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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

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Abstract—How fast can we correct a planned movement following an unexpected target jump? Subjects, starting in an upright standing position, were required to point to a target that randomly and unexpectedly jumps forward to a constant spatial location. Rapid motor corrections in the upper and lower limbs, with latency responses of less than 100 ms, were revealed by contrasting electromyographic activities in perturbed and unperturbed trials. The earliest responses were observed primarily in the anterior section of the deltoïdus anterior (shoulder) and the tibialis anterior (leg) muscles. Our findings indicate that visual on-going movement corrections may be accomplished via fast loops at the level of the upper and lower limbs and may not require cortical involvement. © 2010 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: motor flexibility, motor control, goal directed movement, EMG.

How fast can we correct a planned movement if an unexpected target change makes this planning inadequate? Case studies concerning the processing of visual stimuli are somewhat contradictory. Neurophysiological and electrophysiological data in monkeys suggest slower processing than behavioral data. For instance, in the first stage, 80% of neuronal responses occur in the primary visual area (V1) between 25 and 65 ms after the initiation of a visual signal. The second stage occurs in the lateral intraparietal area (LIP) and responses are observed between 70 and 180 ms after an initiation signal (Bullier, 2001). Similarly, Maunsell and Gibson (1992) have recorded neural activity in the striate visual cortex (V1) 30–100 ms after a light flash. Note that in these cases, neural responses were recorded without the need for the animal to program movement or motor correction. More recently, Archambault et al. (2009) examined the activity of cortical area 5 during a pointing task in which the target location changed when the hand was in mid-air. They reported no change in neuronal discharges until 150 ms after the change in target location. These central delays, however, are not representative of the fast motor corrections observed in human behavioural studies where temporal pressure changes can be more easily applied.

Indeed, turning to double-step experiments in humans, Paillard (1996) assessed hand kinematics and established that minimum correction times of around 150–180 ms were required to influence ongoing movement. Other studies have reported shorter latencies of 100–150 ms (Bridgeman et al., 1979; Georgopoulos et al., 1981; Soechting and Lacquaniti, 1983; Gielen et al., 1984; Goodale et al., 1986; Pelisson et al., 1986; Paulignan et al., 1990; Prablanc and Martin, 1992; Desmurget et al., 1999; Day and Lyon, 2000; Prablanc et al., 2003; Diedrichsen et al., 2005). Is 100 ms the lowest limit for implementing a correction after the occurrence of a target jump? This question remains legitimate, at least in certain instances.

First, in most of the experiments cited, motor corrections were detected via hand kinematics. This is insufficient to circumvent inertial, anatomical, and neuromechanical complexities of the subjects, especially in complex movements. Electromyography (EMG) recordings provide more insight into the neural control of multisegmental motion (Corneil et al., 2004). Second, in most of these experiments the target moved to several locations. If the target movement is large, movement durations are approximately lengthened by the duration of a simple reaction time (RT), namely the time required to initiate the movement after the go-signal (Flash and Henis, 1991). However, in the framework of the traditional RT model, it is well established that RTs increase as the number of visual targets increase (Woodworth, 1938, Hick's law 1952). Consequently, multiple jumps may result in an overestimation of the time it takes to make a correction; thus, in the case of a single target location (in a simple RT paradigm), motor corrections should appear earlier. Third, movements were always performed from a seated position, and mostly involved arm movements in a pointing task. However, in

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Abbreviations: BBi, biceps brachii; BFi, biceps femoris; BRi, brachio radialis; DAi, deltoidus anterior; DPi, deltoidus posterior; EMG, electromyography; ESi, erector spinae between L3 and L5; Fep$_{area}$, 95% confidence ellipse area; LDi, latissimus dorsi; PET, positron emission tomography; PSi, pectoralis superior; RAi, rectus abdominis; RFi, rectus femoris of the quadriceps; RT, reaction time; SOLi, soleus; TAi, tibialis anterior; TBi, triceps brachii; 95% CI, 95% confidence interval.

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reaching and grasping tasks, a proximal-to-distal sequence of muscle recruitment is generally observed (Jeannerod, 1986; Crenna and Frigo, 1991; Ma and Feldman, 1995; Stapley et al., 1998, 1999; Adamovich et al., 2001; Bonnetblanc et al., 2004; Bonnetblanc, 2008), suggesting that motor corrections could be observed earlier in proximal muscles.

Altogether, these general considerations suggest that latencies in motor correction may be overestimated when considering kinematics alone, particularly if a pointing task involves complex motor coordination. Certain motor corrections may precede pure arm movement corrections and may be triggered more rapidly at the proximal muscle or lower limb level. We investigated the three previously mentioned limitations further, including whether certain motor corrections precede pure arm corrections and whether they are triggered more rapidly. Thus, we designed an experiment in which subjects had to point, from an upright standing position, to a target, which unexpectedly jumps or moves forward to a constant location, such as in a simple RT model. We then measured, for several muscles, the time it took the individual to correct their arm movement after the target moved.

Finally, based on the above-mentioned contradictions between shorter and longer latencies in motor corrections, Paillard (1996) also suggested that, if movement can be corrected with terminal feedback, early motor corrections are not necessarily involved in the whole correction process. To determine whether correction delays depend on task urgency, we also varied the delay between the go-signal and the target jump. If motor corrections are facilitated with the urgency of the task and if the time-delay is shortened, we should then observe earlier motor corrections when the target change occurs later during the movement.

EXPERIMENTAL PROCEDURES

Seven right-handed adults (all men, age=[20–25]; mean=23 years, height=[175–183]; mean=179.7 m) performed pointing movements with their right index finger. From the starting point, the near and the far targets were located respectively 20, 65 and 90 cm in front of the subject in the sagittal plane and 15 cm below the xyphoid process. The near target could be reached with the arm alone, whereas reaching the far target required an additional forward bending trunk movement. Targets were represented by small visual and tactile 10×10 mm square switches, which could be lit (red colour, luminance=1mcd) and which permitted accurate measurement of time to target contact (see Fig. 1). Subjects were asked to perform pointing movements as quickly and as accurately as possible when a target was lit, in five conditions. In two normal conditions, either the near or the far target was suddenly lit ("go-signal") and remained lit throughout the pointing movement. In three conditions with target jump (3/11 of all trials), the near target was suddenly lit, as in the control trials, but after a variable delay, it was turned off, whereas the far target, the one located beyond reach, was immediately turned on. This forward target jump occurred 120 ms after the first target was lit (i.e. before movement onset: $t<t_0$), after hand movement onset (i.e., when subjects removed their finger from the starting button, t_0), or 50 ms after hand movement onset (t_0+50 ms). Twenty trials were performed for each of the three conditions with target jumps ($t<t_0$, t_0, t_0+50 ms). Eighty unperturbed trials were also performed for near and far target conditions. A total of 220 trials were pseudo-randomized (20 blocks of 11 trials). Each block contained three perturbed trials (at $t<t_0$, t_0, t_0+50 ms), four trials with a stationary near target and four trials with a stationary far target, with trials randomized within a block. All movements were executed in a dimly illuminated room. Each subject performed six trials before data were recorded, and this always occurred in the following order: two trials in the near, two trials in the far and two trials in the t_0 condition.

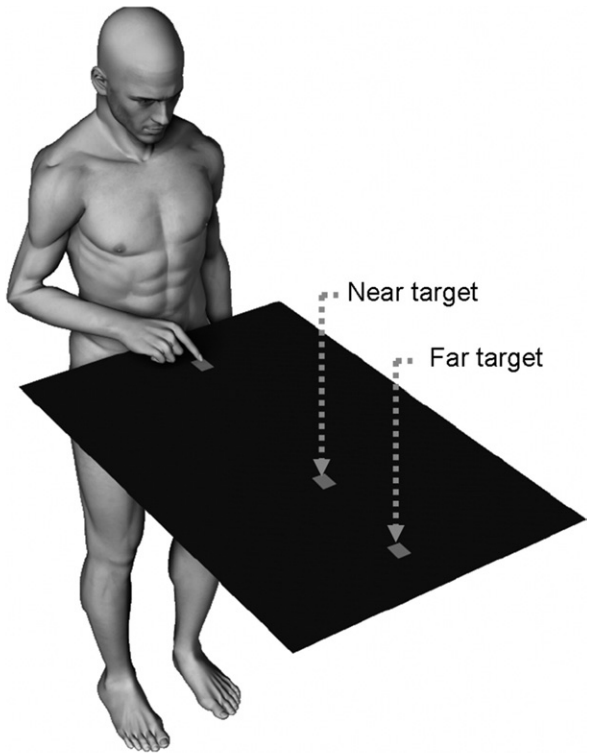

Fig. 1. Experimental pointing task. View from the experimental set-up for the pointing task.

The 3D kinematics of hand movement was recorded with an optoelectronic device (SMART-BTS, Milan, Italy) (120 Hz). The marker was placed on the third phalanx of the right index. All movements were externally triggered. Position signals were filtered (Butterworth 4th order, dual-pass algorithm with a 10 Hz cut-off frequency) before calculating hand kinematics. Velocities and acceleration were computed with a zero phase finite difference algorithm. Statistical analyses were performed using ANOVAs with repeated measures to compare kinematics data from the five experimental conditions (Near, Far, $t<t_0$, t_0, t_0+50 ms). Post-hoc analysis was conducted with the Neuman–Keuls test when necessary.

Surface EMGs were recorded on subjects' right side for the brachio radialis (BRi), biceps brachii (BBi), triceps brachii (TBi), deltoïdus anterior (DAi), deltoïdus posterior (DPi), pectoralis superior (PSi), latissimus dorsi (LDi), erector spinae (ESi) between L3 and L5, rectus abdominis (RAi), biceps femoris (BFi), rectus femoris of the quadriceps (RFi), soleus (SOLi) and tibialis anterior (TAi). All electrodes were placed parallel to the muscle fibres with an interelectrode distance of 2.5 cm. All EMG signals were pre-amplified at the source before a second stage amplification (SMART-BTS, Milan) and were recorded at a frequency of 960 Hz. Raw EMG signals were first bandpass filtered between 20 and 400 Hz and then full-wave rectified and filtered using an averaging moving-window algorithm (window size: 25 ms) (Bonnetblanc et al., 2004; Bonnetblanc, 2008). Trials were averaged for each target location and for stationary or perturbed conditions.

For the $t<t_0$ condition, signals were either synchronized with the "go-signal" (i.e. synchronized with the target jump) or with hand movement onset (in this case, the number of target jumps were averaged). Paired t-tests revealed that both types of synchronization methods led to similar results for all EMG signals, in terms of detecting correction times ($Ps \geq 0.336$). Consequently, both synchronization methods were deemed equivalent. For the sake of clarity, results for the $t<t_0$ condition were obtained by synchronizing signals with hand movement onset. In the t_0 and t_0+50 ms conditions, signals were synchronized with hand movement onset (i.e. with the target jump). We then performed two types of analysis to assess motor correction times.

The first analysis used integrated EMG data and was performed for each subject individually. For each muscle, EMG signals were integrated per 10 ms intervals (iEMG) from −250 ms before the target jump to 800 ms after. We then compared iEMG values from the three perturbed and near conditions for each window width; we used t-tests to estimate the time required to correct motor commands sent to a particular muscle after the target jump had occurred (time to EMG modulation within a 10 ms interval). The moment that the *P*-value was lower than 0.05 for minimum durations of 50 ms, determined the correction time after the target jump, thus avoiding false interference detection (Prablanc and Martin, 1992; Bonnetblanc et al., 2004; Bonnetblanc, 2008). We then computed the correction times for EMG activities and hand accelerations for each perturbed condition and each muscle. Note that repetitive t-tests were not used to answer whether there were differences, but were used to help determine the point at which these differences became significant. There was no summation of the false-positive rate. This difference was subtle, but legitimizing the use of repetitive t-tests in our study. Also, this method has been previously employed in several studies (Prablanc and Martin, 1992; Desmurget et al., 1999; Bonnetblanc et al., 2004; Saijo et al., 2005; Gomi, 2008; Gritsenko et al., 2009).

The second method, involving the use of confidence intervals from unperturbed near trials, was also performed on each subject individually. We computed the 95% confidence intervals (±95% CI) across time for all unperturbed near trials. For each perturbed trial, we subsequently measured the time at which values first exceeded this confidence interval for a minimum duration of 50 ms. Ten of 560 trials fell (i.e. 1.7% of all trials) outside of the 95% CI for the near condition; this corresponded to a maximum of 5 out of 80 trials (i.e. 6.3%) for subject D. These outliers were not taken into account when computing the 95% CI for the near condition.

RESULTS

We examined whether the EMG correlates for motor corrections could be detected less than 100 ms after a target jump in a pointing movement originating from an upright standing position. We also tested how fast they could precede endpoint kinematic arm corrections in some proximal muscles or lower limbs. Therefore, we recorded and analysed both hand kinematics and electromyographic activities of eight muscles located in the legs, trunk and arm.

Hand kinematics

We first computed the 95% confidence ellipse area of the finger endpoint (Fep_{area}), to check whether the accuracy of the pointing movement remained the same. There was no significant difference in the five experimental conditions ($F(4,24)=0.136$ $P=0.966$). Similarly, the hand RT did not significantly vary among all conditions ($F(4,24)=0.101$ $P=0.991$, see Table 1). A Kolmogorov–Smirnov test showed that hand RT did not follow an abnormal distribution for the five experimental conditions for each subject ($ds \leq 0.09$, $Ps \geq 0.05$). It indicated that subjects did not predict or anticipate the target jumps during the experiment.

One factor, five level (Near, $t<t_0$, t_0, t_0+50 and Far) repeated measures ANOVAs were then undertaken to assess mean movement times, peak velocities, and acceleration durations. Neuman–Keuls post-hoc analysis revealed significant differences in movement times between the near condition and all others, between the far condition and the t_0 and t_0+50 conditions, and between the $t<t_0$ condition and the t_0 and t_0+50 ms conditions ($Ps<0.005$). Peak velocities, including time to peak velocities (acceleration durations), were significantly different (see Table 1) between the near and far conditions, the near and $t<t_0$, far and t_0, and far and t_0+50 ms conditions ($Ps \leq 0.001$) (Table 1). We assessed the finger trajectories and velocity profiles of one representative subject under each experimental condition; these profiles were assessed over 20 trials (Fig. 2). Second peaks in the velocity profiles indicated later corrections in hand movement, and were markedly visible if target movements occurred at hand movement onset (t_0) or 50 ms later (t_0+50 ms). By contrast, these were not visible if the target jumped during hand RTs ($t<t_0$): hand trajectory and velocity profiles exhibited no rebound with this condition.

Correction times detected using hand acceleration

To determine if the target jump induced corrections in the hand acceleration profile during the ongoing movement, we computed the finger acceleration rate and averaged it over a single window frame (120 Hz) for each subject. Each averaged value was subjected to a t-test for independent samples. The target jump induced significant mo-

Table 1. Hand kinematics variables. The following hand kinematics variables are averaged for the seven subjects: the 95% confidence ellipse areas of the finger endpoint, the movement times, the reaction times, the acceleration durations, the mean velocities and the peak velocities in the near, far, $t<t_0$, t_0 and t_0+50 ms conditions (mean±standard deviation). For each of these variables, *F* and *P*-values are also reported

	Near	$t<t_0$	t0	t_0+50 ms	Far		
Feparea (cm^2)	0.20±0.01	0.19±0.02	0.20±0.01	0.20±0.02	0.20±0.02	$F(4,24)=0.13$	$P=0.97$
Movement time (ms)	285±23	377±51	519±57	574±70	375±31	$F(4,24)=38.28$	$P<0.001$
Hand reaction time (ms)	352±18	351±27	356±23	357±27	352±20	$F(4,24)=0.101$	$P=0.99$
Acceleration duration (ms)	126±31	154±30	127±30	122±30	168±29	$F(4,24)=12.88$	$P<0.001$
Mean velocity (ms^{-1})	1.7±0.2	1.9±0.2	1.4±0.2	1.2±0.2	2.0±0.2	$F(4,24)=16.34$	$P<0.001$
Peak velocity (ms^{-1})	2.9±0.2	3.3±0.3	2.8±0.2	2.7±0.3	3.5±0.2	$F(4,24)=6.86$	$P<0.001$

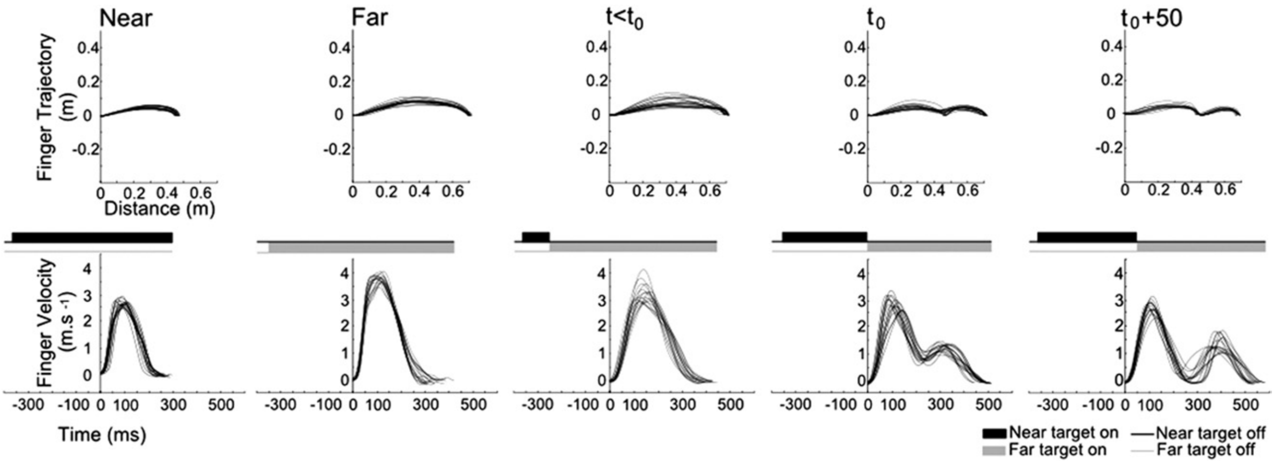

Fig. 2. Hand movement kinematics. Finger trajectories (upper panel) and velocity profiles (lower panel) of a representative subject for the five experimental conditions. For the sake of clarity, two horizontal bars are added to illustrate the ON/OFF pattern of the two targets (black: Near target and grey: Far target). The dimensions are dependent on the occurrence of the two cues.

tor correction (Fig. 3A). Data for the near and the three perturbed conditions for one representative subject are presented. The curves were synchronized with hand movement onset. Thus, in the $t<t_0$ condition, the number of target jumps were averaged and listed with their standard deviation. On average for the seven subjects, significant motor corrections of the finger acceleration profile were detected 164 (±10) ms and 168 (±11) ms after the

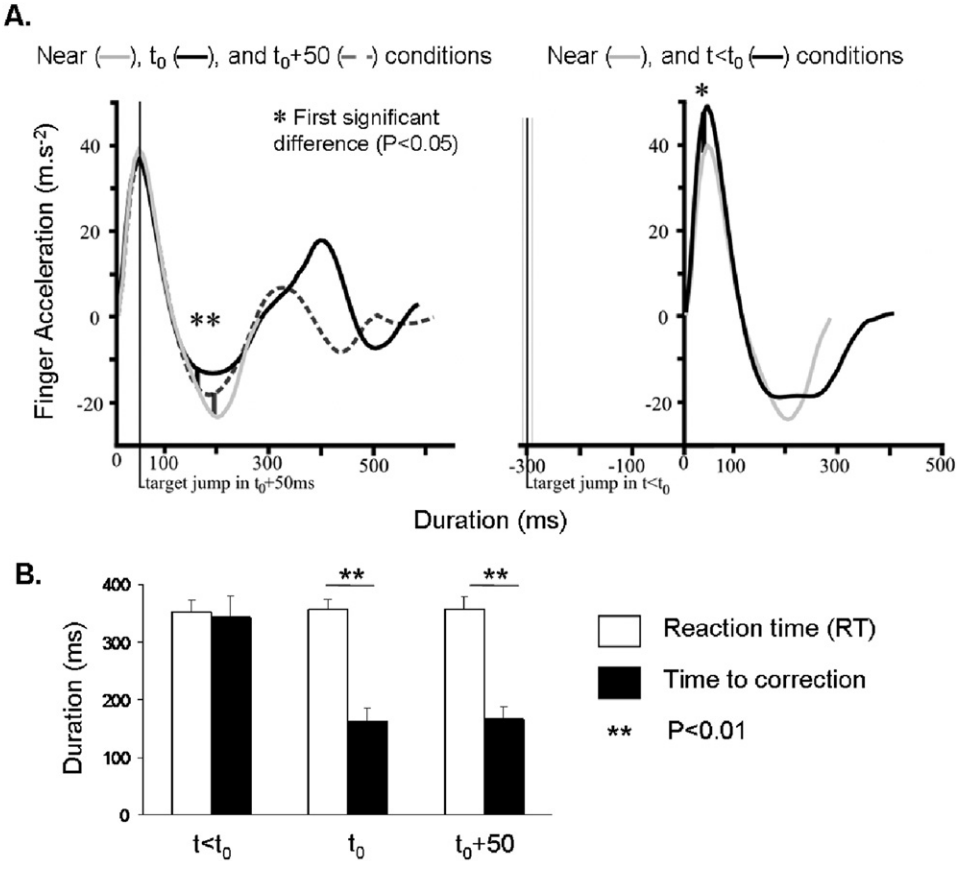

Fig. 3. Acceleration profiles of the hand and reaction times vs. times to motor correction. (A) Acceleration profiles of the hand: raw data. Significant modulations measured on the averaged acceleration profiles (using the t-test method) between the near and perturbed conditions for one representative subject, corresponding to motor corrections induced by the target jump. The curves were synchronized with hand movement onset. Thus, in the $t<t_0$ condition, target jump occurrences are averaged and represented with their standard deviation. (B) Reaction times vs. Times to motor correction. Comparison between the initial reaction times and correction times for finger acceleration in the three conditions with a target jump.

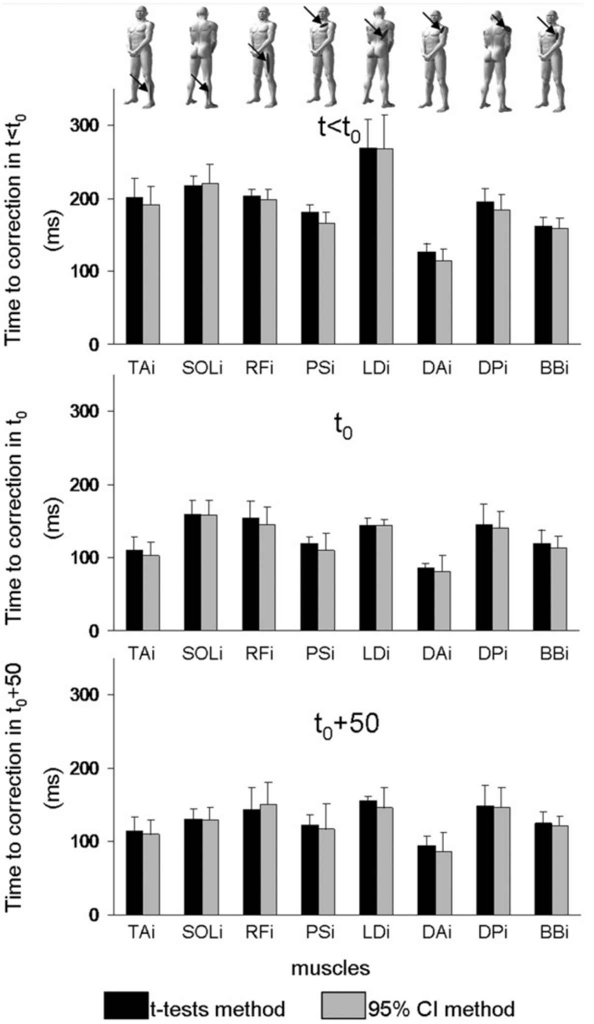

Fig. 4. Mean and standard deviation values for the correction times detected on the EMG activities for all muscles. Histograms of the means and standard deviations of correction times determined using the repetitive t-test method (black bar) and using the 95% CI method (grey bar). Data are presented for all muscles in the three conditions with a target jump. No significant difference was found between both methods.

target jump in the t_0 and the t_0+50 ms conditions, respectively. Interestingly, these correction times were significantly shorter than the initial RT (*P*s$<$0.01) (Fig. 3B). In the $t<t_0$ condition, the time to correction was 345 (±16) ms after the target jump and was associated with a higher finger acceleration peak. In this experimental condition, no significant difference was found between the correction time and the initial RT.

Correction times detected using EMG activities: very rapid corrections were observed for the DAi and TAi muscles

We performed two methods to determine if the target jump induced corrections in the eight recorded EMG activities during ongoing movement. The first method used a repetitive t-test and the second method used 95% CIs (please refer to the materials and methods section for more detail).

Fig. 4 presents the means and the standard deviations of the motor correction times determined with the two methods for all muscles under all perturbed conditions. Overall, EMG activities in TAi, SOLi, RFi, PSi, LDi, DAi, DPi, and BBi were all modified after the target jump. No significant differences were found between the results from the two methods, suggesting that the use of a repetitive t-test on integrated EMG signals or the use of 95% CIs were equivalent when determining motor correction times.

More specifically, both methods showed, in four of seven subjects, that DAi and TAi exhibited the most rapid EMG modulations and motor corrections under conditions t_0 and t_0+50 ms; these corrections occurred less than 100 ms after the target jump. We used repetitive t-tests to assess the four subjects with the most rapid responses. Correction times in the TAi were measured at between 85 ms and 95 ms. Three other subjects exhibited significant differences in correction times—between 125 ms and 155 ms—under similar conditions. Seven subjects demonstrated significant correction times in DAi: correctional responses occurred between 75 ms and 105 ms after the target change of location. Fig. 5 shows, for a representative subject, the average EMG activity in DAi and TAi muscles under t_0, t_0+50 ms, and near conditions. For illustration purposes only, data are presented from −100 ms before synchronization to 250 ms after synchronization.

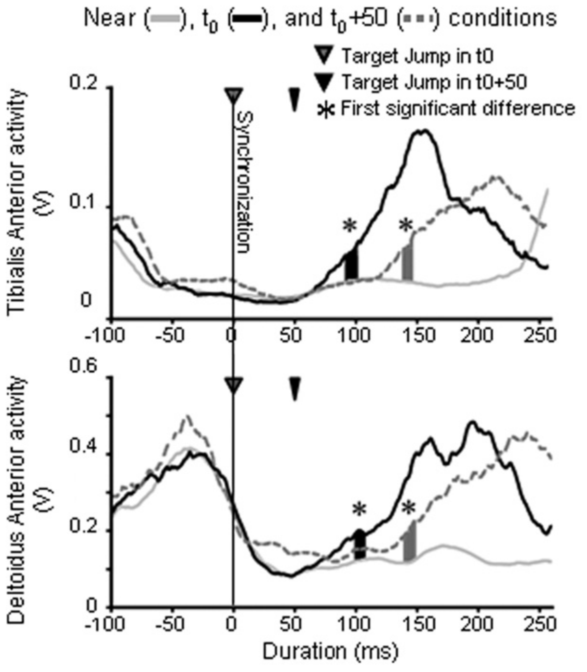

Fig. 5. TAi and DAi EMG activities and the times taken for motor corrections. Significant changes (using t-tests) measured using the magnitude of the EMG activity for the TAi (upper panel) and the DAi (lower panel), for one representative subject. Data are presented for the t_0 (black dashed lines) and the t_0+50 ms (grey dash-dot lines) conditions. Mean EMG activities in the perturbed conditions are superimposed on those for the near condition (grey dashed lines). For illustration purposes, data are presented from −100 ms before synchronization (vertical lines represented hand movement onset) to 250 ms after.

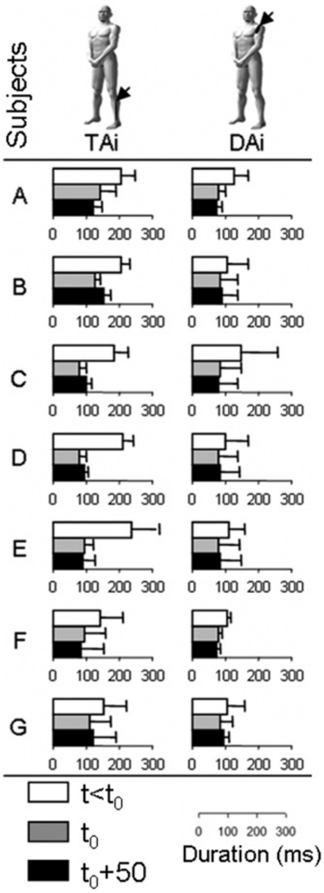

Fig. 6. Time to motor correction for the TAi and DAi muscles in all the subjects. Horizontal histograms with the means and standard deviations for time taken to motor correction for each subject, determined using the 95% CI method. Data are presented for the DAi and TAi muscles, which were the muscles that had the most rapid motor corrections.

Results obtained in TAi and DAi muscles with the second method using 95% CI confirmed earlier findings (Fig. 6). This figure presents the means and the standard deviations of motor correction times obtained for each subject, to illustrate inter-subject variability. Note that very early "motor corrections," occurring less than 65 ms after the target jump, were only detected in 18 of the 420 perturbed trials (4.5%).

DISCUSSION

We aimed to determine whether latencies or delays in motor corrections after a target jump are overestimated when kinematics alone are considered, particularly during a complex motor coordination task, such as pointing. Certain motor corrections may precede pure arm movement corrections and may be triggered more rapidly in proximal muscles or lower limbs. During the task, subjects were standing rather than sitting, and the pointing task was made as simple as possible with only two potential targets.

Pointing from an upright standing position to a target that suddenly and randomly jumps forward to a constant location triggers certain motor corrections within 100 ms, both at the arm and leg levels. In particular, the DAi muscles in 7/7 subjects and the TAi muscles in 4/7 subjects showed motor corrections less than 100 ms after the target jump occurred.

These results confirm our suggestions that discrepancies in the literature reflect a lack of sensitivity in animal studies and artifactual slowing owing to multiple targets in some human movement studies.

First, our findings clearly contrast those reported in previous electrophysiological and animal studies. This discrepancy is even more surprising if we consider the fact that intra-cortical conduction velocities may often be limited to 1–2 m/s, thus slowing cortical processing (Bullier et al., 1988). Note that, in animal experiments, methods for imposing temporal pressure are limited.

Second, shorter latencies may be explained by the simpler experimental model used in comparison with other human movement studies. For instance, Day and Lyon (2000) observed longer latencies for motor corrections with hand kinematics (from 190 to 230 ms). Their study involved pointing at three targets with two possible target jumps. By contrast, Soechting and Lacquaniti (1983) observed shorter latencies with hand kinematics (120–140 ms) for a single random target jump. We used a similar pointing model and report shorter latencies with EMG activities, suggesting that these signals are useful for accurately detecting motor corrections.

Here, correction times (after the target jump) were shorter than the initial RT (after the go-signal). This effect may be explained by the Hick's law principle (1952). Indeed, if subjects have to initiate their movement, there are at least two possibilities for the location of the target (near or far). However, if the target jumps forward, a single possibility for target location remains (only the far target). There is no spatial uncertainty in this condition. As a consequence, the correction time should be equivalent to a simple RT (Hick, 1952; Soechting and Lacquaniti, 1983; Flash and Henis, 1991). However, these correction times were even shorter than simple RTs measured with hand kinematics for simple finger movements. In the classical studies of Woodworth (1938) and Hick (1952) these simple RTs were equal on average to 185 ms. This contrasts with findings by Soechting and Lacquaniti (1983) who found that the time it takes to correct the trajectory measured with hand kinematics was similar to the RT required to initiate the movement. Altogether, these results strongly suggest that both the simplification of the pointing constraints and the use of the EMG technique may have led to these rapid motor corrections. Moreover, Soechting and Lacquaniti experiment subjects were seated and only had to move their arm to reach the target. By contrast, our study subjects were standing, thus reaching the target with their hand involved complex coordination of the whole body, which was initiated in the TA (Bonnetblanc et al., 2004; Bonnetblanc, 2008).

This latter aspect is important, including the fact that motor corrections with approximately the same latency were observed at both arm and leg levels. In this case, TAi activity cannot be a by-product of corrections made by the arm, which are triggered through the reflexive mode. In five of seven subjects, motor corrections in the TAi were observed less than 20 ms after those observed in the DAi. This is inconsistent with the time lapse required to generate a mechanical change from upper to lower limbs and to trigger a reflexive response. This time lapse is also not sufficiently long enough for the mechanical displacement of the upper limb to occur, as the hand kinematics is not yet modified. It rather suggests that there is no hierarchical processing of upper over lower limb motor corrections and that motor flexibility in rapid movements probably involve a complex coordination of the whole body schema. These results are thus important in the understanding of motor correction organization in more complex and ecological movements.

Indeed, in case of urgency, one may suggest that it would be easier to send a motor command to the arm to rapidly correct the focal movement, but as the whole body is involved in the pointing task, the TAi must also be recruited to facilitate the displacement of the centre of mass and to initiate the bending forward motion. In our study, DAi and TAi contractions were limited to a few degrees of freedom. The DAi makes the hand move toward the far target with a trajectory in the sagittal plane, whereas the TAi initiates a forward bending motion of the subject with the foot as a fixed support. This may explain why rapid motor corrections within 100 ms were only observed in these two muscles and not in the other ones. Other muscles may be solicited with greater variability, as their involvement is not fixed in space. This may explain inter-subject variability. Indeed, the variability we observed between subjects at the EMG level may also be explained by large differences in movement requiring complex coordination. Coefficients of determination were very low ($R^2 < 0.44$) between correction times measured using the DAi and TAi EMG activities and those measured using hand acceleration, suggesting that the time to correct the movement at the muscle level was not representative of the time to correct the movement at the kinematics level. In other words, the subjects may use various types of muscular coordination to correct their movement. This interpretation is reinforced by the fact that inter-subject variability, measured by the coefficient of variation, for RTs was lower than that observed for times required to make a correction (0.07 vs. 0.26). However, the observed inter-subject variability at the level of EMG activities may also be explained by several other factors. For instance, differences in attention levels or the ability to alert or react may explain this variability. To investigate whether these were indeed the reasons for these differences, we compared correction times measured using DAi and TAi EMG activities and RTs measured on the same muscles. We found very low coefficients of determination ($R^2 < 0.38$). This suggested that the time to initiate the movement was not representative of the time to correct the movement, lending further support to this hypothesis. As a consequence, the motor coordination sequence employed to correct the movement may be an important factor influencing inter-subject variability in our experiment.

Another (unlikely) functional interpretation of these rapid motor corrections is that these fast EMG modulations are non-specific and are similar to an alarm response. In this case, we would probably observe distributed EMG modulations (not on agonistic muscles only) of the same latencies for all target jump conditions. However, motor corrections were delayed if the target jump was triggered during the RT before hand movement onset. This is in accordance with Paillard's hypothesis (1996), which suggests that if movement is corrected with terminal feedback, early motor corrections are not necessarily involved in the whole correction process.

Under such pre-defined conditions in which a single target jump is involved, the cortical processing of the visual signal may be very simple and rapid, with the subjects being able to pre-plan a particular motor correction and perform it at the occurrence of the visual input, despite the fact that they do not know when the target jump will occur. This may facilitate information processing, especially in the parietal cortex, in which retinal signals are known to be transformed into motor coordinates (Johnson et al., 1996; Duhamel et al., 1997; Burnod et al., 1999; Buneo et al., 2002). Consequently, the cortical loop involved in the motor response could be faster and involve fewer synaptic relays than in conditions with several possible targets for the jumps.

An alternative suggestion, and one we advocate, is that motor corrections following the target jump may also be triggered by lower level loops involving few synaptic relays. In contrast to the slow signal processing within the cortex, some studies have shown quicker adjustment in cat limbs during goal-directed movement, suggesting that subcortical structures are involved in these rapid motor corrections (Alstermark et al., 1987; Pettersson et al., 1997; Pettersson and Perfiliev, 2002). These authors suggest that visual control is exerted via ponto–cerebellar pathways. In a patient with a complete agenesis of the corpus callosum, Day and Brown (2001) observed similar adjustments in latency, irrespective of the target jump direction or the hand used; once again suggesting that visual control was not necessarily cortical.

Gaveau et al. (2003) have more recently reported very fast motor corrections using eye kinematics, occurring only 50 ms after visual double-step stimulation during saccadic eye movements. These authors suggest that the superior colliculus could be involved in these functional corrective loops. Similarly, Corneil et al. (2004) demonstrated that visual target presentation elicits a time-locked, lateralized recruitment of neck muscles at extremely short latencies (55–95 ms) in the orientation response. These authors suggested that the superior colliculus engaged the tectoreticulospinal pathway to move the head independently of gaze shift. Interestingly, neurons of the dorsal Superior Colliculus have been shown to display persistent levels of low-frequency activity in advance of target presentation (Glimcher and Sparks, 1992; Basso and Wurtz, 1997; Dorris and Munoz, 1998). Moreover, the superior colliculus has also unequivocally been shown to be a key structure in so-called express saccades. Lesions of the superior colliculus abolish express saccades but still admit the monkeys to perform fast regular saccades (Schiller et al., 1987).

Finally, working with reaching movements of the arm, Saijo et al. (2005) have shown that a sudden visual background displacement induces motor corrections at the arm level with 100 ms EMG latencies. These quick responses seem to be functional, as subjects were unable to cancel the initial correction even if instructed to move in an opposite direction. Altogether, these results have recently led Gomi to develop an integrated model of multilevel motor control (Gomi, 2008), in which some implicit low level visuomotor controls exist and interact with higher ones. At such a low level, fast reactions are automatically triggered; this is, however, detrimental to the flexibility and complexity of higher-level motor adjustments. Although we cannot make unequivocal conclusions on the nature of the loops involved in the motor corrections we measured, their short latencies appear to be with this model, at least with respect to the initiation of the motor correction process.

In these types of corrections, parts of the networks identified by positron emission tomography (PET) functional neuroanatomy are known to involve the posterior parietal cortex and the cerebellum (Desmurget et al., 1999, 2001). Our findings suggest that there are potential rapid cortical or subcortico–spinal corrective loops that remain to be identified in the rapid motor correction process.

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