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Coordination between equilibrium and hand trajectories during whole body pointing movements

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Abstract We examined the coordination between equilibrium and voluntary pointing movements executed from the standing position, using the whole body. It has previously been shown that trunk movement has little effect upon kinematic characteristics of hand pointing when movements are executed in the sitting position. The present study asked if elements of hand trajectory are modified by requirements of large trunk displacements and fine equilibrium control when pointing movements are executed from the standing position. To achieve this, center of pressure (CoP) and center of mass (CoM) displacements were analyzed along with the kinematics of the pointing hand. Results showed that the CoM was not stabilized (it displaced between 23% and $61 \pm 21\%$ of the foot's length), confirming that instead of a compensation of mechanical perturbations due to arm and trunk movements, the present equilibrium strategy consisted of controlling CoM acceleration towards the target. Hand paths were curved and were not distance or speed invariant. Rather than simple inefficiencies in programming or execution, path curvature suggested that different hand movement strategies were chosen as a function of equilibrium constraints. In light of these results, we hypothesize that postural stability may play a role in the generation of hand trajectory for complex, whole-body pointing movements, in addition to constraints placed upon end-effector kinematics or the dynamic optimization of upper-limb movements. A depen-

dent regulation of equilibrium and spatial components of the movement is proposed.

Keywords Whole body pointing · Equilibrium · Hand kinematics · Human

Introduction

A classical approach to examining the coordination between posture and movement has been to analyze equilibrium processes related to arm movements. This approach has largely considered target oriented arm movements as perturbations to postural stability. For example, anticipatory postural adjustments have been interpreted as compensating for the perturbing effects of limb(s) movements upon whole body equilibrium, during arm (Belenkii et al. 1967), trunk (Crenna et al. 1987), and leg (Mouchnino et al. 1992) movements executed in the standing position. The above-mentioned studies have focused almost entirely upon the effects of the focal component (arm or leg movement) upon the equilibrium component of the task (for a review see Horak and Macpherson 1996).

Interestingly, however, the reverse approach, to focus on the effects of equilibrium constraints upon arm movement control, has received little attention. When subjects reach targets from the standing position the central nervous system (CNS) has to specify the spatiotemporal characteristics of the arm movement while maintaining the whole body center of mass (CoM) within the supporting base (the feet). A number of interesting questions arise when considering together the control of equilibrium and arm trajectory formation. For example: (1) are the control laws governing arm movements, laid down largely using planar two-joint tasks and having little or no equilibrium constraints, applicable to multijoint reaching movements (requiring a high degree of equilibrium control)? (2) How are equilibrium constraints integrated by the CNS during the formation of a specific end-point trajectory among a plethora of possible ones?

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In addition to these theoretical considerations we attempted in this paper to understand more fully the relationship between equilibrium and arm movement planning and execution during voluntary whole body pointing movements. Two opposing theories could be considered. It has classically been assumed that upper limb movements represent an internal source of disturbance to equilibrium, and resulting trunk displacements are compensated for in an anticipatory or reactive manner (Massion 1992). In accordance with this concept, in which the postural component compensates for demands imposed on the body by upper arm motion, one can predict that during whole body pointing movements perturbations induced by arm displacements will be cancelled out in order to reach the target regardless of equilibrium constraints produced by the task.

An alternative hypothesis could be that the postural component does not entirely compensate for the perturbing effects of the focal one, but rather facilitates the execution of the movement by shifting the CoM from one position to another within the support area provided by the feet. This has been proposed in previous work from our group (Stapley et al. 1999), and has also been suggested to be the case during arm raising (see Pozzo et al. 2001), a paradigm traditionally used to study posture and movement coordination (Belenkii et al. 1967; Bouisset and Zattara 1987). In this case, upper limb movement planning would take into account equilibrium components and postural constraints would influence arm movement.

Only recently have a few studies begun to investigate the coordination between trunk and arm movements from such a different point of view. For instance, the contribution of the trunk both to postural stability and to hand reaching movements has been shown by Ma and Feldman (1995) and Kaminski et al. (1995). Additionally, Tyler and Hasan (1995) have provided evidence that non-focal muscle activity is not always devoted to postural stabilization during multidirectional pointing movements. All these experiments, however, tested subjects while in a seated position, which has much reduced constraints of equilibrium compared to the standing one.

The present study examined end-point trajectory formation when subjects were faced with large constraints of equilibrium, as a means of further investigating the coordination between posture and voluntary arm movement. We hypothesized that increasing postural constraints significantly affects arm (hand) trajectory, and should therefore be considered as a supplementary factor influencing their formation. Independent measures of equilibrium and the kinematics of end point trajectory were analyzed during a reaching task toward a target located beyond arm's length. Our previous studies have partially demonstrated that reach to grasp (Pozzo et al. 1998) and lifting (Kerlirzin et al. 1999) tasks were subjected to whole body equilibrium constraints and produced curved hand movements.

Materials and methods

Six healthy subjects (all males, 18–29 years, mean height 1.70 ± 0.05 m, weight 71.4 ± 8.7 kg and foot length 0.245 ± 0.059 m) agreed voluntarily to participate in the study. No subject had a previous history of neuromuscular disease. Each subject's written consent was obtained and all experiments were conducted in accordance with legal requirements and international norms.

Subjects were asked to point with the two arms simultaneously, from an upright standing position with the index finger of each hand to a location approximately level with the ends of a wooden dowel (40 cm long and 1 cm in diameter, mounted on two 15-cm-high semicircular supports) placed on the ground in front of them. Although an auditory tone clearly marked acquisition onset and meant that subjects were free to begin their movement, no requirements were given to minimize the reaction time between the tone signal and movement onset. Accuracy was not the primary constraint on subjects during these experiments. Only trials where subjects did not touch the target (and thus possibly use it as a support) were analyzed. No specific instructions were given regarding the strategies required to point using the upper and lower limbs; the latter could indeed be flexed or kept extended (knees straight). However, all subjects chose a strategy of coordinated trunk, knee and hip flexion to point at the level of the bar. Hand position was located initially at the external side of the thigh and thus induced a hand pointing movement in a semipronated position. Each subject executed one block of six pointing movements at normally (preferred) paced (*N*) speed towards a first object distance, corresponding to 5% of their height (*DI*), measured from the distal end of their great toe. The next block of six movements was conducted as fast as possible (*F*), still at *DI*. This order of movement velocity was repeated for pointing movements made to the dowel at a distance of 30% of each subject height (*D2*). For the distant target condition, each subject was able to reach the target from a stable squatting posture without associated forward trunk bending. Therefore, each subject performed a series of four blocks of six pointing movements (a total of 24 trials), in the following order: *NDI*, *FDI*, *ND2* and *FD2*.

The movements of 11 retroreflective markers (15 mm in diameter) placed at various anatomical locations on the body were measured using an optoelectronic measuring device, Elite (BTS, Milan, Italy). Two infra-red-emitting cameras were attached to a vertical pole 1 and 2 m from the ground on the left side of the subject, at a distance of 3 m from each subject's left hemibody. The 11 markers were used to define eight links (see Fig. 1, left inset), and were attached on the left side of the body, at the head (the external canthus of the eye and the auditory meatus), the upper limb (the acromial process, the lateral condyle, the styloid process and the tip of the index finger), the trunk (the level of the lumbosacral L5–S1 vertebra), and the lower limb (the greater trochanter, the knee interstitial joint space, the external malleolus and the fifth metatarsophalangeal of the foot).

The 11 markers permitted the computation of the sagittal position of the whole body center of mass (CoM) using a seven-segment mathematical model consisting of the following rigid segments: head-neck, chest, abdomen-pelvis, both thighs (as one segment), both shins, upper arms and forearms. Using the model, the position of the center of mass was calculated via standard procedures and documented anthropometric parameters (Winter 1990). The model used to determine whole body CoM position has previously been validated for similar whole body reaching movements (Stapley et al. 1999). This previous publication compared modeled CoM and measured CoP position using a force platform, during quiet stance as well as the times series of measured and estimated (modeled) ground reaction forces. It was concluded that our model provided a realistic representation of sagittal whole body CoM position.

Positions of the center of foot pressure (CoP) were recorded using an AMTI force platform (Watertown, USA) set at a sampling frequency of 500 Hz. As the CoP displacements are directly influenced by neuromuscular activity at the ankle joint level (Morasso and Schieppati 1999), it was chosen as a parameter used

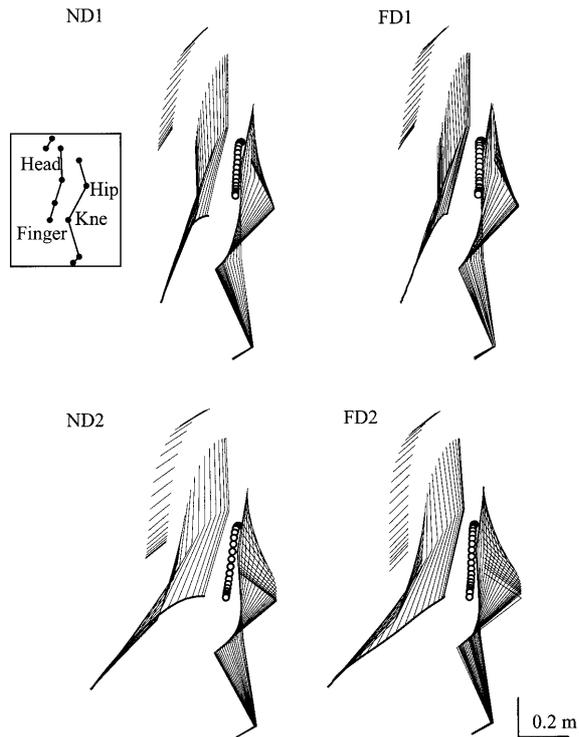


Fig. 1 Stick figures illustrating whole body pointing movements to targets located on the ground in the four experimental conditions. For clarity, only one stick every 50 ms has been plotted. Curving finger trajectories are shown by thick black lines joining successive images. Center of mass positions at 50-ms intervals are indicated by clear circles (*N* movement at normal speed, *F* movement at rapid speed, *D1* target at distance of 5% of each subject's height, *D2* target at distance of 30% of each subject's height)

to illustrate the dynamic effects upon whole body posture induced by the four experimental conditions. Consequently, large displacements of the CoP could be taken to signify a greater degree of muscular control needed to maintain the CoM within the base of support. Anteroposterior (A/P) displacements of the CoM and CoP were expressed as a percentage of the distance between the two markers of the foot (the external malleolus and the fifth metatarsophalangeal of the foot), giving a measure of relative base of support (BoS).

Kinematic parameters in three dimensions (*X*, *Y* and *Z*) were calculated from successive frames taken at 10-ms intervals. Kinematic variables were low-pass filtered using a digital second-order Butterworth filter at a cut-off frequency of 5 Hz. Intentional movement onset (t_0) of the marker located on the finger was established from curvilinear velocity profiles derived from position traces. From their unimodal (bell-shaped) characteristics, t_0 was defined as the first 10-ms time interval where velocity profiles showed a sustained deflection above zero. Finger path curvatures were estimated by studying the deviation from path straightness. This was calculated by interpolating a straight line between the initial and final index finger end points (*L*) and measuring the maximum perpendicular distance (*Dmax*) from the actual path to the interpolated straight line. The quantification of finger path curvatures was made using the ratio $Dmax/L$. The position along the path where *Dmax* occurred was calculated as a percentage of the total amplitude of the path.

Main effect differences between dependent variables (the four experimental conditions: two velocities, *N* and *F*, and two distances, *D1* and *D2*) were evaluated using a 2×2 multivariate analysis of variance (MANOVA). Post hoc analyses were conducted using a Neuman-Keuls test. Any interaction effect has been mentioned

only when it reached statistical significance at the 0.05 confidence level.

Results

General pointing movement characteristics

Figure 1 clearly illustrates that whole body pointing movements were characterized by large angular displacements of shoulder, hip, knee and ankle joints and thus large displacements of the CoM in the sagittal plane, while the support base remained the same. All marker trajectories were oriented in a forward direction, except for hip and L5–S1 markers, which moved in the opposite direction (backwards). It is of interest to note that backward compensatory hip movements, similar to those known to characterize axial synergies during trunk bending (Crenna et al. 1987), were not sufficient to stabilize the CoM at the same AP position. Indeed, the CoM moved significantly forwards within the base of support and mean amplitudes averaged across the four experimental conditions were 6.3 cm, or 40% of the distance between recorded foot markers. Subjects' initial standing posture remained consistent, and the SD of each markers' initial position (with respect to ankle marker) averaged across trial and experimental conditions never exceeded 1 cm for the six subjects tested.

Center of pressure displacements along the anteroposterior axis

Figure 2 shows mean CoP displacements for all trials along the A/P axis in the four experimental conditions for one typical subject and illustrates nicely general trends that were found across subjects. The analysis of CoP displacements across conditions permitted the identification of three general patterns. At normal speed (*ND1* and *ND2*, Fig. 2, upper two curves) the first detectable mechanical event was a backward displacement of the CoP. Immediately following this initial backward CoP displacement was a large forward displacement, after which there were small adjustments of final CoP position at the forward end of the BoS. A second pattern could be identified during pointing movements made at rapid speed and the first target distance (*FD1*). Here the successive backward and forward displacements increased in amplitude and velocity, producing an additional rapid backward CoP to the whole sequence midway through the reaching movement. Finally, when postural constraints were perhaps at their maximum (*FD2*), a much exaggerated pattern similar to that seen in *FD1* was recorded, but with an additional rapid forward CoP movement appearing just before the final adjustment of CoP displacement.

Figure 3 summarizes displacements of the CoP and CoM in the four conditions. It clearly shows that move-

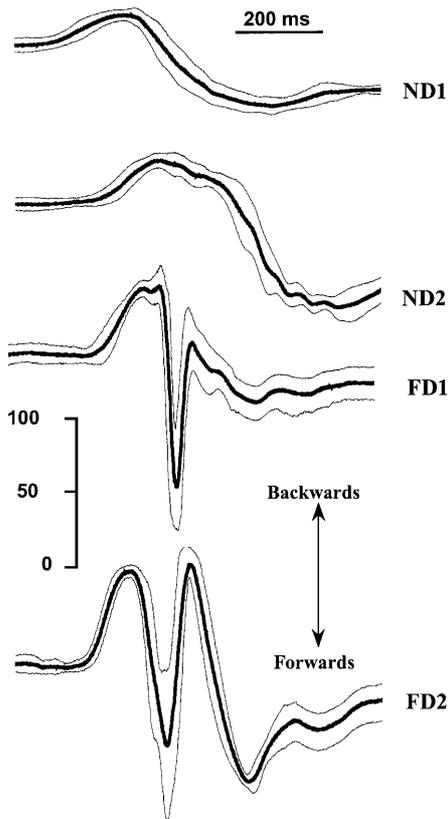


Fig. 2 Average center of pressure (CoP) displacements along the anteroposterior axis for one subject in the four experimental conditions (for abbreviations of the experimental conditions, see Fig. 1). Displacements of CoP are quantified as a percentage of the distance between the markers of the external malleolus and of the fifth metatarsophalangeal, so that the real base of support was in fact larger and peak-to-peak CoP position sometimes exceeded 100%. Also shown is ± 1 SD of the mean (*thin traces*)

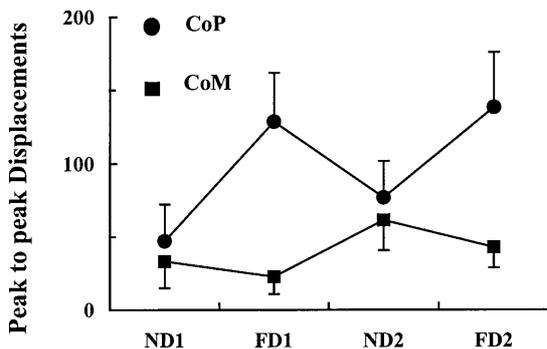


Fig. 3 Average peak-to-peak center of mass (CoM, black square) and center of pressure (CoP, black dot) displacements along the A/P axis for all six subjects, and in all four conditions. Values are expressed as a percentage of relative base of support length (the distance between markers placed on the fifth metatarsophalangeal and the external malleolus). Also shown is 1 SD of the mean (*N* movement at normal speed, *F* movement at rapid speed, *D1* target at distance of 5% of each subject's height, *D2* target at distance of 30% of each subject's height)

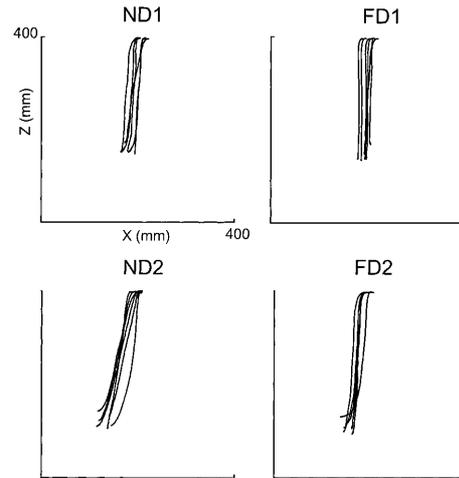


Fig. 4 Path of the center of mass displacements in the sagittal plane for one typical subject in the four experimental conditions. Each trace has been shifted rightwards in order to more clearly visualize the shape of the paths (*N* movement at normal speed, *F* movement at rapid speed, *D1* target at distance of 5% of each subject's height, *D2* target at distance of 30% of each subject's height)

ment velocity induced a greater increase in peak-to-peak CoP displacements than did the distance of the target for the four experimental conditions. Indeed when compared to the *ND1* condition, peak-to-peak CoP displacements were enhanced by a factor of about 1.5 at *D2* and by about 2.6 when executed at rapid speed. However, ANOVA showed significant main effects of velocity ($F_{(1,5)}=43$, $P=0.0001$) and distance ($F_{(1,5)}=19$, $P=0.0001$).

Whole body center of mass displacements

Actual mean values (all subjects) of forward CoM displacements ranged between 0.036 ± 0.017 m (*FD1*) and 0.095 ± 0.03 m (*ND2*). This range of values represented respectively $23 \pm 12\%$ and $61 \pm 21\%$ of relative BoS length (the distance between foot markers). Across subjects, these amplitudes significantly decreased during movements performed at rapid speed ($F_{(1,5)}=13.04$, $P=0.01$). Figure 3 clearly shows the opposite effect of velocity on CoP and CoM displacements. CoM horizontal displacement significantly increased, however, when subjects pointed to distant targets ($F_{(1,5)}=36$, $P=0.001$).

Figure 4 illustrates sagittal plane trajectories of the CoM for one representative subject in all four pointing conditions. It may be noted that CoM trajectories commonly demonstrated two components: the initial part of the path was curvilinear and oriented forwards and was followed by a straight downward movement. This trend was seen in all six subjects tested.

In order to quantify the contribution of the upper limb to CoM forward displacement, successive positions of the CoM have been calculated without considering the hand, the forearm and the upper arm in the mechanical

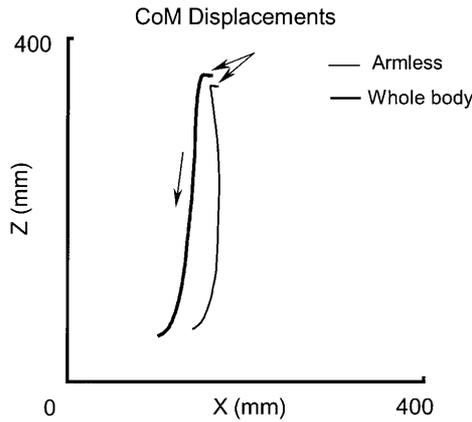


Fig. 5 A comparison of real and remodeled center of mass displacements in the sagittal plane for one typical subject at the distant target and normal speed. The *thicker line* indicates CoM displacements calculated by considering all the eight segments. The *thinner line* shows successive positions of the CoM calculated without considering the hand, forearm and arm in the mechanical model. *Arrows in the upper part* mark the initial horizontal and forward displacement of both armless and whole body CoM displacements

model (Fig. 5). When pointing to close and distant targets at normal speed, contributions of arm movements to the total A/P CoM displacement were on average 27% and 38%, respectively. This indicates that the arm, which represents a mere 10% of the total body weight, has a significant contribution to the coordination of multiple segments and joints and ultimately moves the CoM forward within the BoS. If a priori this value is not surprising since the arm is at a significant distance from the center of the body, Fig. 5 shows qualitatively how forward arm movements contribute to total CoM displacements in one typical subject, in the *ND2* condition. In the armless condition, a slight but noticeable initial forward CoM displacement was produced independently of arm movements and probably in response to anticipatory backward CoP displacements (as suggested by Stapley et al. 1998). Following this, the CoM commonly displayed a downward and backward displacement that reversed approximately midway to the target. Interestingly, when the arms were incorporated in the calculations, the CoM displacement was always oriented forwards, with the contribution of the arms to the forward whole body displacement occurring at the end of the initial horizontal CoM displacement.

Hand trajectories

It can be noted that finger paths, for both distances, presented noticeable curvatures which were more pronounced for movements executed at normal speed compared to those executed at fast speed. Furthermore, variability between paths increased when subjects pointed at distant targets.

The effects of movement speed and target distance on the shape of finger path in the sagittal plane are qualita-

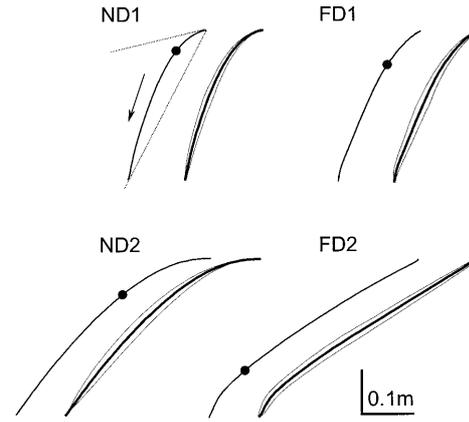


Fig. 6 Means (*thick lines*) ± 1 SE (*thinner lines*) of finger paths in the sagittal plane for one typical subject throughout the four experimental conditions. *On the left part of each trace*, the position of the maximum curvature (D_{max}) along the mean path is indicated (*black dots*) in order to qualitatively show the effects of the experimental condition on shape curvature. In the *upper left part of the figure (ND1)*, *arrows* indicate movement direction and the *dotted lines* give an approximation of the direction of the finger path at the initiation of the pointing movement and the target direction (*N* movement at normal speed, *F* movement at rapid speed, *D1* target at distance of 5% of each subject's height, *D2* target at distance of 30% of each subject's height)

tively shown in Fig. 6. Paths were normalized (in terms of distance and initial and final positions) within each experimental condition in order to more clearly show their form independently of variations in their start and final positions.

In Fig. 6 average and standard deviations of all subjects' finger paths are depicted separately for each experimental condition (right traces). For movements executed at normal speed the initial part of the path was curvilinear and oriented forwards about 45° away from the target location while for fast movements the initial part was less curved for the near distance and it was absent for the farther distance. Average values of D_{max}/L were 0.090 ± 0.032 , 0.72 ± 0.012 , 0.103 ± 0.049 , and 0.096 ± 0.045 , for the *ND1*, *FD1*, *ND2* and *FD2* conditions, respectively. Despite a trend of producing straighter finger paths at rapid speed, no significant main and interaction effects of experimental condition were found upon absolute D_{max}/L values ($F_{(1,5)}=0.92$, $P>0.05$ for the distance condition and $F_{(1,5)}=0.91$, $P>0.05$ for the speed condition). Furthermore, variability between paths increased when subjects pointed at the distant targets (see SDs of D_{max}/L).

The absence of a statistically significant effect of D_{max} does not mean, however, that target distance and movement speed had no effect upon finger path shape. Rather, and as can be noted in Fig. 6, the position of D_{max} along the path (the black dot on left traces) was displaced downwards, being situated further from the starting finger position with increasing speed (on average 0.37 ± 0.06 , 0.38 ± 0.04 , 0.42 ± 0.008 , 0.50 ± 0.010 , for the *ND1*, *FD1*, *ND2* and *FD2* conditions, respectively). Statistical analysis revealed a main effect of movement

speed ($F_{(1,5)}=12.5$, $P<0.02$) and target distance ($F_{(1,5)}=8.24$, $P<0.003$) on the position of D_{max} along the finger path. The average durations of finger paths were 855 ± 139 ms, 508 ± 41 ms, 882 ± 106 ms, and 556 ± 67 ms, for the *NDI*, *FDI*, *ND2* and *FD2* conditions, respectively. There was a highly significant effect of movement speed ($P<0.001$) due to the instructions given to subjects, but there was no effect of target distance ($P>0.05$).

Discussion

The purpose of the present study was to investigate the coordination between equilibrium and arm trajectories during pointing beyond arm's length. Based on previous results reported in the literature, one should have expected a minimization of horizontal CoM displacement in order to compensate for equilibrium perturbations caused by pointing movements. On the contrary, we found that when subjects reached the target located at different distances the CoM was not stabilized but accelerated toward the targets, moving inside the base of support. This result contrasts with previous studies which have suggested that equilibrium is significantly affected by arm movements in the standing position and that an invariance of the anteroposterior CoM position is necessary to achieve the goal of the task.

The significant CoM displacements recorded during the present task extend the results previously obtained when subjects had to grasp and lift a bar located on the ground (Stapley et al. 1998, 1999) and demonstrate that CoM forward displacement is also present in a whole body pointing task. Together, these results support the idea that during such tasks, rather than a strict CoM stabilization by the compensation of mechanical perturbations due to upper limb movements, the equilibrium strategy consists of controlling CoM acceleration toward the target.

However, an alternative hypothesis could be that CoM displacement reveals a hidden constraint of the task and that target reaching cannot be performed without CoM displacement. This possibility has been previously tested through a simulation study for a similar whole body reach and grasp movement (Stapley et al. 2000). The results of the simulation showed that the two constraints of hand trajectory for object grasp and CoM stabilization could theoretically be fulfilled, suggesting that CoM displacement was not task dependent and did not represent a necessity of the whole body grasping task. Consequently, for the present pointing task in which subjects did not have to grasp and lift a load (which incidentally represents an additional equilibrium constraint compared to the present pointing task), and which can be performed without trunk bending from a squatting position (see "Materials and methods"), it seems difficult to accept the idea that the shift of the CoM is task dependent. Indeed, if the task used here necessitated CoM displacements, we should have recorded greater (or at least similar) CoM displacements during fast pointing movements to the distant target compared to normal velocity.

However, our results showed smaller CoM displacements for rapid pointing movements.

Besides addressing the recurrent issue of CoM control within the support base, our study has also considered how equilibrium is maintained while the CNS predicts the mechanical consequences of CoM acceleration upon arm pointing movements. In our view, arm trajectory analysis during standing is thus an important medium for understanding how the brain resolves such a dichotomy.

Hand path

The analysis of arm kinematics showed that subjects reached the targets with curved finger paths. This result is in agreement with other studies performed in the sagittal plane from the sitting position (Atkeson and Hollerbach 1985; Pellegrini and Flanders 1996; Papaxanthis et al. 1998), where arm trajectories were found to be curved. Furthermore, it suggests that curved hand paths are specific to the sagittal plane whatever the subject's position, sitting or standing, and contrast with the relatively straight end-point paths previously obtained in the horizontal plane (Morasso 1981; Abend et al. 1982; Osu et al. 1997; Haggard and Wing 1998).

An important new result highlighted by the present study was that the shape of the path, but not the overall curvature, changed with target distance and movement speed. Indeed, the position of D_{max} along the finger path increased for distant target approaching approximately the middle of the path.

This result, associated with the finding that finger paths were significantly curved for the experimental conditions tested, may be attributed to a perturbing effect of CoM acceleration on arm movement execution. In other words, we could interpret this finding as an inaccuracy in arm trajectory planning because of different spatial and temporal characteristics of the arm and trunk movement constraints specific to whole body pointing movements. Indeed, flexion of the body strongly contributes to the vertical component of hand movement, in addition to a greater trunk inertia, a segment which moves more slowly compared to the arm. Nevertheless, the following experimental facts seem to indicate, however, that such an assumption is not substantiated.

If subjects planned equivalent paths in all the conditions but were unable to achieve such a path due to uncontrolled mechanical effects of arm and trunk forward acceleration, path curvature should have been more greatly affected at rapid speed, because of dramatic increases in dynamic torques associated with the faster movements.

However, in the rapid speed condition of the present study while the time available to regulate the movement decreased, mechanical changes due to fast movement execution did not significantly affect path curvature. In addition, strong evidence against such an interpretation is that for movements to the near target (the experimental condition in which equilibrium constraints were reduced compared to other conditions) the initial component of

the pointing movement was oriented at about an angle of 45° with respect to the line connecting initial and final positions. Therefore, in the case of such an inaccuracy hypothesis, one has to accept the idea (although somewhat questionable) that the CNS performs arm movements with such large differences between the actual trajectory and a programmed straight line.

Moreover, dynamic and equilibrium constraints should also affect movement time as has been previously reported for the effects of inertial anisotropy on the execution time of horizontal arm movements (Gordon et al. 1994). In our study the duration of arm movement execution was not affected by target distance for the two speeds tested, indicating that dynamic changes due both to different joint angular displacements (when pointing to further target distances) and movement speeds are anticipated. Rather than simple inefficiencies in programming or execution, our results seem to indicate the adoption of different hand movement strategies as a function of equilibrium constraints.

The present results contrast with the data obtained when seated subjects are required to move the trunk in order to reach a target placed outside his/her extrapersonal space. In this case, the hand moves along a similar path despite there being multiple segments involved (Kaminski et al. 1995; Ma and Feldman 1995). These authors suggested that two independent synergies existed: one ensuring the hand reaching movement to the target, and the other coordinating trunk and arm movements, leaving the position of the endpoint unchanged. In a similar kind of experiment, Saling et al. (1996) suggested that movements may be programmed in terms of reaching endpoint kinematics in space. Such independent synergies may indeed be generated in movement without equilibrium constraints. Interestingly, Flanders et al. (1999) found that during a reaching task where subjects were forced to take a step as the target was located beyond arm's length, hand path was speed invariant.

The interaction of focal and equilibrium task components

Simultaneous arm and CoM forward movements are important mechanical components that the CNS must take into consideration in order to point to the target. The CNS must know the simultaneous effects of one component (equilibrium) on the other (arm trajectory), or vice versa. A curved hand trajectory performed at rapid speed will be a greater perturbation to whole body equilibrium compared to a straight hand path, and this must necessarily be taken into account during the planning of the task. It may indeed explain the observed changes in finger path with speed in the present study.

One possibility of integrating focal and equilibrium components of the task in the same motor plan would be that the CNS builds up such whole body reaching strategies by using internal models similar to those described by Wolpert and Kawato (1998) and Kawato (1999). We propose that during motor learning of such movements

the CNS would create an inverse and a forward model. The inverse dynamic model would include the mechanical interaction of the moving limbs with the environment and the reciprocal effects of the two components of the task, while the forward model would associate sensory signals of position and velocity to motor commands, thereby allowing the prediction of the future position of the arm or the CoM during movement execution given the actual motor command (as proposed by Miall and Wolpert 1996 and Wolpert et al. 1995a, 1995b). This internal model allows subjects to overcome the problem of both minimizing whole body horizontal momentum and producing the required forward angular momentum to rapidly reach the target. It is well known that the value of the subtraction between the positions of the CoM and CoP is directly proportional to CoM acceleration (Morasso and Schieppati 1999). We propose that the CNS solves such a problem by using greater anteroposterior displacements of the CoP (Stapley et al. 1998), which needs an accurate internal knowledge of limb dynamics and kinematics. In this way, ankle moments increase, thus fulfilling the need both for increased speed of whole body movement toward the target and for the conservation of equilibrium. In the same vein, it can be noted that speed had a greater effect upon peak-to-peak CoP displacements than did distance, as during rapid movements, CoM displacements decrease. Optimization of equilibrium control during such a goal-directed task may make pointing movements more accurate.

Conclusion

The present study has shown that end effector trajectories were curved during a whole body pointing task and that the shape of finger path varied according to movement speed and target distance. These results indicate a difference between the planning and execution of whole-body pointing and simple upper-limb point-to-point reaching movements which have revealed kinematic invariants despite modifications to the speed of the movement, target location or load. Results from the present study suggest that: (1) the straight-path model cannot be systematically applicable for complex movements, (2) equilibrium constraints play a role in end-point trajectory formation, and (3) focal and equilibrium components of the movement are functionally difficult to separate. As an alternative proposal to a hierarchical model whereby the postural component would be subordinate to the focal one and would assist in its execution, we also proposed that when pointing involves body movement, motor commands to upper and lower limbs would share a common goal of displacing the CoM forwards within the BoS in order to achieve a postural transition.

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