) for a representative subject (S9). The y-intercepts of the regression lines across most subjects and most conditions were largely positive, which indicates that most of the corrective postural muscle activity started before the onset of the corrective reaching muscle activity (Table 2). The advance activation of the leg muscles with respect to arm muscles ranged from 16.9 ms (lPerl before rPDel) to 390.8 ms (lPerl before rTric). The slopes ($m$) of each of the regression lines ranged from 0.256 (lPerl vs. rTric) to 1.71 (lSol vs. rTric).

Fig. 4. Typical arm- and leg-muscle activity in relation to the 3D ground reaction forces produced for a reach movement (A) and an online correction movement to the target placed 45° to the right of midline, corr45 (B). In each, the muscles plotted in gray are those recorded in the right leg. The vertical dashed line indicates initial movement onset, and the full vertical black line represents movement end. In B, the shaded gray area indicates the area in which arm and postural adjustments occurred. r, right; l, left; ADel, anterior deltoid; PDel, posterior deltoid; Tric, triceps; Bic, biceps; Sol, soleus; TA, tibialis anterior; Perl, peroneus longus.
When data were pooled for each corr condition, the activation of the leg muscles consistently preceded those of the arm (positive y-intercept), and the leg muscles evolved earlier during the corrections than arm-muscle activation (slope analysis). To verify whether the predictive activation of leg vs. arm muscles held across target shifts of different amplitudes (eccentricity), we performed the same linear regression analysis for the pooled corr conditions for each subject. Table 2 provides a complete breakdown of these relationships. Of the 49 linear regressions performed (3 muscles for 9 subjects), all but nine showed significant $r^2$ values. Importantly however, only five revealed that arm-muscle activation preceded leg-muscle activation ($y$-intercept values $<0$ and $m$ values $>1$). For most comparisons, values of slope were $<1$ and as low as 0.107 (rADel vs. lPerl for S6), confirming, as with the pooled data, that the activation of postural muscles evolved more rapidly than arm muscles. Therefore, when all conditions and muscles were considered, our results supported a predictive control of postural activity in relation to arm-muscle activity across all target directions.

**DISCUSSION**

This study investigated how the two components of posture and voluntary movement interact when changes in ongoing reaching movements are produced while standing. We proposed two possibilities: 1) when faced with an unexpected change in visual target position, for which a reaching movement had been initiated, postural adjustments would occur after the adjustments seen in the arm muscles correcting the trajectory of the hand toward the target; 2) postural adjustments would occur before any change in arm-muscle correction and kinematic change of hand position, and posture would therefore be predictive with respect to the voluntary component of the action. Our results supported the latter of these two possibilities, i.e., modifications in leg-muscle activity preceded those of arm muscles when target position changed, regardless of how far a correction was required to be made with respect to the midline (eccentricity). We will begin by discussing some methodological differences between our paradigm and previous visuomotor-correction paradigms. Then we will highlight the functional role of the postural adjustments, situate our kinematic correction results within existing literature taken from “double-step” experiments carried out in seated subjects, and finish by placing our findings within a theoretical framework of predictive motor control.

**Methodological considerations.** In this study, we used a digital signal, derived from a switch detecting the onset of right finger movement, to trigger the change in visual target from the initial central one to one of the other three targets. Different delays resulted between when the finger began to move and when the first and second lights extinguished and illuminated, respectively. This paradigm was intended to provide us with a means of investigating how humans adapt posture and movement when programmed actions must be modified online after they have begun. Our paradigm cannot, however, be regarded as a classical double-step paradigm, one that involves a change in gaze saccade after an initial one has been initiated, a paradigm traditionally used to probe the properties of the
Fig. 6. Multiple comparisons of differences between EMGcorrect values of arm and leg muscles. A: average differences EMGcorrect differences per corr target. Values for all 3 arm and leg muscles have been pooled (averages for each corr target \( \pm 95\% \) confidence interval, CI). Positive differences indicate postural muscle corrections before arm corrections (see direction of arrow, top right). B: average differences \( (\pm 95\% \) CI) EMGcorrect (all arm muscles pooled) per leg muscle. Values for EMGcorrect measures were pooled for all arm muscles and expressed as differences with each leg muscle in turn (positive differences also indicate postural muscle corrections before arm muscles). C: EMGcorrect differences \( (\pm 95\% \) CI) per phase of reach, i.e., before peak velocity (acceleration) or after peak velocity (deceleration). D: average differences \( (\pm 95\% \) CI) EMGcorrect (all arm muscles pooled and all leg muscles pooled) per subject.

Fig. 7. Linear regressions calculated between postural and arm muscles participating in the online corrections to unexpected visual perturbations of target position. Each graph shows the postural muscle correction latencies (EMGcorrect) as the dependent variable (A: ISol, B: IPerl, C: ITA) with the regressions performed between the 3 arm-muscle correction latencies (rPDel, rADel, and rTric). Times (in ms) are expressed along each axis from the onset of the initial reach movement. Values are significant at \( *p < 0.05 \) and \( **p < 0.010 \).
Table 2. Complete breakdown of linear regression analysis for the pooled corr conditions for each subject

<table>
<thead>
<tr>
<th>Subject</th>
<th>Arm Muscle</th>
<th>Leg Muscle</th>
<th>lPerl</th>
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<td>rTric</td>
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Slope (m), y-intercept (Yi), r² values, P value for the strength of the regression fit (P), and P value for the intercept (P-int) for linear regressions conducted between the leg and arm muscles selected to characterize the online corrections to all targets for each subject. Values are significant at *P < 0.05 and †P < 0.01. n/a, no significant modulation of electromyogram between corr and reach conditions. *Multiple comparisons of intercepts between subject are significant when P-int is ≥ α of 0.0057 (Sidak-Bonferroni correction for 9 tests between muscles per subject). lPerl, left peroneus longus; rPDel, right posterior deltoid; rADel, right anterior deltoid; rTric, right triceps; ISol, left soleus; ITA, left tibialis anterior.

ouculomotor system (Becker et al. 1979; Westheimer 1954; Wheless et al. 1966). This is principally because our light-target changes (from L1 to L2) were not triggered using the onset of the initial gaze shift, as in other arm-movement studies (Goodale et al. 1986; Gritsenko et al. 2009; Prablanc and Martin 1992). Nevertheless, our paradigm can be likened to a number of arm-movement studies that have used a double-step paradigm triggered on the onset of movement, either a one-step (amplitude), double-step (Gielen et al. 1984; Megaw 1974), or a two-step (amplitude and direction) one (Day and Lyon 2000;...
Georgopoulos et al. 1981; Soechting and Lacquaniti 1983). For the purposes of this study, however, using delays from the onset of finger movement provided us with a window of time sufficiently long in which to investigate changes in arm movements (and the EMG activity related to them) and their associated postural adjustments. Given that our L2 latencies averaged between 365–394 ms, and Fcorrect latencies between 556–565 ms, we were sure that we had a window of time (± 200 ms) long enough to perform our analysis of both arm and postural muscles. Moreover, during this period (and beyond) our focus was on the relationship between arm- and postural muscle activity to produce the corrections.

Postural adjustments contribute to the execution of voluntary movement. An interesting aspect of our results, with regard to the postural corrections associated with the change in hand trajectory, was that the postural muscles showed activity that effectively increased the shear force under the limb contralateral to the reaching arm before Fcorrect. The vertical force under this limb also showed loading during the same period. This would suggest that the postural corrections acted to push out and down with the left foot, thus helping to rotate the body rightward toward the new target (see shaded area, Fig. 4B). With this in mind, the postural corrections can be described as being a component of the voluntary movement, rather than ensuring the maintenance of equilibrium. In other words, they accelerated the body in the direction of the target and did not stabilize posture or compensate for the impending arm correction. Had the latter been the primary objective of the postural adjustments produced between L2 and Fcorrect, significant activation of right limb muscles would have been recorded to counter the impending rightward rotation of the body when the arm was oriented toward the new target. In light of this, it would seem difficult to divide so-called posture and movement components of the motor act, as has often been the case during voluntary movement studies (Cordo and Nashner 1982; Hess 1954; Saltzman 1979). Rather, our results corroborate earlier work suggesting an integration of postural and focal commands at higher levels of the CNS (Aruin and Latash 1995; Commissaris et al. 2001; Stapley et al. 1999). Our results show that postural adjustments contribute to focal corrections of voluntary movement.

Effects of standing on the characteristics of online corrections of the arm. An interesting question that arises when examining the online correction of arm movements during stance is to what extent upright posture influences the time taken to initiate a correction once target position changes. It is out of the scope of this study to make definitive conclusions with regard to this question from an experimental perspective because 1) we did not directly compare online corrections in seated and standing conditions and 2) to obtain significant postural adjustments, the amplitudes of target shift used by us far exceeded those adopted in seated studies. Nevertheless, comparisons can be made between our study and previous ones in terms of the percentage of total MT taken to initiate a corrective response, even though the mode of target shift should also be accounted for (see above).

A detailed description of the early kinematic response and its relation to the amplitude of target displacement has recently been reported by Gritsenko et al. (2009). They used target shifts of 15-cm amplitudes in eight possible directions from a central one. Light changes were triggered during a period of saccadic suppression of the initial saccade to the first light and were estimated to occur on average 50 ms before the onset of initial hand movements, which were executed at preferred speeds (as in our study). For perturbed movements that were on average 403 ms in duration, Gritsenko et al. (2009) reported that corrections occurred at 35% (average 140 ms) of total MT. Longer ranges of 38–61% have, however, been reported by Prablanc and Martin (1992). Our correction values occurred at an average 47% of total MT across the three target positions. Thus it is likely that the mode of target shift trigger (gaze vs. first hand movement) plays a role in the onset of the online correction. Despite this, our results demonstrate that standing does not impede the early onset of the correction, which is to some extent comparable to online corrections produced when humans are seated.

Nevertheless, it is evident that both the total MTs and times to online correction (Fcorrect) reported by us were far slower (almost double) than those reported during seated movements (Goodale et al. 1986; Gritsenko et al. 2009; Komilis et al. 1993; Pélisson et al. 1986; Prablanc and Martin 1992; Sarlegna et al. 2003). Previous studies using the double-step paradigm to perturb arm movements during stance have reported correction times as low as 164–168 ms (Fautrelle et al. 2010). However, these authors used target changes that required corrections in the sagittal plane only and triggered target position change before or just after (50 ms) hand-movement onset. To our knowledge, the only other study of double-step perturbations during stance investigated differences in reaction time or MT with the likelihood of a double-step perturbation (Martin et al. 2000). Other recent studies have investigated online corrections of the foot during walking or a single step (Reynolds and Day 2005b; 2005a). The foot online correction onset has been reported to be between 239 and 402 ms after the foot off the ground for a step (Reynolds and Day 2005a), whereas during swing phase of locomotion the foot online correction onset has been reported to be more similar to that for the arm, 114–151 ms (Reynolds and Day 2005b). This suggests that the delayed onset of foot online correction during a step and, possibly, the delayed onsets of online correction observed in this study are attributable to the increased information processing of equilibrium constraints, which may be simplified during a predictive shift of CoM thought to occur during locomotion (Day et al. 1997). Furthermore, Hollands et al. (2004) showed that, during tasks involving body rotation when standing, the onset of saccadic eye movements to targets is also delayed, possibly by additional information processing of equilibrium constraints. Interestingly, however, taken together with studies of arm correction in seated subjects and foot correction of stepping subjects, our results provide evidence for a constancy of times to online corrections of arm movements regardless of postural configuration. Both Gritsenko et al. (2009) and Prablanc and Martin (1992) reported no significant differences in the time to correction across different target amplitudes, and our Fcorrect data also showed no significant differences across the three corr conditions.

It may be debated that the outward (rightward) curvature (rather than a straight trajectory toward the central target) seen for the reach trials was influenced by the expectation of a change in target position. It is outside the scope of the present study to definitively rule out whether expectation was or was not the cause of that curvature. However, it is interesting to note that trajectories
displayed for reaches to the same central target during a paradigm of multidirectional reaching (Leonard et al. 2009) also displayed a similar curvature (Leonard JA, Brown RH, Stapley PJ, unpublished observations). Moreover, in a seated online correction task, Day and Lyon (2000) also showed similar curvatures of straight reaches. However, further study is warranted to investigate the role of target-change expectation in trajectory formation, in both the seated and standing positions.

Implications for the control of posture and movement. Skilled voluntary movement, such as reaching with the arm, relies upon the prediction of the future state of the motor system because of the inherent delays associated with information processing. Studies of anticipatory adjustments of grip force with load during object manipulation (Flanagan and Wing 1997; Johansson and Cole 1992; Kawato 1999) have shown that the CNS “predicts” the dynamic effects of upcoming movements. Interestingly, such a grip force/load force predictive relationship is preserved and precedes arm-movement online corrections, which is strong evidence of the use of predictive motor mechanisms by the brain (Danion and Sarlegna 2007). Other studies of the initiation of stepping suggest that the CoM is controlled predictively by the CNS to maximize the efficiency of movement (Day and Lyon 2000; Day et al. 1997). These studies and others that have examined the execution or learning of seated arm movements and have proposed that forward, or predictive, internal models are employed to anticipate the consequences of actions based on efference copy of outgoing motor commands (Miall and Wolpert 1996). Efference copy is used to estimate the sensory feedback likely to result from the motor command, which results in accurate predictions of current motion (Davidson and Wolpert 2005; Desmurget and Grafon 2000).

The use of such predictive models for controlling equilibrium during arm movements has also been documented. The specific characteristics of anticipatory postural adjustments occurring before the onset of movement (APAs) depend on the prior knowledge of arm and body dynamics (Bouisset and Zattara 1981; 1987). However, APAs are predictive with respect to the initial onset of movement and are programmed with the CNS anticipating the consequences of the impending act. Our results have shown that, when the initial goal of a programmed reach movement unexpectedly changes after it has been initiated, the postural adjustments required to execute the online corrections consistently lead any changes in arm EMG or kinematics (Figs. 6 and 7). Moreover, our results also show that, even for small amplitude changes in target requiring smaller corrections of hand trajectory and posture, a predictive mode of postural control is still largely adopted (leg-muscle corrections led those of the arm consistently across corr conditions, Fig. 7). Therefore, we suggest that postural adjustments in this situation are largely predictive in nature and not based on feedback from the moving limb. Our results corroborate those described by Ruget et al. (2008), who showed that human subjects are able to modify components of weight shift online during the anticipatory period preceding the onset of stepping.

How do our findings fit with what is known about the neural control of arm movements and posture as well as forward models of reaching movements? It is known that there is a significant cortical involvement in predictive postural behavior. Mackinnon et al. (2007) demonstrated a facilitation of the muscles involved in APAs, whereas anticipatory adjustments of arm muscles were absent in patients with damage to their motor cortex (Viallet et al. 1992). Moreover, animal studies have suggested that the cortex contributes to motor planning of reaching during stance (Martin and Ghez 1985; Perfilliev 2005; Perfilliev 1998; Vicario et al. 1983) and the feedforward adjustments accompanying the reach (Yakovenko and Drew 2009). Thus the CNS may send a global command that specifies the planning and execution of movement and posture as one. Even though evidence has been given in support of global, hierarchical signal in which pathways for movement give off collaterals for posture (Gahery and Nieoullon 1978), the findings of a number of studies would suggest that parallel, independent commands exist for the postural adjustments preceding the movement, accompanying the movement, and indeed the movement itself (Horak et al. 1984; Schepens and Drew 2004; Schepens et al. 2008).

Although our results do not allow us to elucidate the origin and specific anatomical structure of the pathways involved in posture and movement, we can speculate about what happens, in terms of the production of postural adjustments in relation to arm-muscle activity, when the expected outcome of a reach does not materialize, such as when target location unexpectedly changes after movement onset. Figure 8 proposes a simplified model of how commands for movement and posture would fit with a forward model of arm movements. The model shows that the motor cortex sends a global planning command for movement and posture (Gritsenko et al. 2009). Efference
copy of commands for the execution of both the arm movement, APAs for initiating the reach, and aPAs accompanying the movement (right side of figure) ensure that discrepancies of the expected movement are detected (Desmurget and Grafton 2000). All the time the expected reach movement mirrors that actually being executed (above the gray horizontal bar), rapid feedback loops adjust and refine the movement in real time. When the target shifts, the expected movement no longer reflects that which must be produced, and a delay ensues. It is here that adjustments of accompanying postural commands (aPA adjustments) must occur before those of the arm (arm adjustments) in order that the dynamic constraints of the task be satisfied. Once posture is updated, predictively of the arm movement, the online correction can be made and the target attained.

Conclusions. We have shown that, when online corrections of ongoing arm movements are required, the CNS adopts a predictive mode of postural control, rather than a purely feedback-based mode. This was shown by the adjustments of postural muscle activity consistently leading those of the arm muscles responsible for correcting the trajectory of the arm to the target (Figs. 6 and 7). Had the CNS relied on information from a change in arm movement to update posture, adjustments of arm-muscle activity would have led those of the postural muscles. This was not seen even for the smallest amplitude target corrections (15° to the right), which could have been executed without significant threats to stability.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

REFERENCES


