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Postural adjustments for online corrections of arm movements in standing humans

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Running head: Postural adjustments during arm movement corrections
Abstract

The aim of this study was to investigate how humans correct ongoing arm movements while standing. Specifically, we sought to understand if the postural adjustments in the legs required for online corrections of arm movements are predictive or rely upon feedback from the moving limb. To answer this question we measured online correction 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 target locations 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 EMG 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 CNS does not depend upon 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 based on the required task demands.

Keywords: Human, Posture, Reaching, Visuomotor control, Online correction, Prediction
Introduction

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 towards 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 to 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 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 Latash 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 based upon 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

137 correction, the postural control system participates in the movement component of the

138 action. We hypothesized that because a change in the trajectory of the arm in response

139 to an unexpected shift in target position could potentially destabilize one’s balance, the

140 CNS predicts the postural adjustments necessary to execute smooth online corrections

141 of arm movements. In other words, when the target shift occurs, leg muscle activity is

142 updated and precedes the necessary changes in ground reaction force in advance of

143 changes in arm muscle activity or in trajectory toward the new target. We show that this

144 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) years 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 set-up

Subjects stood barefoot on two triaxial force plates (model FP4060, Bertec, Columbus OH) that recorded ground reaction forces (GRFs) and moments in the mediolateral (x), anteroposterior (y) and vertical (z) axes at 1000 Hz. Each subject stood with their feet positioned according to their preferred mediolateral stance width, which was based on the average distance between the 2 heels calculated immediately after 3 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 4 target lights arranged about a semi-circular 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 light-emitting diode (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 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 centre 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 1000 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 (lTA and rTA), soleus (lSol, rSol), peroneus longus (lPerl, rPerl), rectus femoris (lRF, rRF), biceps femoris (lBF, rBF) and tensor facia latae (lTFL, rTFL). Additionally, recordings of muscle activity of the reaching arm (right) included anterior and posterior deltoid (rADelt and rPDelt, respectively), long head of the triceps (rTric) and the long head of the bicep muscle (rBic). Bilateral kinematics were collected using a 6-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 EMG system was done using the Vicon controller.

Experimental procedures

Subjects began each trial standing with the head forwards 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 2 principal types of trials: regular reaches (‘reach’ trials) to the central (90°) target and trials that required corrections of arm trajectory
towards 3 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 (90º 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 secs). For some trials, the target light would shift from L1 to any one of the other 3 targets, 75º (‘corr75’), 60º (‘corr60’), or 45º (‘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 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 the online detection of a voltage drop that occurred when subjects released the chest switch. Figure 1B illustrates a representative timeline for a typical corr45 trial at 442 ms after movement onset. The first light (L1) illuminated approximately 250 ms after the auditory tone. The subject reacted to L1 onset by initiating a movement of the finger (‘movt onset’ in Fig. 1B). At this time, chest switch voltage dropped to zero. After 442 ms, L1 turned off and light 2 (L2) illuminated. In this example, the corr45 movement resulted in a lengthening of movement time (MT) of 322 ms with respect to the mean ‘reach’ movement.

FIGURE 1 ABOUT HERE

A variable delay existed between when the controlling Labview routine received the switch signal (shift from 5 to 0V indicating movement onset) and when it simultaneously extinguished L1 and illuminated L2. This was estimated to be on average 62.1 (± 35.1) ms. Thus, even though standard delays of 200 and 350 ms between movement onset and light (L2) change were used, actual delays of the light changes were calculated on a trial by trial basis, using the rising edge of the L2 5V signal (see centre grey line on
Fig. 1B). In order to standardize when L2 changes occurred, delays were represented as a percentage of mean ‘reach’ trial MTs. The distribution of L2 onsets as a percentage of ‘reach’ MT is shown in Fig. 1C. Even though light shifts occurred within the acceleration phase of ‘reach’ trials (open bars), a higher percentage occurred during the deceleration phase (grey bars).

Each experimental session began with subjects performing a series of acclimatization trials, consisting of 5 regular reaches to each target in turn. Following the acclimatization period, trials were organized in a random order. We required subjects to execute a total of 60 ‘reach’ trials to the central target, and at least 15 correction trials to each of the 3 other target positions. Fifteen trials were given during which no target illuminated (catch trials). In some subjects, more than the standard number of corr trials was collected to ensure that a large enough database was established. Catch trials were included in an attempt to prevent subjects from predicting and begin moving to the target before L1 illuminated. All catch trials were eliminated from subsequent analysis.

For experimental conditions to have adequate controls, at least three times the number of control trials compared to experimental trials must be collected (Zar 1999). For our analysis the ‘reach’ trials were to act as controls for detecting differences in the ‘corr’ trials. Thus, we aimed to collect at least 120 trials from each subject (1080 for all 9 subjects). A breakdown of the total number of trials collected and retained after trial selection procedures (see Data analysis) is given in Table 1. Subjects performed blocks of 40 trials between which they would take 5-minute rest periods to reduce fatigue. Each data collection period lasted 45-60 minutes.

Data analysis

Data analyses were performed offline using custom routines written in Matlab (The MathWorks, Natick, MA). Kinematic data and GRFs were low-pass filtered using a digital second-order Butterworth filter, with a 10Hz and 100Hz cutoff frequencies, respectively. Raw EMG signals were high-pass filtered at 35 Hz, demeaned, rectified, and low-pass filtered at 10 Hz, using a 2nd-order Butterworth filter. All trials were
visually inspected for stability of Fz during the background period (500 ms of quiet stance before the first target light illuminated). Any trials showing significant variation in Fz were eliminated from further analysis.

FIGURE 2 ABOUT HERE

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 based on each subject’s average trajectories. These included: fcorrect (the deviation of a ‘corr’ trajectory from the mean of all regular reaches), EMGcorrect (the times at which particular EMG traces during ‘corr’ trials significantly deviated from an average of ‘reach’ trials) and GRFcorrect (times at which forces in the 3 axes significantly deviated from the average force exerted for ‘reach’ trials). The online correction of focal movement (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 to 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
(fc_correct), occurring for this particular trial at 460 ms, 169 ms after the change in the
target light (L2). Similar methods were used to calculate EMG_correct and GRF_correct,
but corrections were detected using a threshold of mean ±2SDs, rather than 1SD for
fc_correct (kinematics). Mean ± 2SDs was found to be more robust for detecting
EMG_correct and GRF_correct than mean ± 1SD. An illustration of the calculation of these
variables is given in the relevant section of the 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 9 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 soleus muscle activity for the same 'corr45' trial as in Figs
2A 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 (fc_correct). EMG_correct was computed for a total of the 3 leg muscles in the left
leg as well as the 3 identified in the right arm (ISol, ITA, IPerl, rADel, rPDel and rTric)
and additionally rBic. A similar algorithm was used to detect when shear (Fx) and
vertical (Fz) force also increased above the force produced during a regular reach (Fig
2D).

Statistical analysis
In order to detect significant differences in total movement times and fcorrect values between ‘reach’ and ‘corr’ conditions a one-way analysis of variance (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 4 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 if 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 (ISol, IPerl, and ITA), 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 alpha (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 (Yi), 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 rightwards 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 inwards towards 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 3 targets. This deviation became more accentuated as corrections were required further towards the right target (45°). However, subjects were able to successfully correct their trajectory, attain the targets and remain balanced.

FIGURE 3 ABOUT HERE

The curvilinear velocity of the right finger (rFin) 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 ('mvt 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). Movement times and fcorrect values for all 'corr' conditions are given in Table 1. Movement times increased between each of the 4 conditions from 815.5 ms (reach) to 1294.6 ms (corr45) and there was a significant main effect of condition between reach, corr75, corr60, corr45 (F(3,772)=492, p=0.00). However, there was no significant difference between the fcorrect times to any of the 3 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, and times to L2 onset and fcorrect for all conditions.

TABLE 1 ABOUT HERE

Corrective forces and electromyographic 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 6 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. Towards the end of the movement, the posterior deltoid and, to a lesser extent the triceps and biceps 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 approximately 500 ms after movement onset. Forces showed that during this phase of the movement both feet exerted force forwards (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 light 2 onset (L2) onset and fcorrect (shaded areas of EMG traces in greyed bar, Fig. 4B) and produced distinct changes in Fx and Fz components of GRF under the left foot, as compared to ‘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, ‘approx. 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 3 right arm muscles (rADel, rPDel and rTric).

FIGURE 4 ABOUT HERE

Arm muscle activity responsible for corrections of finger trajectory

Of the right arm muscles recorded, we investigated 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 4 muscles, it can be seen that 3 (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 3 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, based upon this, we sought to determine if the left leg postural activity evoking changes in shear (Fx) and vertical force (Fz) that reoriented the body towards the new target during online corrections, preceded or not the corrective arm muscle activity in each of the 3 right arm muscles that were correlated to fcorrect (rPDel, rTric and rADel).

FIGURE 5 ABOUT HERE
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 approximately 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 not-significant 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 inter-trial 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 2 of 9 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 were 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 9 linear regressions between postural and reaching muscles (data for all 'corr' trials were pooled) for a representative
subject (S9). The Y intercepts (Yi) 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 (IPerl before rPDel) to 390.8 ms (IPerl before rTric). The slopes (m) of each of the regression lines ranged from 0.256 (IPerl vs. rPDel) to 1.71 (ISol vs. rTric).

**FIGURE 7 and TABLE 2 ABOUT HERE**

When data was 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). In order to verify if 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 x 3 muscles for 9 subjects), all but 9 showed significant r² values. Importantly however, only 5 revealed that arm muscle activation preceded leg muscle activation (Yi values < 0 and m values >1). For most comparisons, values of slope were <1, and as low as 0.107 (rADel vs. IPerl 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 towards 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 corrections paradigms. Then we will highlight the functional role of the online 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 light target from the initial central one to one of the other 3 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 been used to probe the properties of the oculomotor
system (Becker et al. 1979; Westheimer 1954; Wheeless 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 1-step (amplitude), double-step (Gielen et al. 1984; Megaw 1974), or a 2-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 prior to 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 rightwards towards 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 only 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
towards 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 does upright posture influence 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, as 1) we did not directly compare online corrections in seated and standing conditions, and 2) in order 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 8 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, on average 47% of total MT across the 3 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 (tcorrect) 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 targets 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), while 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 be delayed onset of foot online correction during a step and, possibly, the delayed onsets of online correction observed in this study are due 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 correct data also showed no significant differences across the 3 ‘corr’ conditions.

It may be debated that the outward (rightward) curvature (rather than a straight trajectory towards 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 if expectation was the cause or not, 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 (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 maximise 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, 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 Grafton 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. 6,7). 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 upon 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 behaviour. Mackinnon et al. 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; Perfiliev 2005; Perfiliev 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).

While 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 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) ensures 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 grey 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. 6,7). Had the CNS relied upon 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.
Acknowledgements

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Figure legends

Figure 1. Experimental set-up and data collection schema. A. Subjects stood 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 15º increments to the right of centre. B. Explanation of the changes in voltage related to the sequence of light changes. When the signal rose to 5V 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. C. A 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.

Figure 2. Determination of the online correction of finger trajectory (fcorrect). A. Plan view (x,y) of rFin average ‘reach’ trajectories +/- 1SD (dashed line with shaded grey area) in relation to one ‘corr45’ trial (full black trajectory). Filled black circle is the onset of light 2 (L2 onset) and the open circle is the time at which the corr45 x,y trajectory exceeded the average ‘reach’ trajectory plus 1SD for subject S6. B. Average (dashed line) plus 1SD of curvilinear rFin velocity for a reach movement and one ‘corr45’ trial (full black line). Black vertical line is light 2 (L2) onset, grey vertical line is the time of online correction (fcorrect). Each corr condition has been displaced rightwards and downwards for clarity, but the starting position was the same for each. C, D: Explanation of how the correction of the EMG activity and GRFcorrect associated with online corrections were determined. C. Calculation of EMGcorrect. The muscle shown is the left soleus muscle, but the same procedure was used with all other muscles studied (see Methods). The dashed trace and grey traces represent respectively, the mean ‘reach’ soleus muscle activity ± 2SDs above and below the mean. The dark full trace represents the soleus muscle activity produced during an online correction movement, in this example a corr45 movement. The open circle indicates the time at which the corr45 soleus muscle activity exceeded the mean+2SD ‘reach’ activity level. This time was taken as the EMGcorrect time (for more detailed explanation, see Methods and Results). Abbreviations as previous figures, except Movt end=movement time. D. Calculation of GRFcorrect. Method for determining GRFcorrect is shown for the left shear force (Fx). The dashed trace and grey traces represent respectively the mean ‘reach’ Fx and ± 2SDs above and below the mean. The dark full trace represents the Fx exerted during an online correction movement (in this example corr45). The open circle indicates the time at which the exerted force was significantly different from the mean forces exerted in a ‘reach’ trial.

Figure 3. Reaching movement kinematic characteristics and profiles of curvilinear velocity. Shown are averages plus 1SD for all trials for subject 2 in each of the 4 conditions studied. A. Plan view (x,y) kinematics of rFin trajectory for ‘reach’ trials and each of the correction conditions. B. rFin curvilinear velocity also for all 4 conditions. fcorrect=kinematic correction of finger trajectory, mvt end=end of the focal movement (reach and corrected movements).
Figure 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 grey are those recorded in the right leg. The vertical dashed line indicates initial movement onset (‘Mvt Onset’) and the full vertical black line, movement end (‘Mvt End’). In B., the shaded grey area indicates the area in which arm and postural adjustments occurred. For muscle abbreviations, see Methods. L2 ons et=light 2 onset, fcorrect=time of kinematic correction of the rFin marker. Fx=mediolateral force, Fy=anteriorposterior force and Fz=vertical force.

Figure 5. Linear regressions calculated between the four arm muscles recorded in the right arm and the fcorrect latencies calculated using the curvilinear kinematics of the rFin marker. A. right posterior deltoid, B. right triceps, C. right anterior deltoid and D. right biceps. Yi=the value of the Y intercept when X is zero.

Figure 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 +/- 95% confidence interval, CI). Positive differences indicate postural muscle corrections before arm corrections (see direction of arrow, top right of figure). B. Average differences (+/- 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 (+/- 95% CI) per phase of reach, i.e. before peak velocity (Acceleration) or after peak velocity (Deceleration). Filled circles show mean EMGcorrect differences for all targets, while open circles show only data for corr45; shaded area represents 95% confidence interval. D. Average differences (+/- 95% CI) EMGcorrect (all arm muscles pooled and all leg muscles pooled) per subject.

Figure 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. lSol, B. lPerl and C. lTA) 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.

Figure 8. Suggested control schema illustrating the interaction of movement and posture during online corrections of arm movements. APA = anticipatory postural adjustment, aPA = associated postural adjustment (see text for explanation).

Table 1. Average movement times, light 2 (L2) onset and time to correction of finger trajectory (the latter 2 for the applicable conditions) for all experimental conditions tested. Latencies are calculated relative to the onset of the initial finger (reach) movement. N = Number of trials.
Table 2. Slope (m), Y intercept (Yi) and r2 values for linear regressions conducted between the leg and arm muscles selected to characterize the online corrections to the all targets pooled (corr75, corr60 and corr45) for each of the 9 subjects.
Table 1. 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.

<table>
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<th>Condition</th>
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<th>N retained</th>
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<th>L2 onset (ms)</th>
<th>fcorrect (ms)</th>
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<td>360.1 (127.4)</td>
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<td>340.1 (91.4)</td>
<td>566.5 (90.1)</td>
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Table 2. 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.

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<tr>
<th>Subject</th>
<th>Yi</th>
<th>m</th>
<th>r²</th>
<th>p</th>
<th>p-int</th>
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* and ** = significant at p < 0.05 and < 0.01 respectively. n/a = no significant modulation of EMG between corr and reach conditions. + = Multiple comparisons of intercepts between subject are significant when p-int is ≥ alpha of 0.0057 (Sidak-Bonferroni correction for 9 tests between muscles per subject).
References


Fautrelle L, Prablanc C, Berret B, Ballay Y, and Bonnetblanc F. Pointing to double-step visual stimuli from a standing position: very short latency (express) corrections are observed in upper and lower limbs and may not require cortical involvement. In: NSC2010, p. 697-705.


Péliston D, Prablanc C, Goodale MA, and Jeannerod M. Visual control of reaching movements without vision of the limb. II. Evidence of fast unconscious processes
correcting the trajectory of the hand to the final position of a double-step stimulus.

Leonard et al.  Postural adjustments during arm movement corrections


Leonard et al.  

Postural adjustments during arm movement corrections


A. Experimental set-up, plan view

B. Perturbed reach 90° to 45°, delay 442 ms

C. L2 onset as percent time to mean 'reach' peak velocity
A. Plan view of finger trajectory

B. Tangential finger velocity

C. Left soleus EMG - reach and corr45

D. Left shear force (Fx) - reach and corr45
A. *rFin*, average trajectories (plan view)

B. *rFin*, tangential velocity (all conditions)
A. Reach only

approx. area of correct (corr trial)

B. Online correction - corr45

Leonard et al. Figure 4
Leonard et al. Figure 5

A. \( rP\text{Del} \) vs. \( f\text{correct} \)

\[ r^2 = 0.45 \]
\[ p = 0.00 \]
\[ Y_i = -104.5\text{ms} \]

B. \( r\text{Tric} \) vs. \( f\text{correct} \)

\[ r^2 = 0.50 \]
\[ p = 0.00 \]
\[ Y_i = -101.8\text{ms} \]

C. \( r\text{ADel} \) vs. \( f\text{correct} \)

\[ r^2 = 0.88 \]
\[ p = 0.00 \]
\[ Y_i = -30.4\text{ms} \]

D. \( r\text{Bic} \) vs. \( f\text{correct} \)

\[ r^2 = 0.03 \]
\[ p = 0.24 \]
\[ Y_i = 450.3\text{ms} \]
A. Difference: EMGcorrect, all arm vs all leg muscles

B. Difference: EMGcorrect (all arm) vs each leg muscle

C. Difference: EMGcorrect, all arm vs all leg, phase

D. Difference: EMGcorrect, all arm vs all leg, each subject
Leonard et al. Figure 7

A. ISol vs. Arm muscles

\[
\begin{align*}
\text{rPDel:} & \quad r^2=0.359^* \quad p=0.011 \\
\text{rAdel:} & \quad r^2=0.891^{**} \quad p=0.000 \\
\text{rTric:} & \quad r^2=0.724^{**} \quad p=0.000
\end{align*}
\]

- \( Y_i=154.7 \)
- \( m=0.621 \)

B. IPerl vs. Arm muscles

\[
\begin{align*}
\text{rPDel:} & \quad r^2=0.957^{**} \quad p=0.000 \\
\text{rAdel:} & \quad r^2=0.808^{**} \quad p=0.000
\end{align*}
\]

- \( Y_i=96.3 \)
- \( m=0.862 \)

C. ITA vs. Arm muscles

\[
\begin{align*}
\text{rPDel:} & \quad r^2=0.539^{**} \quad p=0.000 \\
\text{rAdel:} & \quad r^2=0.460^{**} \quad p=0.000
\end{align*}
\]

- \( Y_i=346.3 \)
- \( m=0.148 \)

Leonard et al. Figure 7
global planning
movement & posture

APA Movt aPA

Forward model
(efference copy)

APA Movt aPA

rapid feedback loops

target shift

delay

aPA adjustments

Arm adjustments

kinematic correction and movement end
(target attainment)