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Accuracy of pointing movements relies upon a specific tuning between anticipatory postural adjustments and prime mover activation

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Abstract

Aim: Equilibrium-perturbing forces associated with a voluntary upper-limb movement can be strong enough to displace the whole-body centre of mass. In this condition, anticipatory postural adjustments (APAs), developing in muscles other than the prime mover, are essential in maintaining the whole-body balance. Here, we test the hypothesis that APAs preceding an upper-limb target-reaching movement could play a role also in controlling the movement accuracy.

Methods: Standing subjects (10) were asked to flex the right shoulder and touch with the index fingertip the centre of a target positioned in front of them. The reaching task was also performed while wearing and after doffing prismatic lenses (shifting the eye field rightward). EMGs from different upper- and lower-limb muscles and the mechanical actions to the ground were recorded.

Results: (i) Before wearing prisms, subjects were very accurate in hitting the target, and the pointing movements were accompanied by APAs in quadriceps (Q) and tibialis anterior (TA) of both sides, and in right hamstrings (H) and soleus (SOL). (ii) After donning prisms, rightward pointing errors occurred, associated with a significant APA increase in right Q and TA, but without changes in the recruitment of right anterior deltoid (prime mover) and biceps brachii. (iii) These pointing errors were progressively compensated in about 10 trials, indicating a sensorimotor adaptation, and APAs returned to values recorded before wearing prisms. (iv) After doffing prisms, pointing errors occurred in the opposite direction but changes in APAs did not reach significance.

Conclusion: We propose that, besides preserving the whole-body balance, APAs are also tailored to obtain an accurate voluntary movement.

Keywords anticipatory postural adjustment, human, pointing, prismatic lenses, sensorimotor adaptation, voluntary movement.

Anticipatory postural adjustments (APAs) are known to be unconscious muscular activities, preceding any voluntary movement, aiming to prevent the *segmental* and *whole-body* equilibrium disturbances caused by the movement itself (see Massion 1992).

In a multilink structure as the human body, movement may perturb the equilibrium because (i) the contraction of the prime mover exerts forces on both the

distal and the proximal tendon (typically, the former transmits the intended movement, while the latter acts on the posture of more proximal segments; Zatsiorsky 2002), (ii) the forces acting on one segment not only arise from the pertinent muscles but also include the 'interaction forces' deriving from movement of other distal segments (Hollerbach & Flash 1982) and (iii) by changing the body geometry, movement

displaces the projection of the whole-body centre of mass on the ground (CoM; e.g. Bouisset & Zattara 1987; see also the next paragraph).

The importance of proper *whole-body stabilization* is immediately apparent when considering standing subjects performing voluntary movements that involve large masses. In such motor acts, the equilibrium-perturbing forces would cause a whole-body imbalance, by displacing the trunk and the whole-body CoM (Bouisset & Zattara 1987, Bouisset & Do 2008, see also Hess 1943). On the other hand, in those motor tasks in which the whole-body balance is not threatened, the importance of an accurate *segmental stabilization* might look less obvious. In our previous papers (Caronni & Cavallari 2009a,b), it has been reported that when the index finger is flexed, an APA chain develops in several upper-limb muscles to stabilize the *segmental* equilibrium of the arm. According to a mechanical simulation showing the consequences of a poor APA control on the movement trajectory (Caronni & Cavallari 2009a), we proposed that APAs could be crucial to guarantee movement accuracy by an appropriate stabilization of the proximal segments. Further studies showed that a short-term immobilization of the wrist and fingers leads to a APAs impairment in proximal arm muscles, resulting into an impaired fixation of the elbow joint (Bolzoni *et al.* 2012). Moreover, a growing body of evidence clarifies the contribution of the proximal segments on both movement trajectory and speed of distal segments (e.g. Kaminski *et al.* 1995, Archambault *et al.* 1999, Pigeon *et al.* 2000, Pozzo *et al.* 2002, Bortolami *et al.* 2008, Kim *et al.* 2009).

At our knowledge, information about the linkage between APAs and accuracy of voluntary movements may only be figured out from studies analysing the pointing to targets of different size (e.g. Bonnetblanc *et al.* 2004, Nana-Ibrahim *et al.* 2008, Bertucco & Cesari 2010). Indeed, these studies show that Fitts' law¹ (1954) governs both the prime movement speed and the associated APAs. This observation actually provides an indirect suggestion that APAs are involved in attaining the movement precision necessary to accomplish the imposed accuracy constraint. However, APAs are known to be scaled according to movement speed (Lee *et al.* 1987, Shiratori & Aruin 2007); thus, the linkage between target and APAs size could then be just an epiphenomenon of the former relationship.

Aim of the present study is to seek a direct proof of the relationship between the APAs amplitude and the

endpoint of a target-reaching movement. A reaching task was thus performed with the upper limb, before and after donning prismatic lenses, which are known to shift the binocular eye field and cause the subject to miss the target (Redding *et al.* 2005). After some movement repetitions, subjects adapted to the new condition, compensating for the prisms effect and hitting the target again. As a novelty, we will show that the prism-induced pointing error specifically underlies changes in APAs amplitude with no changes in the prime mover activation, thus sustaining the hypothesis that a successful and accurate pointing movement relies upon a specific tuning between APAs and prime mover activation (see Caronni & Cavallari 2009a). Moreover, we also ruled out any bias caused by changes in movement velocity because prismatic lenses do not affect the target size, thus leaving the movement speed unchanged.

Materials and methods

Ten right-handed subjects (four women) were engaged (mean age \pm SD: 26.9 \pm 3.28 years). They reported no history of orthopaedic or neurological disorder; none of them reported a reduction in the visual acuity. Each volunteer gave his/her informed consent to the experiment. This study is conform with Good Publishing Practice in Physiology (Persson & Henriksson 2011).

Motor task

Subjects stood barefoot on a force platform, with the feet normally apart in a natural upright position, and both upper limbs lying along the body. After an acoustic *go signal*, delivered every 5 s so as to mark the overall temporal cadence, subjects had to perform a self-paced index-finger pointing movement, using right shoulder flexion, which was as fast and accurate as possible. Subjects never anticipated the *go signal*. A variation of the 'Belen'kii *et al.* (1967) has been adopted: subjects were asked to point-and-touch a target placed in front of them, watch the final position they attained for no more than 1 s, return to the initial position at their preferred speed and finally relax before starting a new movement. The task was also performed while wearing and after doffing prismatic goggles.

By monitoring the EMG traces during the experiment, it was apparent that they returned to their baseline within 3 s from the movement onset. The target consisted in two lines drawn on a Plexiglas screen, 1 mm thick \times 2 cm long, one vertical and one horizontal, so that its centre was clearly visible. The anterior-posterior, vertical and lateral position of the target was regulated for each subject: the target was

¹Movement duration increases with movement amplitude and decrease when the target size increases, i.e. when the accuracy constraint loosens.

positioned at the shoulder height on the subject's midline, one upper-limb length from the subject's shoulder. Care was taken to align the subject's sagittal plane to the platform midline; feet position was then marked on the platform and checked throughout the experiment. Before starting each exercise, care was taken that the CoP position (calculated online by the SMART system) fell on the platform midline.

Experimental design

A couple of prismatic lenses (Fresnel 3M[®] Press-On, St. Paul, MN, USA, 20 dioptres) were mounted on conventional safety goggles to produce a rightward shift of the binocular eye field of about 11°. This corresponds to a 12-cm linear shift of the target, placed at 60 cm (about one arm length) in front of the subject. While wearing prisms, subjects realized the shifting in the binocular eye field only when they performed the first pointing movement. Indeed, only when the finger reached the Plexiglas screen, they became aware they had missed the target, also because the fingertip underwent the same visual position bias as the target itself. Subjects were asked to close their eyes when donning and doffing goggles and not to move their arms before the new recording session started.

Each experiment was arranged into three sessions of repeated target reaching: before donning (BEFORE), while wearing (DURING) and after doffing (AFTER) goggles with prismatic lenses. In each session, 25 trials of the target-reaching task were performed. Between two subsequent sessions, subjects did rest for 5–10 min. Subjects donned the goggles just before starting the DURING session and kept them on throughout the following rest period. Goggles were removed only right before starting the AFTER session. No subject reported fatigue. They were allowed to familiarize with the motor task by practicing, without goggles, at least 15 target-reaching movements before the first experimental session.

Recordings

In each experiment, electromyographic (EMG) activity, right upper-limb movement, target position and the forces exerted onto the ground were synchronously recorded.

Electromyographics were recorded from two muscles of the right upper limb (anterior deltoid, AD; biceps brachii, BB) and four muscles of both the right and left lower limbs (quadriceps, Q; hamstring, H; tibialis anterior, TA; soleus, SOL). For each muscle, conventional disposable bipolar electrodes (1 cm diameter) were glued 25 mm apart on the skin covering the muscle belly. Skin was cleaned with abrasive

cotton discs and alcohol. The EMG system was a set of customized BTS pre-amplified electrodes (gain $\times 10$, pass band 30–500 Hz), followed by GRASS IP511 amplifiers (total gain 1–10k).

A 3D motion analysis system (SMART-D, BTS[®], Garbagnate Milanese, Italy; six infrared cameras) was used to record both the right upper-limb movement and the target position. Reflecting spherical markers (1.5 cm \varnothing) were taped to the dorsal aspect of the metacarpophalangeal joint of the second finger, radius distal end, olecranon and acromion. Reflective tape was applied directly to the distal phalanx of the index finger so as to resemble a hemispherical marker. This avoided placing a marker directly on the fingertip, which could interfere with the pointing movement. This method allowed the kinematics acquisition device to track the centre of the fingertip as all the other markers, with the same accuracy (± 0.5 mm). A positive deflection on the marker trace indicates a leftward (x , right–left axis), forward (y , posterior–anterior axis) or downward (z , up–down axis) displacement. To identify target position, two hemispherical markers were glued on the Plexiglas screen, equidistantly above and below the target cross. Thus, target position was recognized as the xyz coordinates of the 'virtual' marker placed midway on the line connecting the two.

A dynamometric platform (AMTI[®] OR6-7, Watertown, MA, USA) was used to record forces (F) and moments (M) discharged to the ground with reference to the above axes.

Data acquisition was accomplished by the SMART-D workstation. EMG and platform signals were A/D converted at a sampling frequency of 1120 Hz, while cameras sampling rate was 70 Hz. EMG, kinematics and force signals were digitalized with 16-bit resolution and stored on a PC for offline measurements.

Data analysis

As stated above, subjects were asked to start the target-reaching movement with a right shoulder flexion. Thus, AD muscle will be referred to as the pointing *prime mover*.

Movement onset (0 ms) was identified as the time when the y position trace of the elbow marker crossed a threshold (set at the mean elbow position in the 500 ms preceding the go signal $+2$ SDs) for at least 100 consecutive ms. *Movement end* was instead identified, by the same threshold method, from the y coordinate of the target 'virtual' marker, signalling the impact of the index finger on the Plexiglas screen. Systematically, timing measurements were visually checked and independently confirmed by two of the authors (AC and FB). The pointing movement was assumed to terminate when the finger touched the Plexiglas screen.

We define *pointing error* the distance between the index-fingertip position on the screen and the target (see, for example, Luauté *et al.* 2009, Chapman *et al.* 2010, Ronchi *et al.* 2011). For each trial, the horizontal (x) and vertical (z) components of the pointing error were measured. Movement onset was chosen as reference point to leave enough time for APAs to fully develop. Moreover, this reference allowed us to quantify the amplitude and latency of the premovement activation of AD and BB. In addition, this analysis allowed quantifying APAs amplitude in their mechanical actions on the ground, which develop together with or even after the prime mover activation.

Platform recording analysis was conducted on the three components of the forces exerted to the ground (F_x , F_y and F_z), on the displacement of the centre of pressure ($CoPx$, $CoPy$) and on the torque exerted about the z axis passing through the CoP (Tz). The position of the CoP and the value of Tz were derived from the recorded platform signals; Tz was calculated according to the following formula:

$$Tz = Mz + CoPy * Fx - CoPx * Fy \quad (1)$$

with Mz : moment about the vertical axis passing through the platform centre; $CoPx$ and $CoPy$: right-left and posterior-anterior CoP coordinates in the platform plane respectively.

CoP coordinates were calculated as $CoPx = -My/Fz$ and $CoPy = Mx/Fz$; being Mx and My the moments about the x and y axes passing through the centre of the platform surface. For each trial, both EMGs and platform recordings were re-aligned on movement onset (0 ms). EMGs were rectified and then smoothed by a running average (time window 35 ms).

In each session, analysis of EMG and platform recordings was performed on trials 1–5 (1st BLOCK), in which pointing error resulted to be significantly different among sessions, and trials 11–15 (2nd BLOCK), in which the pointing error was similar in the three sessions.

The EMG and the platform traces within each block were then averaged to obtain a *block mean trace* (BMT). For each muscle, BMTs were normalized on the mean amplitude of the BMT recorded in the 1st BLOCK of the BEFORE session, thus allowing comparison between EMGs recorded from different subjects. Background activity (i.e. the mean amplitude of the BMT from –1000 to –500 ms) was finally subtracted from the EMG and platform BMTs. Voluntary EMG onset in arm muscles and APA onset in postural muscles, as well as in force platform traces, were identified as the time when the BMT crossed ± 2 SDs of the mean background activity level and remained above that threshold for at least 50 ms. All onset timings were visually checked and independently

confirmed by two of the authors (AC and FB). APAs amplitude, or amplitude of premovement activation in AD and BB, was quantified as the mean amplitude of the BMT in a time window arbitrarily set from –25 to 0 ms (see also Caronni & Cavallari 2009a). It is also worth to note that in the great majority of recordings (except for left Q in BEFORE), APAs and prime mover activation level at the 0 ms corresponded to the highest premovement amplitude, and that APAs onset in EMG and platform recordings were, on average, much earlier than –25 ms. Data were analysed by a custom-made software.

Statistical analysis

A two-way repeated-measures ANOVA, with prisms (BEFORE, DURING and AFTER) and trials (1–25) as factors, was applied to horizontal and vertical pointing errors. A similar test *prisms* (BEFORE, DURING and AFTER) \times *blocks* (1st and 2nd BLOCK) was also applied to (i) the amplitude and timing of APAs, or of premovement activation in AD and BB and (ii) the mean movement duration of trials 1–5 and 11–15. When ANOVA resulted in a significant main effect and/or interaction, Tukey's HSD test was used for post hoc comparisons. Significance level was set at 0.05.

Results

Prismatic lenses induce pointing errors in a target-reaching movement

Before wearing prismatic lenses, subjects were very accurate in reaching the target: in each of them, the index finger final position scattered within a circle of 15 mm radius from the target centre (white dots in Fig. 1a,b). When the same movement was performed while wearing goggles (Fig. 1b, black dots), the index fingertip hit the Plexiglas screen to the right of the target. However, within ten trials (*prisms adaptation*, see Fig. 1c,d), pointing fell again within the 15-mm circle. Pointing after goggles removal (Fig. 1b, grey dots) caused the subject to hit to the left of the target and, also in this case, the error faded away (*recovery from prisms after-effect*) after a few movement repetitions.

The mean time course of the horizontal and vertical components of the pointing error (H and V respectively) for each of the three experimental conditions (BEFORE, DURING and AFTER wearing prisms) is detailed in Figure 1c,d. When subjects performed the motor task before wearing prismatic lenses, neither the mean H-error (2.0 ± 1.6 mm, mean \pm SEM) nor the mean V-error (0.9 ± 1.0 mm) was different from 0 (one-sample t -test, $P > 0.25$ for both variables).

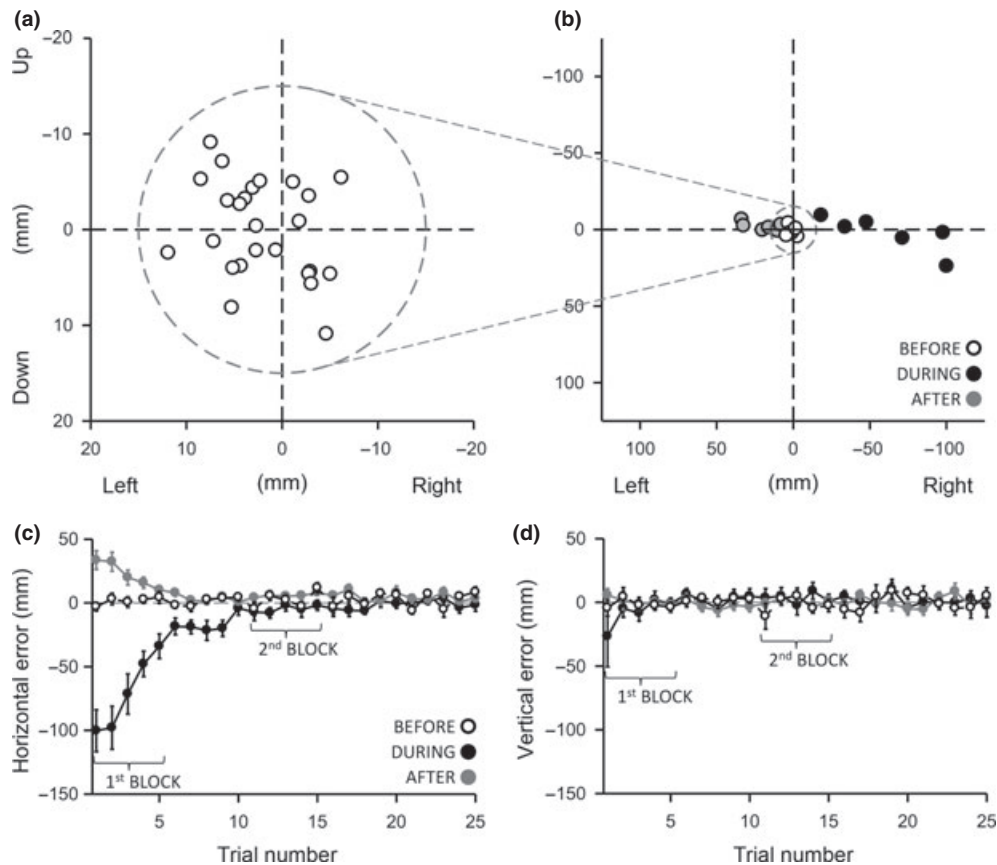


Figure 1 (a) Final position of the index finger (average of all subjects) in each of the 25 pointing movement trials performed BEFORE wearing goggles with prismatic lenses (white dots). All points fell within a circle of 15 mm radius from the target centre (grey dashed circle). (b) Final position of the index finger (average of all subjects) in the first six pointing trials, performed in the three successive experimental sessions (BEFORE, DURING and AFTER wearing prismatic goggles). While wearing prisms (DURING, black dots), the index fingertip missed the target and pointing terminated on its right. After doffing prisms (AFTER, grey dots), the error reversed and pointing terminated on the target left, signalling an after-effect. (c, d) Average horizontal and vertical pointing errors (\pm intersubject SEM) in each movement trial for the three experimental sessions (same labels and symbols as in b). The rightward horizontal pointing error observed in the DURING session recovered, in about 10 trials, to values comparable to those of the BEFORE session. The leftward error in the AFTER session had a lower amplitude than that in the DURING one and recovered more quickly. A *prisms* \times *trial* ANOVA found that the horizontal pointing error was significantly different among sessions only in trials 1–5. The same ANOVA design, instead, did not find any significant change in vertical pointing error. Thus, electromyographic (EMG) and platform data from trials 1–5 (1st BLOCK) were matched to those of other five trials (11–15, 2nd BLOCK), in which pointing error was comparable among sessions, that is, both adaptation to prisms and recovery from after-effect were completed.

When subjects performed the first target-reaching trial while wearing the prismatic lenses, a large rightward H-error occurred (-100.3 ± 16.4 mm; $P < 0.001$), while V-error was not different from 0 (-26.7 ± 23.9 mm; $P > 0.25$). Also after doffing goggles, a considerable H-error occurred (33.5 ± 7.3 mm; $P < 0.001$), but now all subjects ended the pointing to the left of the target. Conversely, V-error (5.7 ± 5.1 mm; $P > 0.25$) was again not different from 0.

Two-way ANOVA on H-error showed a significant effect of both *prisms* ($F_{2,18} = 26.19$, $P < 0.001$) and *trials* ($F_{24,216} = 8.18$; $P < 0.001$), as well as a significant

interaction ($F_{48,432} = 14.92$, $P < 0.001$). Post hoc comparisons revealed that *trials* (i.e. time) had no effect in the BEFORE session, while there was a significant difference between BEFORE and DURING sessions for trials 1–5 (P always < 0.001) and, only for trial 1, between BEFORE and AFTER ($P < 0.002$). Note also that the adaptation process (trial 1–5 with prisms) is considerably longer as compared to the after-effect recovery (trial 1, after prisms). As a two-way ANOVA showed no significant modification on the V-error, the following analysis will focus on the H-error only.

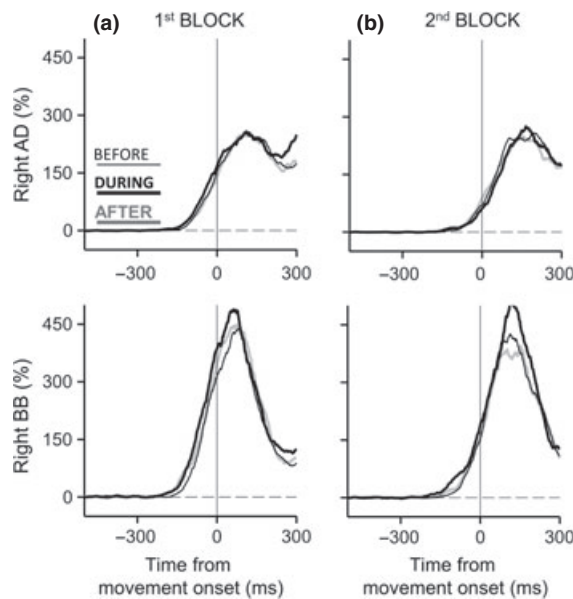


Figure 2 Rectified and smoothed (see Methods) electromyographic (EMG) recordings from the prime mover anterior deltoid (AD) and from the biceps brachii (BB) muscles. Averaged traces of one representative subjects, obtained in trials 1–5 (a – 1st BLOCK) and in trials 11–15 (b – 2nd BLOCK) of the three experimental sessions: BEFORE (thin black line), DURING (thick black line) and AFTER (thick grey line) wearing prismatic goggles. Note that in each BLOCK, the premovement (before 0 ms) EMG activity was nearly indistinguishable in all sessions.

Prismatic lenses modify APAs of a target-reaching movement

As shown above, pointing errors of trials 1–5 were significantly different among sessions, thus a comparison of EMG and platform data from these trials (1st BLOCK – BEFORE, DURING and AFTER sessions) was carried out. Similar *between-sessions* comparisons were also drawn in a second BLOCK of five trials (11–15, 2nd BLOCK), in which adaptation to prisms and after-effect recovery were apparently completed, and pointing errors were comparable among sessions.

EMG recordings. The EMG activity recorded in the prime mover AD and in BB muscle when the right shoulder is flexed and the index finger points to the target is shown in Figure 2 for a representative subject. Note that in both muscles, premovement activity in the 1st BLOCK (before 0 ms) was nearly indistinguishable in all sessions, thus pointing errors were not due to changes in the prime mover activation.

For what concerns lower-limb muscles (Fig. 3), when the reaching movement was performed without prisms, so that pointing was accurate, excitatory or

inhibitory APAs developed in all muscles, except left H and left SOL (1st BLOCK, BEFORE). The latter two will be then ruled out from analysis, because EMG amplitude at movement onset was not significantly different from the background activity (paired *t*-test, $P > 0.5$ for both muscles). When reaching was performed immediately after donning prisms and the subject's index fingertip hits the Plexiglas screen to the right of the target (1st BLOCK, DURING), APAs in Q and TA of both sides increased in amplitude (compare thick to thin black lines). When prisms were removed and subjects missed the target to the left (1st BLOCK, AFTER), APAs in Q and TA of both sides decreased to values similar to those observed in the BEFORE session. It is worth noting that the leftward deviation induced by the after-effect recovered much more quickly than the rightward deviation. To group together the same number of trials in each BLOCK, the 1st BLOCKS of the AFTER session had to include four trials in which the leftward deviation was not significant. The absence of significant APAs' changes in the AFTER vs. BEFORE session may be seemingly ascribed to this. In contrast, both when adaptation to prisms completed and when after-effect recovered (2nd BLOCK; Figs 2b and 3b,d), premovement EMG activities in AD and BB, as well as APAs in lower-limb muscles, were similar in all experimental sessions.

In summary, when prisms induce a pointing error, the movement seems to be associated with stronger lower-limb APAs, not paralleled by changes in the activation of the prime mover.

Quantitative analysis of the EMG recordings. Figure 4a, c shows the mean amplitudes of the premovement activation in AD and BB and of the APAs in lower-limb muscles. Two-way ANOVAS (*prisms* \times *blocks*), computed on premovement EMG amplitude of the two upper-limb muscles, showed no *prisms* nor *interaction* effect, while a significant *blocks* factor resulted for both AD ($F_{1,9} = 117.13$, $P < 0.001$) and BB muscles ($F_{1,9} = 52.74$, $P < 0.001$). Two-way ANOVAS (*prisms* \times *blocks*) on the right Q and the right TA resulted in a non-significant *prisms* main effect, a significant *blocks* main effect ($F_{1,9} = 5.67$, $P < 0.05$ and $F_{1,9} = 11.72$, $P < 0.01$ respectively) and a significant *interaction* ($F_{2,18} = 3.57$, $P < 0.05$ and $F_{2,18} = 4.81$, $P < 0.05$ respectively). According to the post hoc comparisons, *prisms* affected only the 1st BLOCKS, in which right Q EMG was larger in the DURING than in both BEFORE and AFTER sessions, while right TA was larger in DURING than in BEFORE session only. ANOVAS on right H, right SOL and left Q showed neither main effects nor interactions, while a significant *blocks* main effect was found in left TA ($F_{1,9} = 7.6$, $P < 0.05$).

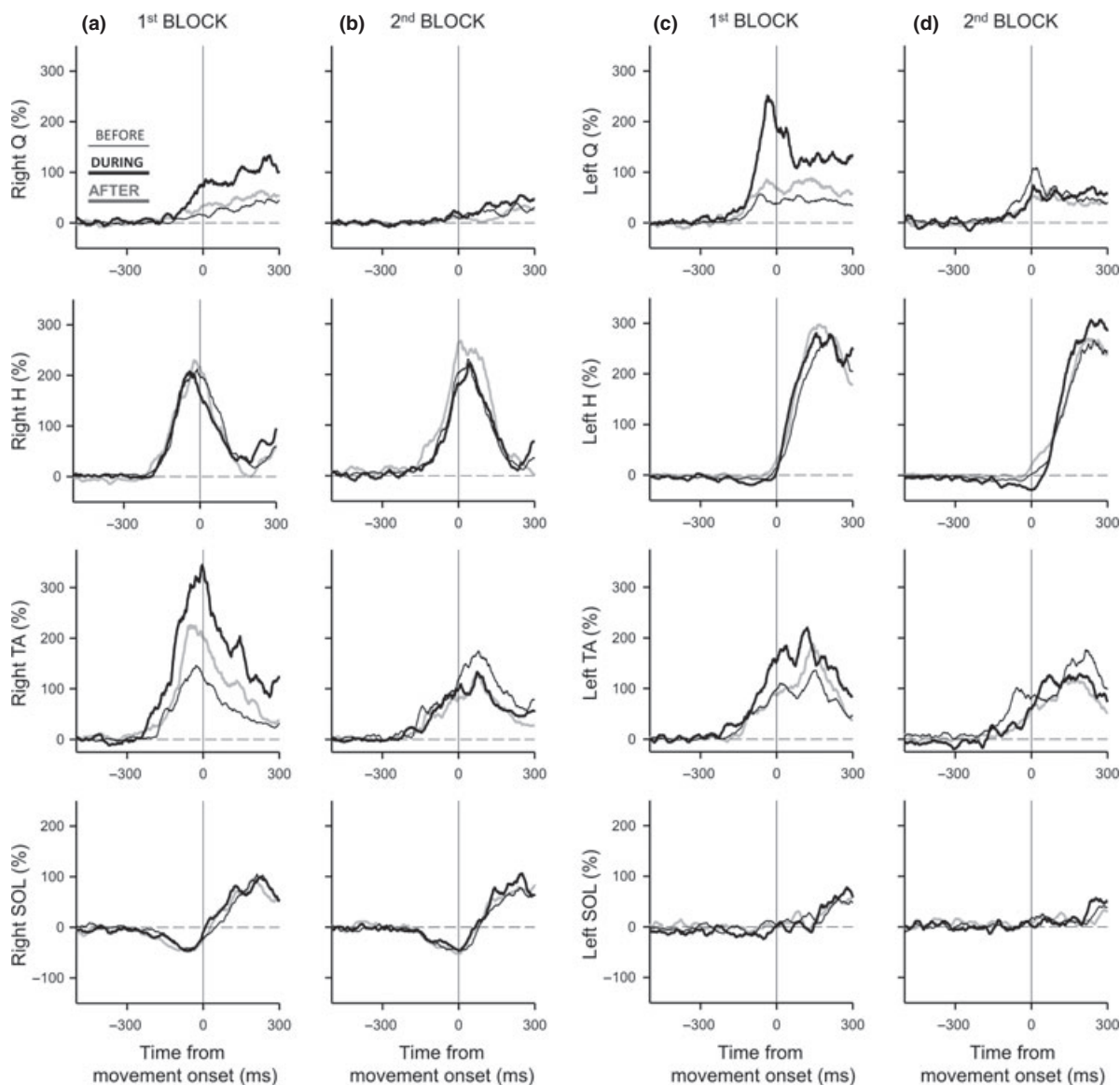


Figure 3 Rectified and smoothed electromyographic (EMG) recordings from the lower-limb muscles quadriceps (Q), hamstring (H), tibialis anterior (TA) and soleus (SOL) of the right (a, b) and left (c, d) sides. Averages of the traces of one representative subjects, obtained in trials 1–5 (a, c – 1st BLOCK) and in trials 11–15 (b, d – 2nd BLOCK) of the three experimental sessions: BEFORE (thin black line), DURING (thick black line) and AFTER (thick grey line) wearing prismatic goggles. BEFORE wearing prisms, excitatory or inhibitory anticipatory postural adjustments (APAs) developed, prior to the movement onset, in all muscles except left H and SOL. In the 1st BLOCK of the DURING session, APAs in Q and TA of both sides increased, while when prisms were doffed (1st BLOCK of AFTER session), APAs decreased to values similar to those of the BEFORE session. In contrast, in the 2nd BLOCK, when adaptation to prisms and after-effect recovery were completed, APAs in lower-limb muscles were similar in all experimental sessions.

Despite the strong increase in APAs strength in left Q and left TA, prisms did not produce significant changes.

Figure 4 summarizes also the latencies of the pre-movement activation and of the APAs. Two-way ANOVAs (*prisms* × *blocks*) resulted in non-significant *prisms* main effect nor interaction, while *blocks* factor was significant in AD, BB, right Q, right TA and left TA (in all cases, $F_{1,9} > 7$, $P < 0.05$), that is, those muscles that showed *blocks* main effect on the EMG amplitude.

Platform recordings. Before wearing prisms, platform recordings changed prior to the movement onset, when all of them significantly differed from the corresponding background level (paired *t*-test, P always < 0.05). As shown in Figure 5a – 1st BLOCK, the force vector pointed backward, rightward and downward; the CoP moved backward and rightward, and the vertical torque turned clockwise. The largest prisms effect occurred in the APA revealed by the

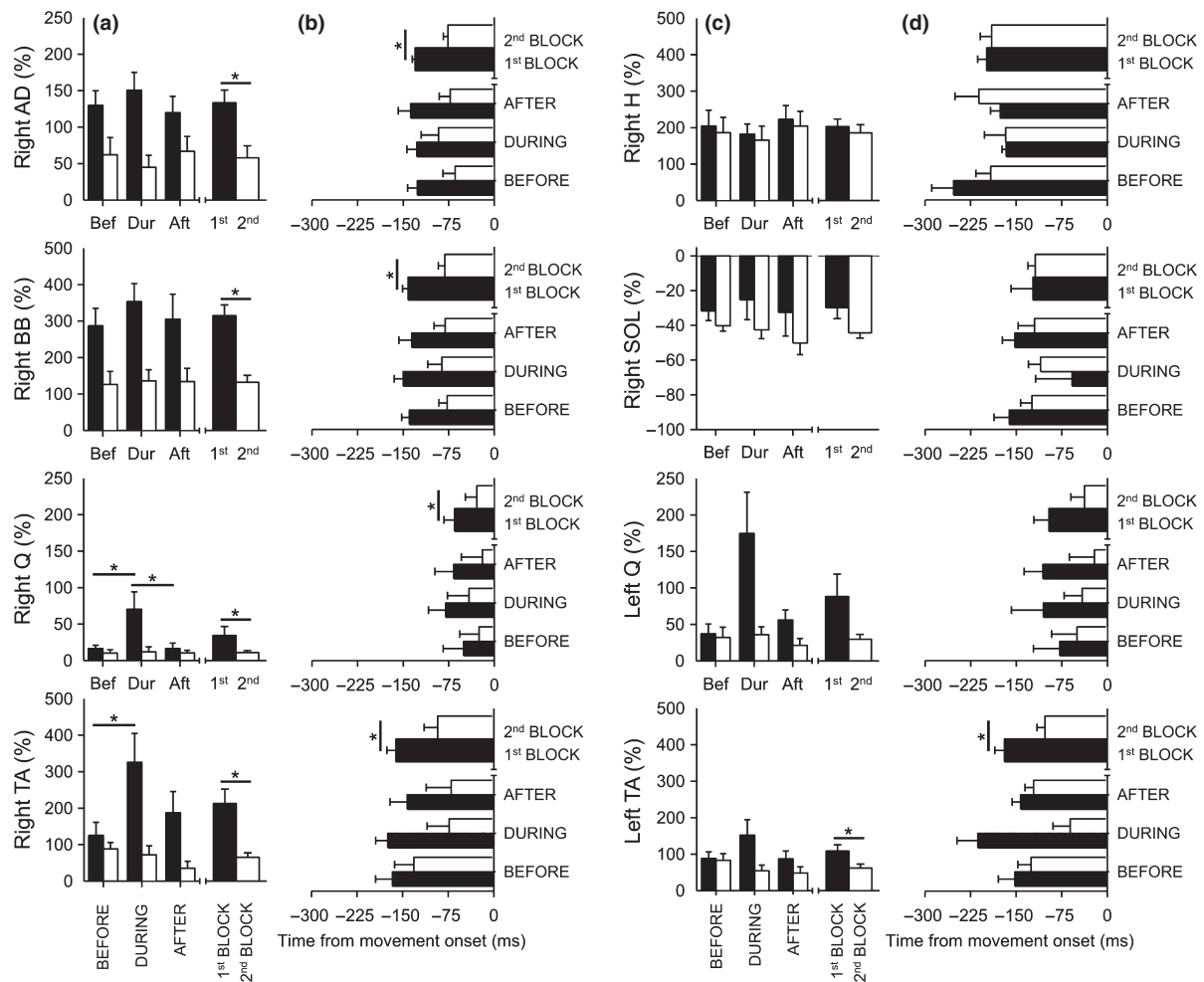
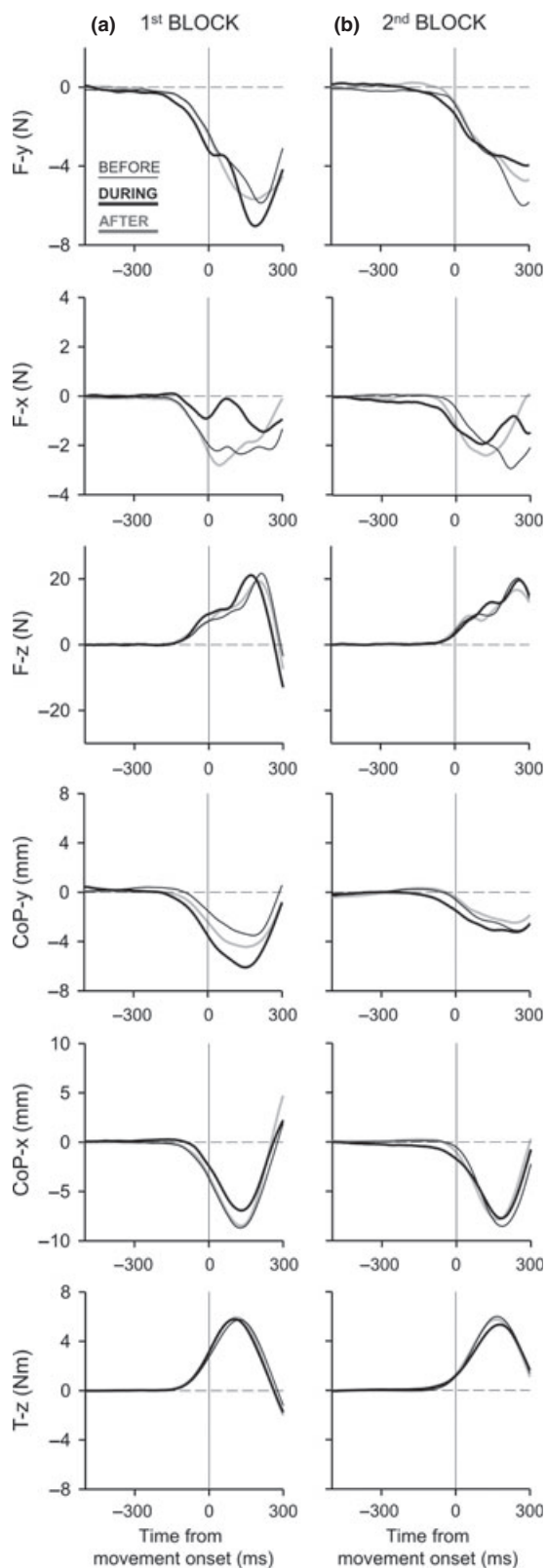


Figure 4 Mean normalized amplitude (a, c) and mean latency with respect to movement onset (b, d) of pre-movement activation in right arm muscles and of anticipatory postural adjustments (APAs) in lower-limb muscles (raw traces in Figs 2 and 3). Plotted values refer to the 1st and 2nd BLOCK (black and white bars respectively) of each experimental session (BEFORE, DURING and AFTER wearing prismatic goggles). Error bars mark the intersubject SEM. Significant differences (*prisms* × *block* ANOVA on each muscle) are marked by asterisks. For each BLOCK, the average of the values recorded among the three sessions is also reported, after the axis break, so as to illustrate the main effect of the ANOVA *block* factor. The APAs increase in Q and TA muscles of both legs observed in the 1st BLOCK of the DURING session (Fig. 3) reached significance only in the right limb. Moreover, a significant *block* factor was observed in the size and latency of pre-movement activations in AD and BB as well as in the size and latency of APAs in right Q and in right and left TA. Finally, in the 2nd BLOCK, non-significant effect of prisms was found on size or latency of pre-movement activations or of APAs, again in agreement with Figures 2 and 3.

CoPy (antero-posterior) displacement. When prisms were just donned (Fig. 5a – 1st BLOCK), the anticipatory displacement increased, while after doffing them, it reduced in size. When adaptation to prisms and after-effect recovery were completed (Fig. 5b – 2nd BLOCK), the APA size in CoPy was again comparable among the three sessions.

Quantitative analysis of platform recordings. Figure 6a shows the mean amplitudes of the APAs in platform recordings. Two-way ANOVA (*prisms* × *blocks*) on APA amplitude in CoPy resulted in a non-significant *prisms* main effect, a significant *block* main

effect ($F_{1,9} = 4.93, P < 0.05$) and a significant *interaction* ($F_{2,18} = 13.19, P < 0.001$). According to the post hoc comparisons, *prisms* affected only the 1st BLOCK, in which the anticipatory displacement was larger in the DURING than in both BEFORE and AFTER sessions. Two-way ANOVAs on the remaining recordings highlighted only a significant *block* main effect in all traces (Fx: $F_{1,9} = 21.33, P = 0.0012$; Fy: $F_{1,9} = 12.71, P = 0.0060$; Fz: $F_{1,9} = 19.75, P = 0.0016$; CoPx: $F_{1,9} = 20.18, P = 0.0015$; Tz: $F_{1,9} = 26.80, P = 0.0005$). The same ANOVA design on APAs latencies (Fig. 6b) showed no *prisms* main effect nor *interaction*, but a significant *block* main effect in



Fy, Fz and CoPy (Fy: $F_{1,9} = 5.90$, $P = 0.038$; Fz: $F_{1,9} = 62.38$, $P < 0.0001$; CoPy: $F_{1,9} = 11.89$, $P = 0.0072$).

Figure 5 Force platform recordings: components of the force exerted on the ground along the three Cartesian axes (Fy, positive when directed forward; Fx, positive leftward; Fz, positive downward), displacement of the centre of pressure (CoPy, positive forward; CoPx, positive leftward) and torque about the body vertical axis passing through the CoP (Tz, positive clockwise). Averaged traces of one representative subjects, obtained in trials 1–5 (a – 1st BLOCK) and in trials 11–15 (b – 2nd BLOCK) of the three experimental sessions: BEFORE (thin black line), DURING (thick black line) and AFTER (thick grey line) wearing prismatic goggles. BEFORE wearing prisms, all platform recordings changed prior to the movement onset, thus showing APAs. Prismatic goggles induced the largest change in the APA of CoPy, which increased when prisms were just donned (1st BLOCK, DURING) and reduced in size after doffing them (1st BLOCK, AFTER). When adaptation to prisms and after-effect recovery were completed (2nd BLOCK), the size of APA in CoPy was again comparable among the three sessions.

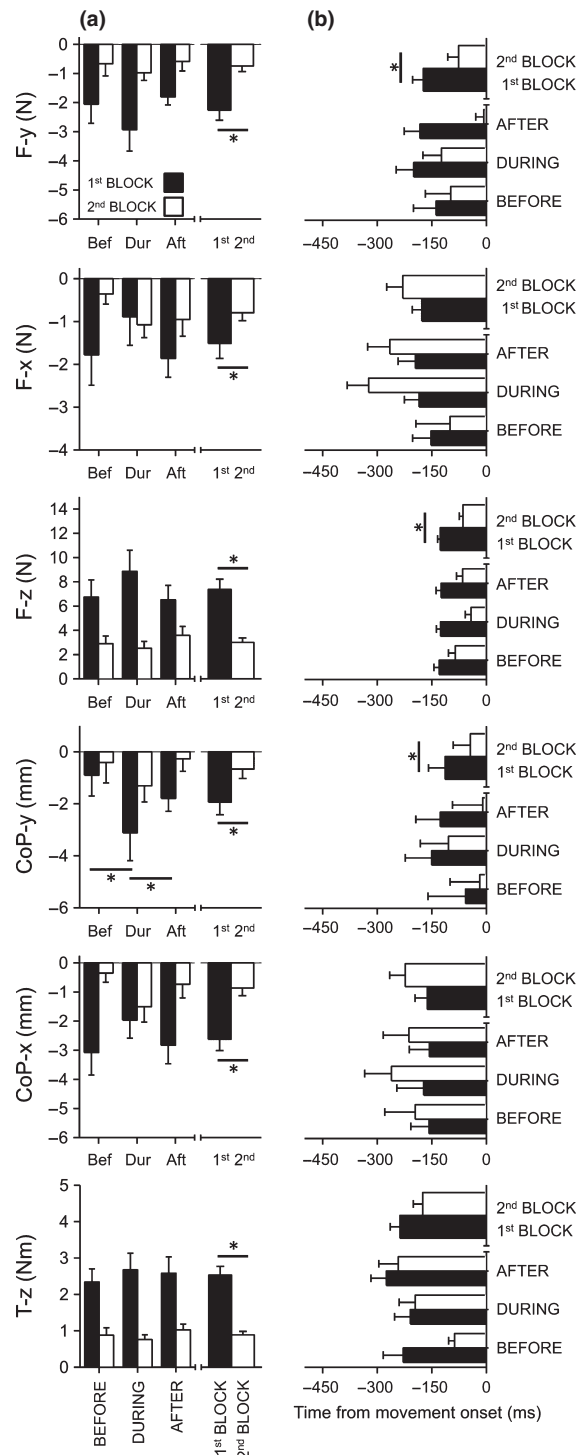
Control analysis – duration of the target-reaching movements

As it is widely reported that APAs are scaled in amplitude to movement duration (faster movements are associated with larger APAs, Lee *et al.* 1987; Shiratori & Aruin 2007), we carefully verified whether this parameter changed during the experiment. Figure 7 shows the mean duration of the target-reaching movement in the two blocks of trials, collected in the three experimental sessions. Two-way repeated-measures ANOVA (prisms \times blocks) highlighted only a significant blocks main effect ($F_{1,9} = 63.45$, $P < 0.001$). Thus, within each block, movement duration was similar in the three sessions, indicating that the APAs' changes observed in the EMG and platform recording, within the 1st BLOCK, should not be ascribed to changes in movement velocity. On the other hand, all the APAs' changes between the two blocks (1st BLOCK vs. 2nd BLOCK comparisons) may be affected as well by the increase in movement duration observed in the second BLOCK.

Discussion

The novelty of our study is that by using prisms, we induced out-of-target movements that were found not to be associated with changes in the prime mover activation, as it might be expected, but only to changes in the APAs size. This observation reinforces the hypothesis that a successful on-target pointing movement relies upon a specific tuning between APAs and prime mover activation, as that obtained at the end of the adaptation phase.

In the following, we will first deal with the origin of the pointing error, then we will recall that accurate



motion of a segment (e.g. the hand) requires a proper coordination between distal (e.g. the upper limb) and proximal (e.g. the trunk) body parts. Thereafter, we will examine evidences suggesting a relationship between APAs and movement accuracy, and finally, we will discuss specific aspects of our results and their possible interpretation.

Figure 6 Mean amplitude (a) and mean latency with respect to movement onset (b) of anticipatory postural adjustments (APAs) in the force platform recordings (raw traces in Fig. 5). Plotted values refer to the 1st and 2nd BLOCK (black and white bars respectively) of each experimental session (BEFORE, DURING and AFTER wearing prismatic goggles). Error bars mark the intersubject SEM. Significant differences (*prisms* × *block* ANOVA on each force platform recording) are marked by asterisks. For each BLOCK, the average of the values recorded among the three sessions is also reported, after the axis break, so as to illustrate the main effect of the ANOVA *block* factor. The CoPy APA increase observed in the 1st BLOCK of the DURING session (Fig. 5) reached significance. Moreover, a significant *block* effect was observed in the size of APAs in all platform variables and also in the latency of APAs in Fy, Fz and CoPy. Finally, in the 2nd BLOCK, non-significant effect of prismatic goggles was found on size or latency of APAs, in agreement with Figure 5.

Origin of pointing error

Pointing to a visually displayed target requires a neural transformation from a visual representation of target location to an appropriate pattern of arm muscles activity. According to Soechting & Flanders (1989a,b); see also Soechting & Flanders 1992 for a

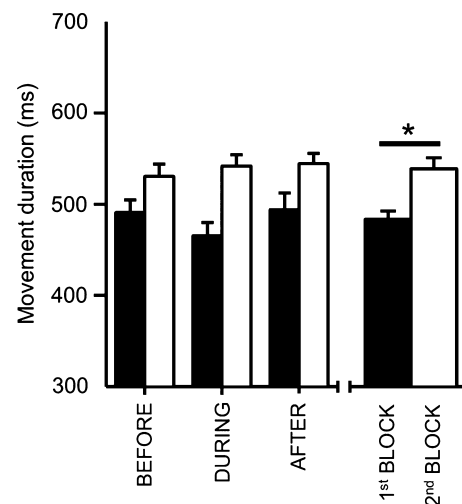


Figure 7 Mean duration of the target-reaching movement. Plotted values refer to the 1st and 2nd BLOCK (black and white bars respectively) of each experimental session (BEFORE, DURING and AFTER wearing prismatic goggles). Error bars mark the intersubject SEM. Significant differences (*prisms* × *block* ANOVA) are marked by asterisks. For each BLOCK, the average of the values recorded among the three sessions is reported, after the axis break, so as to illustrate the main effect of the ANOVA *block* factor. Note that the only significant difference was an increase in movement duration in the 2nd vs. 1st BLOCK, while prisms had no effect in either BLOCK.

review), errors in such a movement derive from errors in the sensorimotor transformation from the visual representation of the target to the kinematics representation of the planned trajectory. Indeed, such transformation is intrinsically nonlinear, but subjects usually employ a linear approximation when they have to remember the target location and point to it. These authors also showed that when subjects have to reach a position, which has been previously appreciated kinaesthetically (thus after having empirically built up the exact transformation), pointing errors dramatically reduce. Several evidences were collected that the parietal cortex plays a critical role in integrating visual and somatic inputs for building up this sensorimotor transformation (see [Kalaska et al. 1997](#) for a review).

In our study, pointing errors were apparently due to the changes in the sensorimotor transformation induced by prisms. In a few trials, thanks to the visual feedback, our subjects empirically solved the new sensorimotor transformation and succeeded in reaching the target. The same occurred (in the opposite direction) after doffing goggles. An increase in pointing error when requiring to change the sensorimotor transformation, for instance by asking to reach a target in an horizontal workspace while looking at the initial position of the hand and target on a vertical screen, was also observed by Messier & [Kalaska \(1997\)](#).

Coordination between proximal and distal body segments

There is growing evidence from the literature showing that the performance of dexterous motor tasks, such as pointing and reaching, relies on the exact coordination between proximal (e.g. trunk) and distal body segments (e.g. hand).

Several motor control studies (Ma & Feldman 1995, Archambault et al. 1999, Pigeon et al. 2000, Robertson & Roby-Brami 2011) provide evidence that motion of the trunk and the upper limb is appropriately scaled each other to ensure the maximal accuracy when moving the hand towards a target. In their seminal paper, Hollerbach & Flash (1982) offer a model, which describes shoulder–elbow coordination in hand-reaching movements. The same model also predicts the modifications of the distal segments trajectory and its final position when the force exerted at proximal joints is inadequate, a condition in which an out-of-target movement would result. Similarly, out-of-target movements are also expected when the Coriolis force acting on the arm during the simultaneous displacement of the upper limb and torso is not compensated in a feed-forward manner (Bortolami et al. 2008).

Interestingly, [Era et al. \(1996\)](#) have reported that top-level rifle shooters stabilize their whole-body balance better than naive shooters, particularly in the last seconds before the shot. This and other studies investigating the same topic (e.g. Aalto et al. 1990, Mononen et al. 2007) give evidence that shooting accuracy relies on the accurate trunk and lower-limb posture control, allowing coordination of these body segments with the focal trigger pull. In close relation with the idea that postural stabilization influences movement performance, other authors showed that changes in the size of the base of support ([Yiou et al. 2007](#)), or the addition of a secondary motor task, which specific APAs may interfere with those of the primary motor task ([Yiou 2005](#)) might influence the velocity of the focal arm movement.

On these premises, APAs may represent the earliest part of the motor command necessary for proximal and distal body segments coordination, as also supported by our results.

APAs contribution to movement accuracy

Only in recent years, some authors suggested that APAs function is not limited to ensure the whole-body balance, but might also encompass the ability to provide the most appropriate conditions to guarantee an accurate movement execution.

Anticipatory postural adjustments decrease in size as the accuracy demand increases (i.e. when pointing smaller and smaller targets), a feature that has been shown both in the upper limb ([Bonnetblanc et al. 2004](#)) and in the lower limb ([Bertucco & Cesari 2010](#)). Lower-limb pointing was also investigated by [Duarte & Latash \(2007\)](#), who have shown that the faster the movement is, the larger the APAs variability is. It also well described the relationship between movement speed and scattering of the final position around a target ([Schmidt et al. 1979](#), [Fernandez & Bootsma 2004](#)). In the other way round, all these observations suggest that small and less variable APAs should accompany slow but precise movements. [Berrigan et al. \(2006\)](#) reported that when pointing is performed towards small targets (i.e. under high accuracy constraints) from an ‘unstable’ position (i.e. standing vs. sitting), slowing movement speed actually represents a strategy to reduce the equilibrium disturbance and, consequently, the associate APAs.

Conversely, other authors showed that decreasing the stability of the initial posture (passing from seating with 100% ischio-femoral contact to 30% contact) might increase both the amplitude of the APAs and the overall performance of an arm movement like, for example, the maximal velocity of a pointing task ([Teys  d  re et al. 2000](#)) or the isometric maximal force

developed during a pushing task (Le Bozec & Bouisset 2004). Both these effects were ascribed to a greater postural mobility in the unstable (30% contact) condition. However, it should be noted that, in both these studies, subjects were asked to perform as fast as possible movements/pushes, not to exactly reach a particular point or a given force level. Thus, the motor task was quite different from that of Berrigan *et al.* (2006).

Thus, when the accuracy demand increases, movement velocity decreases, that is, movement time increases, as already described by the Fitts (1954). However, as APAs amplitude is known to be proportional to focal movement velocity (Lee *et al.* 1987, Shiratori & Aruin 2007), its reduction might be not directly related to the increased accuracy demand, but to the associated reduction in movement speed. With respect to the above studies, our work is novel because it proves the relationship between APAs and movement accuracy (i.e. the pointing error), rather than the accuracy constraint (i.e. the target size), by ruling out the effect of movement velocity. The latter was indeed constant among sessions thanks to the fact that prismatic lenses influenced just movement direction, as revealed with aiming errors, but did not affect the target.

Further considerations on present results

As pointed out above, a crucial aspect in APAs modulation is movement velocity. However, our experiments show that when movement velocity remains constant among sessions (i.e. within each BLOCK), prism-induced pointing errors are still associated with changes in APA amplitude, thus supporting a linkage between APAs and movement accuracy. When moving fast, stronger prime mover activation is associated with stronger (Lee *et al.* 1987, Shiratori & Aruin 2007) and more anticipated APAs (Horak *et al.* 1984, Zattara & Bouisset 1988). This is in agreement with our results, which show that APAs and prime mover activation in the 1st BLOCK were larger and started earlier than those recorded in the 2nd BLOCK, when movements were slower.

Intriguingly, the relationship between movement speed/prime mover contraction and APAs' changes was limited to Q and TA of both sides (although not significant in left Q), with no modifications in H and SOL, a pattern which suggests that different muscles of the APAs chain could have different roles in equilibrium stabilization. APAs are known to secure the equilibrium in a twofold way (Massion 1992) (i) by counterbalancing the segmental equilibrium disturbance due to the reaction forces developing with the ongoing movement (which grow when movement speed increases) and (ii) by preventing the whole-body

CoM displacement produced by the new configuration of the body (regardless the speed with which that configuration has been reached). Considering that 1st and 2nd BLOCK trials have different movement speed, but similar movement amplitude on the sagittal plane, it can be proposed that anterior lower-limb muscles (Q and TA) may neutralize the time-changing perturbation due to prime mover contraction, while posterior muscles (H and SOL) may neutralize the CoM changes as the movement develops.

Prisms selectively modulate those APAs sensitive to modification in movement speed. When wearing prisms, APAs amplitude was significantly increased in right Q and TA muscles (1st BLOCK – DURING vs. 1st BLOCK – BEFORE); no changes were instead found in APA latency. Thus, APAs timing and amplitude seem to be independently controllable, as also suggested by Nana-Ibrahim *et al.* (2008). Note also that the TA APA contributes to the backward CoP change, which in turn counteracts the perturbation applied by the arm movement on the shoulder. Indeed, the backward CoP change is responsible for the generation of forward-oriented inertial forces, which act to counteract the perturbing force induced by the arm movement (Bouisset & Zattara 1987).

The backward CoP change is apparently larger when wearing prisms. To explain this behaviour, one should consider that (i) to hit the target on the sagittal plane, the subject has to flex and slightly adduct the arm, so that the resulting perturbation is directed backward and slightly rightward; (ii) when committing rightward pointing errors, the shoulder angle in the horizontal plane seems to be unchanged, so that the fingertip endpoint deviation stems from a rightward rotation of the shoulder girdle (produced by a change in the many degrees of freedom along the body, see next paragraphs). As a consequence, the vector of the perturbation should undergo the same rightward rotation. Its projection along the y-axis should then increase, in agreement with the significant increase in TA APAs and CoPy change (Figs 4 and 6). Note also that, in parallel, the projection of the perturbation along the x-axis should instead reduce, in agreement with the slight decrease (although not significant) found in CoPx.

A final comment is worthwhile about the invariance of the upper-limb kinematics during the different sessions. In the absence of whole-body kinematic data, allowing to trace the relative position of the upper limb with respect to the trunk, the invariance of the shoulder angle in the horizontal plane (i.e. adduction/abduction of the arm) may be inferred by the observed invariance in the AD and BB activity (see Fig. 2). Indeed, AD and BB are both involved in shoulder flexion and adduction (see Kapandji 1982). Thus, any rightward deviation of

the upper limb in the horizontal plane should have been either negligible or signalled by a de-recruitment in both AD and BB activity. For the same reason, a different recruitment of other muscles acting on the shoulder, or even of other deltoid portions, should have been accompanied by appreciable changes in AD and BB. On this basis, we are rather confident that the pointing movement, with and without prisms, was performed without major changes in the shoulder angle in the horizontal plane.

Therefore, the pointing error should stem from other muscles acting along the body vertical axis, that is, from changes in the APAs chain, as those witnessed by our results. Data provided in this paper are certainly insufficient to fully appreciate the complex biomechanics of the postural chain. In this regard, the invariance of Tz coupled to the asymmetric changes in left and right Q and TA suggests a mechanical action from the legs to the pelvis that should have been accompanied by a counter rotation in one or more of the many degrees of freedom within the chain. Present data do not allow any speculation about this aspect, but in any case, this does not affect the main result of this paper: the accuracy of pointing movements relies upon a specific tuning between APAs and prime mover activation.

Conclusions

Data reported here suggest that by securing the position of the proximal joints, properly tailored APAs contribute to make the focal movement accurate. Indeed, we showed that prisms induce pointing errors in the upper limb by modifying the balance between APAs in lower limb and prime mover contraction. In other words, 'A movement never responds to detailed changes by a change in its detail; it responds as a whole to changes in each small part, such changes being particularly prominent in phases and details sometimes considerably distant both spatially and temporally from those initially encountered' (Bernstein 1967).

Conflict of interest

Research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

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