

# Sequential control signals determine arm and trunk contributions to hand transport during reaching in humans

Elena Rossi, Arnold Mitnitski and Anatol G. Feldman

Neurological Science Research Center, Department of Physiology, University of Montreal and Research Center, Rehabilitation Institute of Montreal, Montreal, Quebec, Canada H3S 2J4

When reaching towards objects placed outside the arm workspace, the trunk assumes an active role in transport of the hand by contributing to the extent of movement while simultaneously maintaining the direction of reach. We investigated the spatial–temporal aspects of the integration of the trunk motion into reaching. Specifically, we tested the hypothesis that the efficiency (‘gain’) of the arm–trunk co-ordination determining the contribution of the trunk to the extent of hand movement may vary substantially with the phase of reaching. Sitting subjects made fast pointing movements towards ipsi- and a contralateral targets placed beyond the reach of the right arm so that a forward trunk motion was required to assist in transporting the hand to the target. Sight of the arm and target was blocked before the movement onset. In randomly selected trials, the trunk motion was unexpectedly prevented by an electromagnet. Subjects were instructed to make stereotypical movements whether or not the trunk was arrested. In non-perturbed trials, most subjects began to move the hand and trunk simultaneously. In trunk-blocked trials, it was impossible for the hand to cover the whole pointing distance but the hand trajectory and velocity profile initially matched those from the trials in which the trunk motion was free, approximately until the hand reached its peak velocity. The arm inter-joint co-ordination substantially changed in response to the trunk arrest at a minimal latency of 40 ms after the perturbation onset. The results suggest that when the trunk was free, the influence of the trunk motion on the hand trajectory and velocity profile was initially neutralized by appropriate changes in the arm joint angles. Only after the hand had reached its peak velocity did the trunk contribute to the extent of pointing. Previous studies suggested that the central commands underlying the transport component of arm movements are completed when the hand reaches peak velocity. These studies, together with the present finding that the trunk only begins to contribute to the hand displacement at peak hand velocity, imply that the central commands that determine the contributions of the arm and the trunk to the transport of the hand are generated sequentially, even though the arm and trunk move in parallel.

(Received 2 June 2001; accepted after revision 11 October 2001)

**Corresponding author** A. G. Feldman: Research Centre, Rehabilitation Institute of Montreal, 6300 Darlington, Montreal, Quebec, Canada H3S 2J4. Email: feldman@med.umontreal.ca

A central question of how the nervous system integrates multiple degrees of freedom (DFs) of the body in the motor task (Bernstein, 1967) has been addressed in many studies, particularly in those analysing arm-reaching movements involving the trunk (Kaminski *et al.* 1995; Ma & Feldman, 1995; Saling *et al.* 1996; Wang & Stelmach, 1998, 2001; Flanders *et al.* 1999; Gréa *et al.* 2000; Pigeon *et al.* 2000; Adamovich *et al.* 2001). An interesting aspect of this co-ordination is related to the difference in the inertia of the trunk and arm segments. As a more massive body, the trunk cannot move as fast as the arm and, to overcome this difference, control levels may slow the arm motion to effectively synchronize it with the trunk motion (Poizner *et al.* 2000). Reaching a target, however, may be equally efficient without synchronization, as in the case when the arm moves faster than, and stops moving before, the trunk (Wang & Stelmach, 1998; Archambault *et al.* 1999;

Adamovich *et al.* 2001). When the trunk is intentionally involved in reaching to objects placed within the arm’s reach, the influence of the trunk movement on the hand position is neutralized by appropriate changes in the arm joint angles so that the hand trajectory remains invariant (Ma & Feldman, 1995; Adamovich *et al.* 2001), a co-ordination called the ‘compensatory arm–trunk synergy’.

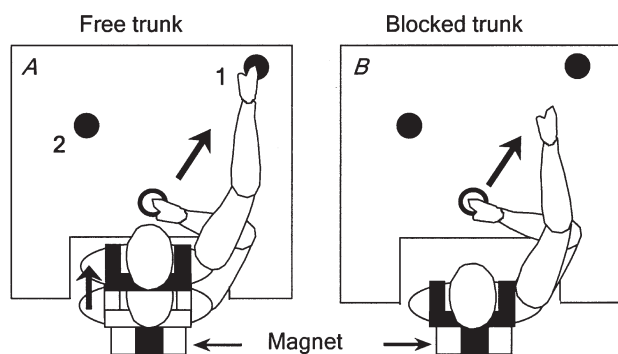
The compensatory synergy concept was further developed to include the notion of gain control (Pigeon & Feldman, 1998; Pigeon *et al.* 2000). This formulation made the concept applicable to movements in which trunk involvement is determined by the task rather than by instruction, as is the case in movement beyond the reach of the arm. Thus, efficiency of the compensatory synergy is characterized by a coefficient called gain ( $g$ ), so that  $g = 1$  when the influence of the trunk motion on the hand position

is fully compensated and  $g = 0$  when no compensation is made. It is likely that the gain can be specified depending on the distance to the target. For example in movements to remote objects, the gain of the compensatory synergy should be attenuated ( $g < 1$ ) in order to allow the trunk to contribute to the pointing extent.

Achieving the required movement extent may not be the only aspect of the integration of trunk motion into reaching. In some behavioural situations, the directions of the trunk and hand motion may not coincide. For example when taking a laterally located glass from a dinner table, we can simultaneously lean the trunk forward, in the sagittal plane, to hear a person on the opposite side of the table better. In this case, while producing the trunk motion, control systems should prevent a change in the hand movement direction, which also requires appropriate co-ordination of the arm and trunk motions. Since these motions may be desynchronized in terms of peak velocities, the gain of the arm–trunk co-ordination may not be constant during reaching.

In the present study, we investigated the spatial–temporal aspects of the integration of the trunk motion into reaching towards targets placed beyond the reach of the arm. Specifically, we tested the hypothesis that the arm–trunk compensatory co-ordination, and thus the contribution of the trunk to the movement extent, may substantially vary depending on the phase of reaching.

Subjects made hand movements in a diagonal direction while leaning the trunk sagittally. The trunk movement was thus intentionally constrained to influence not only the hand movement extent but also direction. There are



**Figure 1. Schematic diagram showing the trunk arrest paradigm for pointing to targets placed beyond the reach of the arm**

A harness with an electromagnetic plate attached to it on the back and an electromagnet attached to the wall were used to block the trunk movement in randomly selected trials. Shown are an initial and a final configuration of the arm and trunk; an initial target (○), and ipsilateral (1) and contralateral (2) targets. A, motion of the arm (diagonal arrow) to the ipsilateral target when the trunk motion (vertical arrow) was not obstructed. B, same as in A when the trunk was blocked.

several possible strategies for combining the arm and trunk motion in pointing to targets beyond the reach of the arm. One strategy would be to initiate the trunk contribution to the hand displacement as soon as the trunk begins to move. Another strategy would be to initiate the trunk contribution some time after the trunk movement onset, when the arm has reached the limit of its contribution to hand movement extent. To determine which strategy was actually used by subjects, the trunk motion was blocked in randomly selected trials, making it impossible for the hand to cover the whole pointing distance. This trunk arrest paradigm has previously been used in the analysis of movements within the reach of the arm (Adamovich *et al.* 2001). In movements beyond the reach, if subjects employed the first strategy in non-perturbed trials, the effect of trunk arrest would be a change in the hand movement direction. In the case of the second strategy, the hand trajectory could remain invariant despite the trunk arrest, up until the arm reached the maximal extent. In addition, the changes in the arm inter-joint co-ordination in response to the trunk arrest may be indicative of the control strategies employed by the nervous system in response to sudden changes in the number of DFs participating in the movement. Some results of the present study have been reported in abstract form (Feldman *et al.* 2001).

## METHODS

### Experimental procedures

Seven right-hand-dominant healthy subjects (students, age 19–26 years) participated in this study. They gave written, informed consent approved by the Ethics Committee of the Montreal Institute for Rehabilitation. All procedures used were in accordance with the Declaration of Helsinki.

Subjects were seated in a cut-out section of a table limiting the range of possible directions of trunk bending ( $\pm 15$  deg from the sagittal plane). The initial target (a light-emitting diode embedded in the table; Fig. 1, open circles) was at a distance of 30 cm from the midline of the chest directly in front of the subject. On a 'ready' cue (light), subjects lifted their right (dominant) arm 2–3 cm above the table so that the tip of the index finger (the arm endpoint) was above the initial target and the forearm–shoulder plane was approximately parallel to the surface of the table. In response to an auditory 'go' signal from a computer, subjects moved the hand from the initial position to one of two targets placed beyond the reach of the arm in either the ipsi- or contralateral workspace (Fig. 1, filled circles). They were required to bend the trunk and the head as a single unit, thus minimizing the relative head-on-trunk displacement. Lateral inclinations of both hand and trunk were permitted in the limits determined by the cut-out section of the table.

The final targets were placed at a distance exceeding the full length of the arm by 30%, at the angles of about 45 deg and 30 deg to the sagittal plane, for ipsi- and contralateral targets, respectively. The length of the arm was measured from the acromion to the tip of the outstretched index finger. To reach the target, subjects were forced to combine arm movements with a forward trunk motion

of about 18–28 cm at the shoulder level produced by a hip flexion, and, when the arm moved backward, to return the trunk to the initial, vertical position.

Subjects received some prior training with full vision (three to five trials) but without trunk perturbations. Subjects wore liquid crystal glasses (Translucent Technologies, Inc., Plato S2 Spectacles) that became opaque about 100 ms before the movement onset and thus blocked vision of the target and the arm. After a holding period of 200–500 ms at the final position, the subject moved the arm back to the initial position, where vision was restored. Movements were thus produced to remembered targets, without knowledge of results (Poizner *et al.* 1998; Adamovich *et al.* 2001).

Subjects wore a harness with an electromagnetic plate fastened posteriorly. Before the ‘go’ signal, the plate was locked to an electromagnet attached to the wall behind the stool on which the subject sat. In 70% of 60 trials, the electromagnet was unlocked 100 ms after the ‘go’ signal, i.e. before the movement onset so that the trunk movement was unobstructed. In 30% of randomly selected trials, the electromagnet remained locked before and after the ‘go’ signal and thus the trunk motion was mechanically prevented, which resulted in an isometric pressure on the harness (the residual trunk motion was less than 3 cm at the level of the shoulder). Movements to the ipsilateral and contralateral targets were made in two separate experiments.

Subjects were allowed to touch the surface of the table only after the arm returned to the initial position, when the glasses became transparent. They were instructed to make movements in a stereotypical way (mean peak velocity of the hand was  $114 \text{ cm s}^{-1}$ , range  $80\text{--}210 \text{ cm s}^{-1}$ ). They were informed that the trunk arrests would be made in an unpredictable manner and they should not anticipate the experimental condition in each trial, nor make corrections of the final hand position in the event of trunk arrest.

#### Data recording and analysis

The analysis focused on movements directed towards but not from the ipsilateral and contralateral targets. Although pointing movements produced above the surface of the table could be considered planar, a 3-D analysis of kinematics was made. The endpoint and trunk positions were obtained using an optoelectronic, 3-D motion analysis system (Optotrak, sampling rate 200 Hz). Infra-red light-emitting markers were placed on bony landmarks – the tip of the index finger, the head of the ulna (wrist), lateral epicondyle (elbow), right and left acromion processes (shoulders), mid-sternum (trunk). The co-ordinates of the fingertip and sternal markers were used to compute, respectively, the arm endpoint and trunk trajectories. Tangential hand and trunk velocities were computed based on a five-point differentiation algorithm applied to respective position data.

We anticipated that since the trunk moved predominantly in the sagittal plane, the most substantial effect of the trunk arrest would be a change in the sagittal components of the hand trajectory and velocity profiles. Therefore, we computed and compared these components for non-perturbed and trunk-blocked trials.

For data averaging, movements were aligned with respect to their onsets. Movement onsets and offsets for the endpoint and trunk were determined for each trial using the time at which hand tangential velocity rose above and fell below 3% of its peak value, respectively. The mean traces ( $\pm 1$  S.D.) for all measured variables were computed for each target in non-perturbed and trunk-blocked movements. For each variable, the onset of divergence of the traces from the two types of trials was identified as the point at

which the mean trace from the trunk-blocked trials first left the  $\pm$  S.D. zone for the mean trace from the non-perturbed trials.

The analysis of inter-joint co-ordination focused on the relationship between elbow flexion/extension and shoulder horizontal adduction/abduction angles. The changes in these angles during arm movements were the most substantial compared to other arm DFs such as shoulder protraction/retraction (mean  $\pm$  S.D. value  $4.1 \pm 2.0$  deg; measured in combined movements as the rotation of the vector defined by the two shoulder markers; cf. Pigeon & Feldman, 1998). Elbow and shoulder angles were computed based on the dot product of vectors defined by the co-ordinates of appropriate markers. The shoulder horizontal adduction/abduction angle was measured as the horizontal projection of the angle between two vectors, one defined by the right and left shoulder markers and the other parallel to the humerus between the right shoulder and elbow markers. The latency of divergences in the angle–angle diagrams in response to perturbation was measured relative to the onset of the divergence of the trunk velocities in the trunk-free and trunk-blocked trials.

Repeated measures ANOVAs for the two conditions (combined, arrested) and the two target locations (ipsi- and contralateral) were performed to assess the effect of trunk arrest on the measured variables in each experiment. The level of significance of  $P < 0.05$  was used in all tests.

The term ‘hand trajectory’ will refer to the trajectory of the tip of the index finger. The terms ‘endpoint trajectory’ and ‘hand trajectory’ will be used as synonyms.

## RESULTS

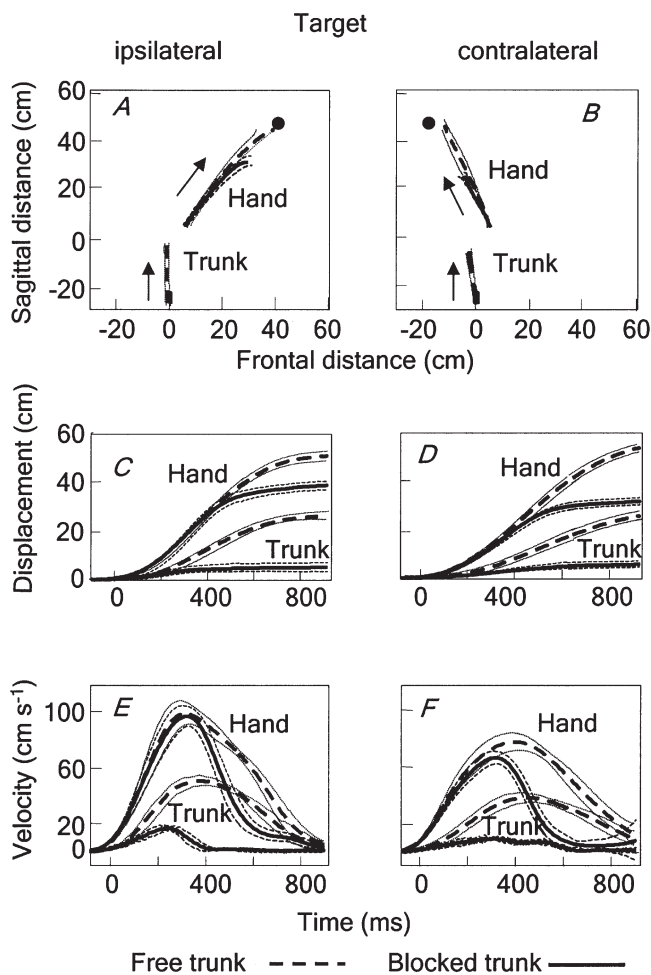
The trunk trajectory did not deviate more than 7 deg from the sagittal plane. Trunk motion was thus basically produced by hip rotation with possible sagittal contributions from other degrees of freedom (DFs) along the spinal column. The mean peak value of the hand tangential velocity in the combined movements to either of the two targets was about two times higher than the trunk peak velocity (Fig. 2*E, F*). In trunk-blocked trials, the trunk displacement was reduced to about 3 cm and the peak velocity to about  $16 \text{ cm s}^{-1}$ . The trunk velocity profiles in the combined and arrested movements started to diverge after some delay (typically  $< 60$  ms), depending on the subject and target.

The trunk began to move and ceased moving practically simultaneously with the hand but the hand and trunk peak velocities were not synchronized (Fig. 2*E, F*); peak velocity of the trunk occurred significantly later than that of the endpoint, by  $75 \pm 44$  ms (mean  $\pm$  S.D.) for the ipsilateral and by  $50 \pm 37$  ms for the contralateral target ( $P < 0.05$ ).

When the trunk was arrested, the hand could not cover the whole pointing distance (Fig. 2*A–D*). However, the hand trajectory and velocity profiles initially matched those from the trials in which the trunk motion was unobstructed and began to diverge comparatively late in the movement, about  $420 \pm 50$  ms for the group, for ipsilateral and  $460 \pm 80$  ms for contralateral target, measured from the beginning of the arm movement (Fig. 2*E, F*). The

divergence occurred near the peak velocity of the hand movement. Depending on the target and subject, the divergence point could occur simultaneously, after or before the hand peak velocity (Fig. 2*E, F*). The time from the peak velocity to the divergence point for the group was  $40 \pm 100$  ms for the ipsilateral and  $10 \pm 120$  ms for the contralateral target.

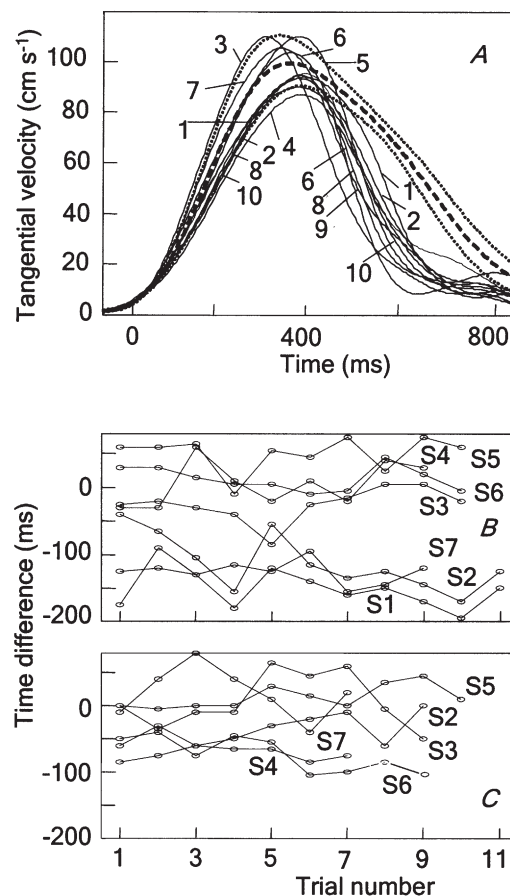
The effect of the trunk arrest became noticeable only after the hand had covered a substantial part of the movement distance in non-perturbed movements ( $56 \pm 13\%$  for the ipsilateral and  $63 \pm 13\%$  for the contralateral target).



**Figure 2. Typical kinematic effects of the trunk arrest in movements to targets located beyond the reach of the arm**

There are shown: mean traces for conditions when the trunk motion was not obstructed (thick dashed lines) or blocked (thick solid lines); thin lines for  $\pm$  s.d. for the means; arrows in *A* and *B* for the hand movement directions, and filled circles for targets. In free-trunk movements, subject S5 (left panels) leaned the trunk forward by about 23 cm (measured at the level of the hand) and subject S4 (right panels) by about 21 cm. These displacements were reduced to about 3 cm in trials in which the trunk movement was mechanically blocked. Despite these differences in the trunk motion, the endpoint (hand) trajectories (*A, B*), displacements along them (*C, D*) and velocity profiles (*E, F*) initially followed the paths in trials in which the trunk motion was free.

Although trials were randomized and subjects were instructed not to anticipate conditions in the forthcoming trial, this may have been insufficient to prevent changes in the control strategy in subsequent, blocked-trunk trials. Such changes also may have been masked by the averaging of kinematic curves. Velocity profiles in the sequential blocked-trunk trials were variable but the variability did not exceed that in free-trunk trials (Fig. 3*A*). We hypothesized that, if present, an adaptive control strategy would be associated with changes in the instance at which the hand reached peak velocity in sequential trunk-blocked trials. In Fig. 3*B*, these instances are shown as a function of the trial number for blocked-trunk trials (the mean time at which the hand reached its peak velocity in free-trunk trials was subtracted from these instances). The consistency of the response to the trunk block was estimated by computing Pearson correlation coefficients between the trial number



**Figure 3. Kinematic characteristics of hand movements to the ipsilateral target in individual blocked-trunk trials**

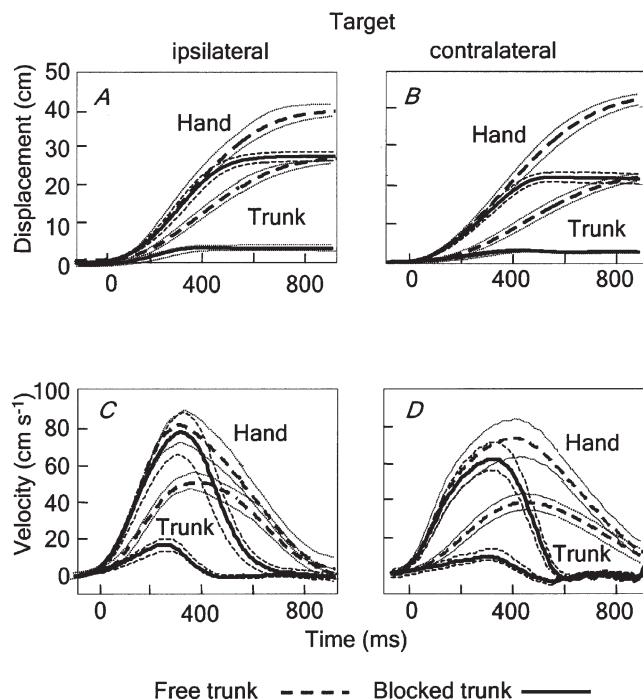
*A*, velocity profiles in individual blocked-trunk trials superimposed on the mean  $\pm$  s.d. (dashed and dotted lines, respectively) velocity profiles for free-trunk trials for subject S5. The sequential numbers of the blocked-trunk trials are shown near the curves. *B* and *C*, the time of the occurrence of the maximum peak velocity in sequential blocked-trunk trials for ipsilateral (*B*) and contralateral (*C*) targets, for different subjects. The mean time at which the hand reached its peak velocity in free-trunk trials was subtracted from these data.

and the time difference between the velocity peak for a given trunk-blocked trial and the averaged peak velocity for the free-trunk movements. Only one subject in each condition (S5 for the ipsi-lateral and S2 for the contralateral target) showed a regular change in the time difference between velocity peaks. Of these two, only in one subject (S5) was there a tendency to decrease the time difference in sequential blocked-trunk trials and thus improve the matching of hand movements in the two types of trials. In the majority of cases, the correlation coefficients were insignificantly different from zero ( $P < 0.05$ ), implying that there were no systematic changes in the sequential responses to the trunk arrest.

Since the trunk moved in the sagittal plane, the most substantial deflection of the hand trajectory in blocked-trunk trials would also be in the sagittal plane, towards the body, if this deflection were not neutralized by appropriate changes in the arm joints. In this connection, we also computed sagittal components of the hand displacement and velocity profile. The effects of the trunk arrest on these (Fig. 4A–D) were similar to those of the tangential components (Fig. 2C–F). Like the tangential components, the sagittal components of hand displacement and velocity profiles began to diverge only when the hand approached or reached its peak velocity (Fig. 4C, D). At the divergence

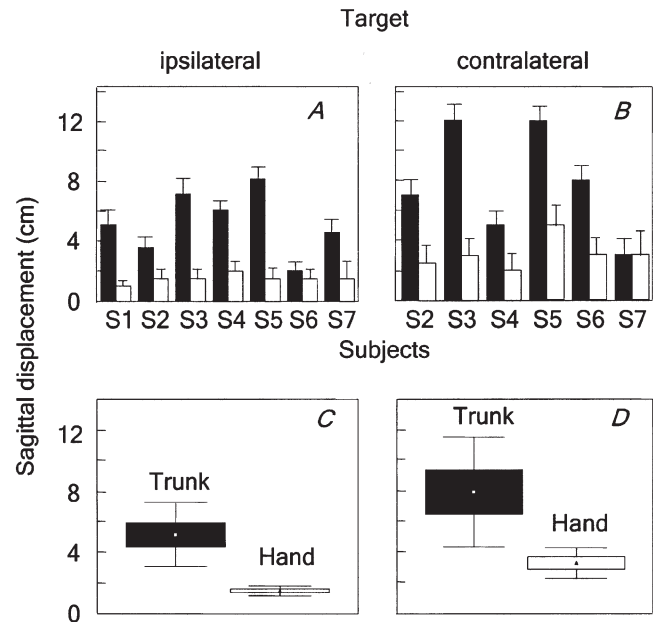
point, the mean sagittal distance between the hand trajectories in the non-perturbed and trunk-blocked trials was  $1.5 \pm 0.3$  cm for the ipsilateral and  $3.1 \pm 1.0$  cm for contralateral target. At the same time, the sagittal distance between the trunk trajectories from the two types of trials was significantly greater:  $5.2 \pm 2.1$  and  $7.8 \pm 3.6$  cm for movements to respective targets (Fig. 5). These findings suggest that the influence of the trunk displacement on the hand position was compensated by appropriate changes in the arm joint angles.

In contrast to the endpoint trajectories and velocity profiles, the elbow and shoulder angles substantially changed in response to the trunk arrest, as could be seen from the comparison of individual kinematic characteristics for the blocked-trunk trials with the respective mean characteristics for free-trunk trials (Fig. 6) or from the comparison of the mean kinematic characteristics in the two types of trials (Figs 7 and 8). While making non-perturbed movements to the ipsilateral target, subjects usually did not fully extend the elbow (Figs 7A and 8A, dashed curves). In blocked-trunk trials, they increased the elbow extension (Figs 7A and 8A, continuous curves). Simultaneously, they inverted the movement direction at the shoulder, from abduction in the non-perturbed trials



**Figure 4.** Sagittal components of the mean displacement and velocity of the hand and trunk for the subjects as in Fig. 2

The displacement and velocity profiles were preserved until about the peak velocity of the hand movements, despite the substantial differences in the trunk kinematics in trials in which trunk movements were unobstructed or blocked.



**Figure 5.** The individual (A, B) and group mean sagittal trunk displacements (C, D) in non-perturbed trials during the time when the hand trajectory remained invariant despite the trunk arrest

The residual trunk displacement in the trunk-blocked trials was subtracted from the total trunk displacement in the non-perturbed trials. The difference was compared to the sagittal displacement of the hand at the time when the mean hand trajectory in the trunk-blocked trials first left the zone of  $\pm$  S.D. for the mean hand trajectory in the trunk-free trials. The trunk displacement was significantly greater than the hand displacement, for both targets.

to adduction in the trunk-blocked trials (Figs 7C and 8C). These strategies were observed in four subjects. In the remaining three subjects, the elbow movements were not significantly different in the non-perturbed and trunk-blocked trials. At the same time, these subjects also inverted the direction of the shoulder horizontal adduction in response to the trunk arrest. While making movements to the contralateral target, subjects preserved the magnitude but changed the timing of the elbow extension and increased the magnitude of the shoulder horizontal adduction in response to the trunk arrest (Figs 7B, D and 8B, D).

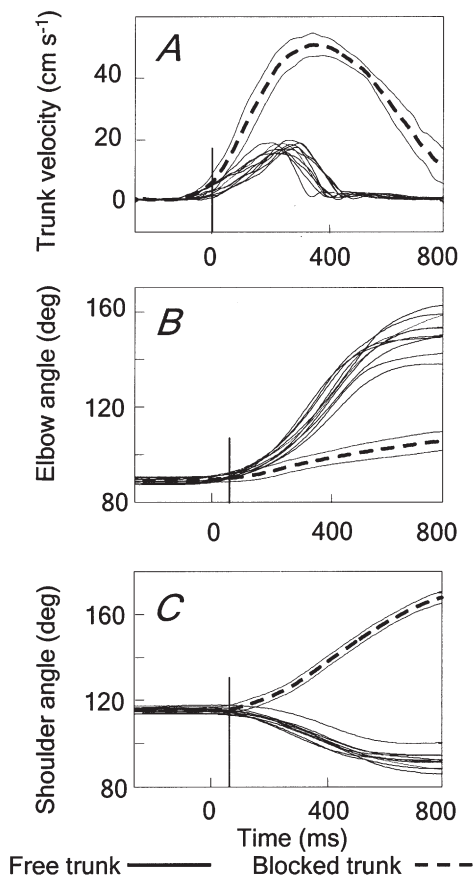
A typical example of averaged elbow–shoulder diagrams is shown in Fig. 9, demonstrating substantial changes in the pattern of inter-joint co-ordination in response to the trunk arrest, especially for movement to the ipsilateral target (Fig. 9A). For this target, the co-ordination profiles for the non-perturbed and trunk-blocked trials in two subjects began to diverge with a minimal latency of 40 ms (for all subjects, the mean latency was  $85 \pm 35$  ms). For

movements to the contralateral target, the changes in the elbow–shoulder co-ordination in response to the trunk arrest were smaller but also evident (Fig. 9B). They occurred at a minimal latency of 62 ms (for the group, mean latency was  $105 \pm 43$  ms; Fig. 10). In contrast, the hand trajectories in non-perturbed and trunk-blocked trials began to diverge significantly ( $P < 0.01$ ) later: the mean latencies were  $346 \pm 79$  ms for the ipsilateral target and  $384 \pm 118$  ms for the contralateral target (computed from the onset of divergence in the trunk velocity profiles to the onset of divergence in the sagittal components of hand velocity profiles).

## DISCUSSION

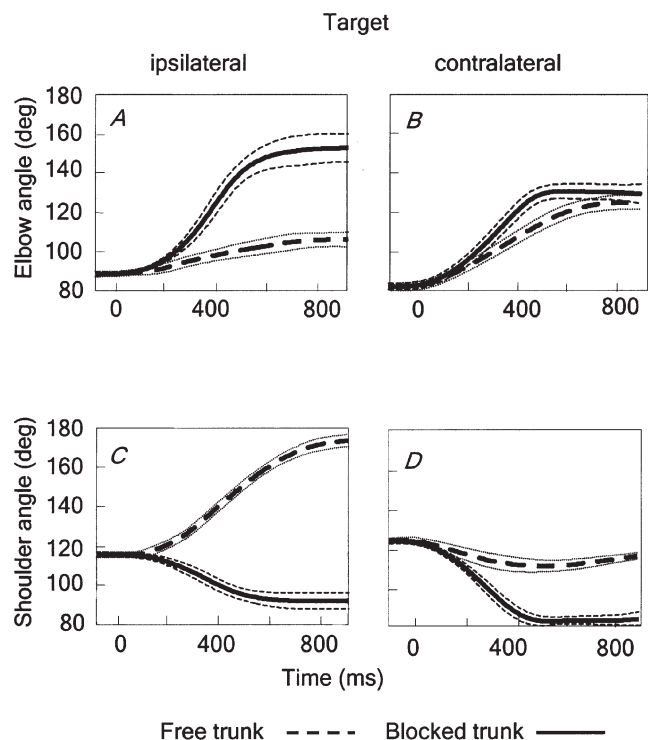
### Basic findings

We investigated the spatial–temporal aspects of the integration of the trunk motion into reaching towards targets placed beyond the reach of the arm. For movements to each target, trunk arrest made it impossible for the hand to cover the whole pointing distance. The hand trajectory and velocity profile initially matched those from trials in which trunk motion was unobstructed, approximately until the time when the hand movement speed reached its maximum or when the hand had covered about a half of the entire movement distance in non-perturbed trials. Although the hand trajectory remained invariant throughout this



**Figure 6.** Effects of trunk arrest on the elbow angle and shoulder horizontal adduction/abduction angle in hand movements to the ipsilateral target

A, trunk velocity profiles in individual blocked-trunk trials superimposed on the mean  $\pm$  s.d. velocity profiles for free-trunk trials. B and C, similar comparison for elbow and shoulder angles. Vertical lines show the average time when the corresponding curves in the two types of trials began to diverge.



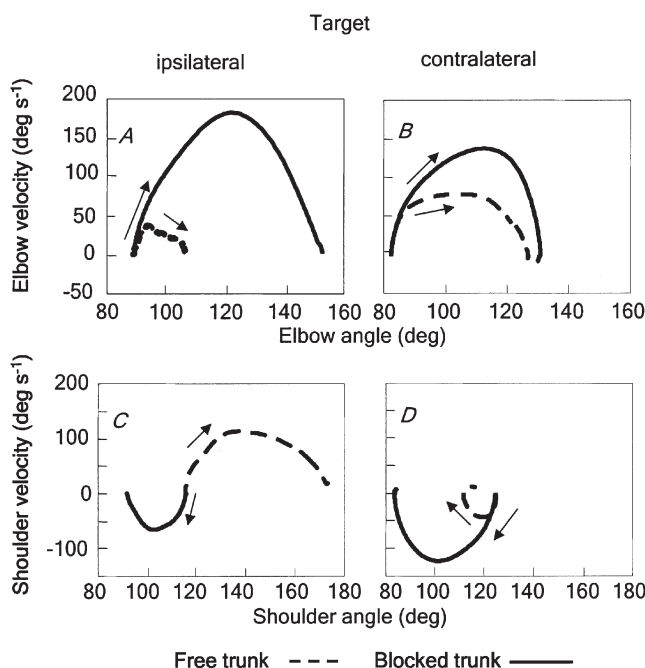
**Figure 7.** Changes in averaged elbow angle and shoulder horizontal adduction/abduction angle in response to the trunk arrest

Larger numbers on vertical axes show elbow extension and shoulder abduction.

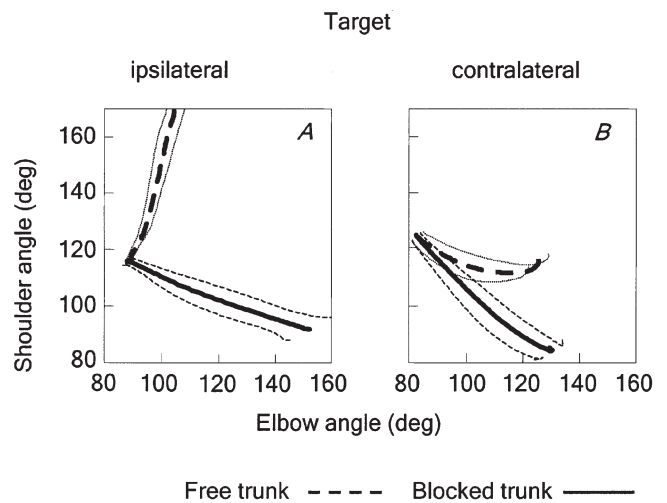
initial phase, the arm inter-joint co-ordination substantially changed when the trunk was blocked, beginning from a minimal latency of 40 ms.

**Neutralization of the influence of the trunk on hand transport during the early phase**

In the present study, the horizontal sagittal displacement of the shoulders due to the trunk motion in non-perturbed trials exceeded several centimetres before the hand trajectory began to diverge from that in the perturbed trials. If transmitted to the hand, this displacement would influence the direction and velocity of the hand movement. If this were the case, then the force resulting from the trunk acceleration and driving the arm forward would decrease with the trunk arrest, as would the kinetic energy transmitted from the trunk to the arm (not less than by a factor of six, according to our estimation based on a comparison of the trunk peak velocities in the two types of trials). Interactive torques (which are proportional to the product of trunk and joint velocities) would also decrease in trunk-blocked trials. Therefore, if the trunk actually contributed to the hand motion before the endpoint peak velocity, a deflection of the hand towards the body in response to the trunk arrest would be observed. Such a deflection, starting from the very beginning of hand movement, has actually been observed in specific experiments in which the trunk motion did contribute to the hand motion (see Fig. 8 of Adamovich *et al.* 2001). In the present study, the hand trajectory and velocity profile in the trunk-blocked trials began to diverge from those in free-trunk trials only when the hand had covered about half the movement distance. It is possible that, prior to this

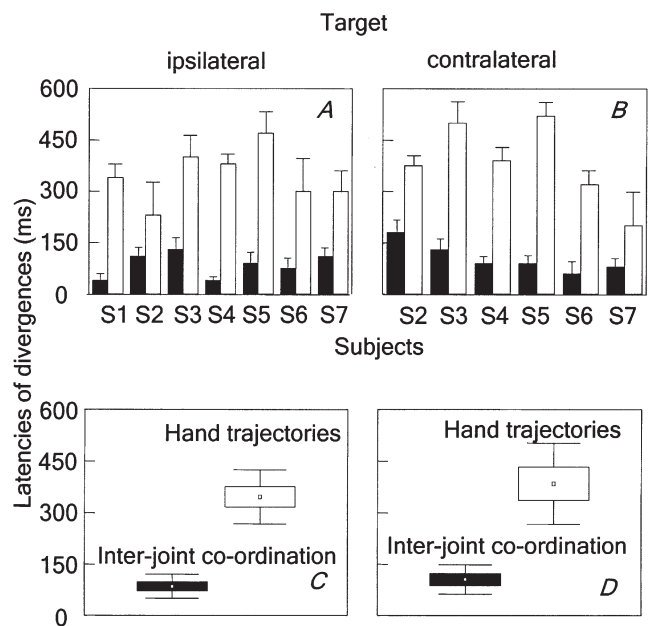


**Figure 8.** Effects of trunk arrest on the position/velocity curves (phase diagrams, averaged) for the elbow and shoulder horizontal adduction/abduction angles



**Figure 9.** Changes in the inter-joint co-ordination in response to the trunk arrest

point, central levels triggered changes in the arm joint angles in response to the trunk arrest to maintain the same direction of the hand trajectory despite the loss of the trunk contribution to it. This could be done, for example, by memorizing the trunk contribution made in free-trunk trials and transforming it into appropriate central commands to elbow and shoulder muscles in the trunk-blocked trials. It has been shown, however, that centrally triggered corrections of arm motion in response to trunk obstruction in randomly selected trials typically start after the hand had approached or reached the final position (for discussion see Adamovich *et al.* 2001). Therefore, in the present study, such triggered reactions were likely to occur



**Figure 10.** Latencies of changes in the inter-joint co-ordination in response to the trunk arrest (■) compared to the time when hand trajectories in the non-perturbed and trunk-blocked trials began to diverge (□)

too late to provide the observed invariance of the hand trajectory and velocity profile at the initial phase. Thus, the hypothesis that in free-trunk trials, the hand trajectory and velocity profile during the initial phase of arm movement essentially depended on the trunk motion conflicts with the observation that the hand trajectory remained invariant in blocked-trunk trials.

The finding that the trajectory and hand velocity profiles remained invariant during the initial half of the hand movement despite the trunk arrest can be explained in the following way. In non-perturbed trials, the influence of the trunk motion on the hand trajectory was actively neutralized by appropriate compensatory rotations in the arm joints linked to the trunk motion. These compensatory rotations could be cancelled with the trunk arrest by a short-latency reflex mechanism, leaving the hand trajectory unchanged. According to this hypothesis, the trunk arrest would result in substantial short-latency changes in the arm inter-joint co-ordination, which was the case in our study (Figs 9 and 10). Changes in the arm inter-joint co-ordination in response to the trunk arrest could be detected kinematically at a minimal latency of 40 ms. This finding suggests a rapid reflex compensatory mechanism driven by vestibular or/and proprioceptive afferent signals. Similar behaviour has been observed during reaching towards targets placed *within the reach* of the arm, except that in this case the whole hand trajectory remained invariant whether or not the trunk motion was prevented (Adamovich *et al.* 2001). In these experiments, the influence of the trunk movement on the hand position was also neutralized by appropriate compensatory rotations of the elbow and shoulder joints (Pigeon *et al.* 2000; Adamovich *et al.* 2001). In contrast, when arm movements were made towards a target moving with the trunk, the arm inter-joint co-ordination did not change in response to the trunk arrest but the hand trajectory rapidly deviated from that in the free-trunk trials (Adamovich *et al.* 2001). It is likely that, in the free-trunk trials of the first task, subjects actively modified arm joint angles to prevent the influence of the trunk motion on the hand displacement. In contrast, in the second task, the trunk-related compensatory modifications of the arm-joint angles were cancelled in order to allow the full expression of the trunk contribution to the hand displacement. In other words, by regulating the gain of the compensatory synergy, the nervous system could transform reaching from a frame of reference associated with the laboratory to one associated with the trunk.

Some possible mechanisms involved in the active compensation of the trunk influence on the hand trajectory in a reaching movement within the reach of the arm (Adamovich *et al.* 2001) or during the early phase of movement beyond the arm's reach, in the present study, include proprioceptive feedback or vestibulo-spinal

pathways targeting motoneurons of arm muscles (Brodal, 1974). The involvement of proprioceptive feedback could result, in particular, from motion at the hip joint. The involvement of vestibulo-spinal pathways could result from the trunk motion and associated motion of the head. These systems could induce short-latency changes in ongoing, whole body movements, as has been shown by galvanic stimulation for the vestibular system (Fitzpatrick *et al.* 1994) and neck muscle vibration for proprioception (Lackner, 1988; Ivanenko *et al.* 2000).

Taken together, the results of our study show that although the hand and trunk moved in parallel, the trunk began to contribute to the hand transport only at a later phase of movement, starting at about the time when the hand reached peak velocity. Indeed, the arm–trunk system is not the only one in which task-specific compensations may come into play. The best-known example is the vestibulo-ocular reflex compensating for the influence of head rotation on gaze shift (Guitton, 1992; Johnson & Sharpe, 1994). Another example is the compensatory change in the vocal tract configuration that preserves a sound despite mechanical perturbations of the jaw (Kelso *et al.* 1984). Spinal frogs, while preparing to wipe a stimulus from the skin, may broadly vary the limb configuration to attack the stimulus in the appropriate direction. Thereby the position of the wiping point of the limb before the attack remains unchanged, implying a compensatory mechanism (Fukson *et al.* 1980; Berkinblit *et al.* 1986). In humans, the arm configuration usually remains the same when subjects produce coactivation of antagonist muscles, implying the existence of some compensatory mechanism balancing the muscle torques when coactivation is made. Finally, compensatory changes in the joint configurations that leave the values of essential task variables unchanged have been reported during sit-to-stand and pistol shooting tasks (Sholtz & Schöner 1999; Sholtz *et al.* 2000).

### **Parallel–sequential organization of the arm–trunk co-ordination**

The organization of arm–trunk co-ordination during reaching can be discussed in the framework of different theories of motor control. We would like to emphasize that we do not consider our data as supporting or rejecting any one motor control theory. The purpose of this section is to determine an appropriate theoretical framework in which our data might be discussed.

Movements considered in the present study represented a transition from an initial to a final equilibrium configuration (posture) of the arm–trunk system and, therefore, our data are relevant to the classical problem in motor control regarding the relationship between posture and movement (Von Holst, 1936; Von Holst & Mittelstaedt, 1950/1973). Different motor control approaches offer different solutions to this problem. In this connection, we will compare three of these – the reafference principle



(Von Holst & Mittelstaedt, 1950/1973), an advanced version of the equilibrium-point (EP) hypothesis (the  $\lambda$  model; Feldman & Levin, 1995), and force control (FC) models. The latter are the models that, although varying in specific details, are united by the idea that the nervous system plans the desired movement trajectories and then, based on some internal representation of the motor apparatus, computes and specifies appropriate electromyographic (EMG) activity, muscle torques and forces to actualize the movement plan (Hollerbach 1982; Shadmehr & Mussa-Ivaldi, 1994; Wolpert *et al.* 1995).

The problem, as Von Holst characterized it, is that there are powerful neuromuscular mechanisms ('postural reflexes') that generate EMG activity and forces in order to resist perturbations that deflect the body from an initial posture. At the same time it is clear that the organism can intentionally adopt different postures. Each new posture adopted by the system might be considered as a deflection from the initial one. The deflection would result in resistance tending to return the system to its initial position. How then is an intentional movement from the initial posture and the achievement of a new posture of the body possible? We will refer to this problem as 'Von Holst's posture–movement paradox'. Indeed, our everyday experiences show that the nervous system has no problem moving the body or its segments away from an initial posture and stabilizing different postures. However, the explanation of how the body can intentionally move away from the initial posture without triggering resistance might be a critical problem for some approaches to motor control.

The posture–movement paradox could be resolved if postural reflexes were completely or partially suppressed by a central pattern generator when the transition to a new posture is made. Von Holst & Mittelstaedt (1950/1973) rejected this suggestion as conflicting with experimental observations. Specifically, any posture of the body is maintained by resisting reactions similar to those seen in the restoration of the initial posture in response to perturbations. Deafferented patients point to the general importance of proprioceptive reflexes in the stability of any posture. Even after years of practice, these patients are unable to stand or walk without assistance, or maintain a steady-state position of the arm without vision (e.g. Levin *et al.* 1995).

Von Holst and Mittelstaedt suggested that, to produce movement, the nervous system influences afferent systems in some way to reset the initial 'postural state' so that the same postural mechanisms that stabilized the initial posture would act to stabilize a new one. This is a major idea underlying Von Holst's 'reafference principle'. A similar idea is inherent in a version of the EP hypothesis, the  $\lambda$  model, with the addition that it explicitly indicates the parameters the control systems can reset to produce an

unopposed movement to a new posture (Feldman & Levin, 1995). Specifically, the model is based on the experimental finding that the nervous system can reset the muscle activation thresholds ( $\lambda$ s) and thus specify new spatial co-ordinates at which an equilibrium posture can be reached and maintained (Matthews, 1959; Asatryan & Feldman, 1965). With the resetting of activation thresholds, the initial posture appears to be a deflection from the newly specified posture. Therefore, the same neuromuscular mechanisms that produce EMG signals and forces in response to deflections from the initial position will produce, without any programming, EMG signals and forces tending to eliminate the deflection from the new posture and thus move the system to it (Feldman & Levin, 1995).

FC models cannot account for how the body or its segments (for example the arm) can actively change position without triggering resistance. The generation of muscle torques would result in the movement of body segments from an initial position. In response, mechanisms of postural stabilization would generate resistance that would tend to return the segments to their initial position. Control signals might attempt to reinforce the programmed action by generating additional torques that counteract this resistance. This strategy would clearly be non-optimal in terms of energy costs, requiring high EMG activity and forces not only for motion but for maintenance of final posture.

For example Schweighofer *et al.* (1998) simulated planar point-to-point arm movements using an FC strategy. Their equations 6 and 8 show that after the movement offset, muscles should generate tonic activity in proportion to the distance between the initial and the final muscle lengths. This implies that the final position is reached by overcoming the resistance to the deflection of the arm from the initial position. Thereby, at the final position, the muscle activity cannot be minimized without driving the limb back to the initial position. This prediction of the FC strategy (see also Bhushan & Shadmehr, 1999) obviously conflicts with the common observation that after transition of the arm to any new position, muscle activation can be minimized without arm motion.

This deficiency of FC models is related to the fact that they have no means for resetting the postural state of the system and thus do not solve Von Holst's posture–movement paradox in a physiologically feasible way. At present, FC models do not incorporate the empirically well-established physiological mechanism of EP shifts – changes in the activation muscle thresholds (Matthews, 1959; Asatryan & Feldman, 1965), a mechanism that, if deficient, results in dramatic movement problems in neurological patients (Levin *et al.* 2000). These models also do not take into account that practically all descending systems have the capacity to regulate the activation thresholds (Feldman & Orlovsky, 1972).

One can assume that the FC model can be reconciled with the EP hypothesis by incorporating the physiologically well-established mechanisms of EP resetting. However, the problem of integration of the two hypotheses is not as simple as it may seem. In FC models, control levels directly programme and specify kinematic, EMG and force variables. In contrast, in the EP hypothesis, these variables are not programmed or computed but emerge dynamically in response to resetting of muscle activation thresholds produced by control levels. These thresholds are regulated, although not necessarily always, independently of muscle forces and kinematic variables. We would be concerned with the logical consistency of a theory integrating conflicting ideas of the two approaches to motor control.

One might think that the FC model is more advanced than the EP hypothesis since it postulates feed-forward commands for an efficient control of movements. Feed-forward control is actually inherent in the EP hypothesis, specifically the  $\lambda$  model. Parameters such as muscle activation thresholds predetermine, in a feed-forward manner, where, in spatial co-ordinates, the system may reach a balance of forces and thus re-establish an equilibrium state. In general, changes in control parameters and resulting shifts in the EP precede changes of EMG activity, muscle forces and kinematics. In fact, all intentional movements, according to the  $\lambda$  model, are guided in a feed-forward manner. This allows the system to effectively use reflexes in the production of even fast movements, ensure stability of posture and movement despite reflex delay, and generate, if necessary, anticipatory reactions preventing undesirable effects of perturbations if they are known in advance. For example in response to a sudden unloading, the arm position changes (Asatryan & Feldman, 1965). In contrast, the initial arm position remains the same if subjects themselves initiate unloading (Forget & Lamarre, 1995), an anticipatory reaction simulated in the  $\lambda$  model (Feldman & Levin, 1995).

Since point-to-point movements necessitate changes in parameters underlying postural resetting, the theoretical framework of the EP hypothesis (specifically, the  $\lambda$  model) appears to be preferable to that of FC models for discussion of our results.

According to the  $\lambda$  model, a hand movement from an initial to a final equilibrium position results from shifts in activation thresholds of arm and trunk muscles. Taken together, these thresholds represent a referent (R) configuration of the arm–trunk system described by appropriate, threshold joint angles (Feldman & Levin, 1995; Lestienne *et al.* 2000). The activation of each skeletal muscle depends on the difference between the actual and the referent configurations of the system. This difference thus represents a global factor that determines, together with local biomechanical and reflex factors, how muscles

are activated and eventually bring the system to an equilibrium configuration. The difference between the equilibrium and the referent configurations represents a measure of the muscle activation and forces that balance the external forces, for example, gravity. In the model, the virtual hand trajectory determined by the shifts in the R configuration is called the referent hand trajectory. The trajectory, comprised of the initial, intermediate and final equilibrium positions of the hand associated with sequential changes in the R configuration, is called the equilibrium hand trajectory.

In the present study, we focused on horizontal components of the hand movements whereas external, gravitational forces acted vertically. Therefore, to a first approximation, we can consider the horizontal projections of the referent and equilibrium hand trajectories to be identical.

The response of the system to the shifts in the R configuration depends not only on external forces but also on the inertia of moving segments, muscle stiffness and damping (the latter two are regulated by specific central commands in the  $\lambda$  model). Therefore, the actual hand trajectory might differ from the equilibrium one. It has been shown by perturbation methods and modelling that for fast arm point-to-point movements not involving the trunk, the difference between these trajectories is small (for details see Won & Hogan, 1995; Gribble *et al.* 1998; Ghafouri & Feldman, 2001). In terms of the  $\lambda$  model, the basic empirical findings in the present study can be interpreted in the following way. At the initial phase of the free-trunk trials, the proprioceptive and/or vestibular afferent signals elicited by the trunk motion result in a modification of the referent configuration of the arm underlying the transport arm motion in the absence of trunk motion. At a later phase, starting approximately when the hand reaches its peak velocity, the effect of afferent signals is attenuated to allow a contribution of the trunk motion into the hand movement direction and extent. The same reflex mechanism arrests the changes in the referent configuration of the arm in response to the trunk block and temporarily provides the invariance of hand trajectory. This description can be extended, based on some additional data showing how the arm transport component is controlled.

A growing number of empirical and simulation studies support the notion that changes in the control variables responsible for the shifts in the equilibrium position of the arm in fast point-to-point movements finish substantially before the movement offset. Specifically, these shifts end approximately at the time of peak velocity of the hand (Flanagan *et al.* 1993; St-Onge *et al.* 1997; Gribble *et al.* 1998; Ghafouri & Feldman, 2001). There are alternative suggestions that the shifts in the equilibrium position underlying fast point-to-point arm movements end only

with the movement offset (Latash & Gottlieb, 1991; Latash, 1993; Gomi & Kawato, 1996). Gribble *et al.* (1998) have shown, however, that these suggestions resulted from simplified assumptions reducing the highly non-linear neuromuscular system to a set of linear spring-like elements (for discussion see also Feldman *et al.* 1998). Gomi and Kawato's conclusions conflict with results of two empirical studies that do not depend on the assumption of linearity of the system: one showing that shifts in the equilibrium point end substantially before the end of the actual reaching movement, about the time when the hand reaches the peak velocity (Ghafouri & Feldman, 2001) and the other that the hand equilibrium and actual trajectories are spatially close to each other (Won & Hogan, 1995).

In combination with the results of the present study, the evidence that the shifts in the equilibrium position underlying fast point-to-point arm reaching terminate early in the movement (Ghafouri & Feldman, 2001), make it reasonable to describe the trunk-assisted reaching in the following way. The control signals underlying the hand transport and trunk leaning are produced in parallel but the influence of the trunk movement on the hand trajectory is initially compensated by appropriate rotations of the arm joints, until the shifts in the equilibrium position of the hand are completed. As has been argued above, this event occurs about the time when the hand reaches the peak velocity. After that, the gain of the compensation of the trunk is attenuated to allow the trunk to contribute to the hand movement extent and direction.

In conclusion, although the hand and the trunk moves in parallel, the arm and trunk contributions to the hand transport are probably determined by central commands that are generated sequentially.

Trunk-assisted reaching may not be the only task in which different segments move in parallel whereas central commands related to important functional components of the task are generated sequentially. In particular, central commands underlying speech production are probably generated sequentially but the motor responses overlap, resulting in an acoustic effect called co-articulation (Fowler & Saltzman, 1993). In addition, Adamovich *et al.* (1994) analysed fast discrete movements while subjects continuously generated rhythmical movements of the forearm. They also found that although kinematically the two movements overlap, they are evoked sequentially at a control level (see also Sternad *et al.* 2001).

The present study is thus relevant to the problem of 'serial order in behaviour' discussed by Lashley (1951). He noticed that components of different behaviours, including locomotion, prehension and language are generated sequentially and that such generation cannot result from moment-to-moment responses to a serially

ordered environment. Rather, the serial order is a manifestation of a control principle guiding the behaviour of the organism. Lashley also suggested that different components of action could be prepared in advance, without specific ordering whereas an independent neural structure, an action scheme or engram (Bernstein, 1967; Latash, 1993) releases these components in a specific order and at a specific rate. The ordering and rate may be determined depending on mechanical and neural factors (Sternad *et al.* 1998). In particular, in the present study, the sequential control strategy may be necessary to account for the difference in the arm and trunk inertia; control systems might be forced to wait until the trunk acquires a speed comparable to that of the arm in order to smoothly integrate both movements and preserve the hand movement direction. Another possibility is that the trunk contribution to the hand displacement is not initiated until the control signals determining the virtual, equilibrium configuration of the arm approach some threshold values related to the biomechanical limits of arm joint rotations. When the extension limit of the arm has been reached, control levels allow other, trunk degrees of freedom to assist in the task completion. In reaching tasks involving grasping, peak velocities of the endpoint, trunk and hand aperture are reached sequentially (Wang & Stelmach, 2001). Indirectly, this may indicate that control signals underlying the grasp component are initiated when the two transport components have been completed, so that the control signals underlying the three components of reaching are also generated sequentially, a hypothesis that can be tested in future studies.

## REFERENCES

- ADAMOVICH, S. V., ARCHAMBAULT, P., GHAFOURI, M., LEVIN, M. F., POIZNER, H. & FELDMAN, A. G. (2001). Hand trajectory invariance in reaching movements involving the trunk. *Experimental Brain Research* **138**, 288–303.
- ADAMOVICH, S. V., LEVIN, M. F. & FELDMAN, A. G. (1994). Merging different motor patterns: coordination between rhythmical and discrete single-joint movements. *Experimental Brain Research* **99**, 325–337.
- ARCHAMBAULT, P., PIGEON, P. P., FELDMAN, A. G. & LEVIN, M. F. (1999). Recruitment and sequencing of different degrees of freedom during pointing movements involving the trunk in healthy and hemiparetic subjects. *Experimental Brain Research* **126**, 55–67.
- ASATRYAN, D. G. & FELDMAN, A. G. (1965). Functional tuning of the nervous system with control of movement or maintenance of a steady posture: 1. Mechanographic analysis of the work of the limb on execution of a postural task. *Biophysics* **10**, 925–935.
- BERKINBLIT, M. B., FELDMAN, A. G. & FUKSON, O. I. (1986). Adaptability of innate motor patterns and motor control mechanisms. *Behavioral and Brain Sciences* **9**, 585–638.
- BERNSTEIN, N. A. (1967). *The coordination and regulation of movements*. Pergamon Press, Oxford.
- BHUSHAN, N. & SHADMEHR, R. (1999). Computational nature of human adaptive control during learning of reaching movements in force fields. *Biological Cybernetics* **81**, 39–60.

- BRODAL, A. (1974). Anatomy of the vestibular nuclei and their connections. In *Handbook of Sensory Physiology, VI/1 The Vestibular System*, ed. KORNHUBER, H. H., pp. 239–351. Springer, Berlin, Heidelberg, New York.
- FELDMAN, A. G. & LEVIN, M. F. (1995). The origin and use of positional frames of reference in motor control. *Behavioral and Brain Sciences* **18**, 723–806.
- FELDMAN, A. G. & ORLOVSKY, G. N. (1972). The influence of different descending systems on the tonic stretch reflex in the cat. *Experimental Neurology* **37**, 481–494.
- FELDMAN, A. G., OSTRY, D. J., LEVIN, M. F., GRIBBLE, P. L. & MITNITSKI, A. B. (1998). Recent tests of the equilibrium-point hypothesis ( $\lambda$  model). *Motor Control* **2**, 26–42.
- FELDMAN, A. G., ROSSI, E. & MITNITSKI, A. (2001). How the trunk contributes to the hand movement during reaching. In *Neural Control of Movement*, Society for the Neural Control of Movement, NCM 2001 Poster Abstracts, ed. STRICK, P., Seville, Spain.
- FITZPATRICK, R., BURKE, D. & GANDEVIA, S. C. (1994). Task-dependant reflex responses and movement illusions evoked by galvanic vestibular stimulation in standing humans. *Journal of Physiology* **478**, 363–372.
- FLANAGAN, J. R., OSTRY, D. J. & FELDMAN, A. G. (1993). Control of trajectory modifications in target-directed reaching. *Journal of Motor Behavior* **25**, 140–152.
- FLANDERS, M., DAGHESTANI, L. & BERTHOZ, A. (1999). Reaching beyond reach. *Experimental Brain Research* **126**, 19–30.
- FORGET, R. & LAMARRE, Y. (1995). Postural adjustments associated with different unloadings of the forearm: effects of proprioceptive and cutaneous afferent deprivation. *Canadian Journal of Physiology and Pharmacology* **73**, 285–294.
- FOWLER, C. & SALTZMAN, E. (1993). Coordination and coarticulation in speech production. *Language and Speech* **36**, 171–195.
- FUKSON, O. I., BERKINBLIT, M. B. & FELDMAN, A. G. (1980). The spinal cord takes into account the scheme of its body during the wiping reflex. *Science* **209**, 1261–1263.
- GHAFOURI, M. & FELDMAN, A. G. (2001). The timing of control signals underlying fast point-to-point arm movements. *Experimental Brain Research* **137**, 411–423.
- GOMI, H. & KAWATO, M. (1996). Equilibrium-point hypothesis examined by measured arm stiffness during multijoint movements. *Science* **272**, 117–120.
- GRÉA, H., DESMURGET, M. & PRABLANC, C. (2000). Postural invariance in three-dimensional reaching and grasping movements. *Experimental Brain Research* **134**, 155–162.
- GRIBBLE, P. L., OSTRY, D. J., SANGUINETI, V. & LABOISSIERE, R. (1998). Are complex control signals required for human arm movement? *Journal of Neurophysiology* **79**, 1409–1424.
- GUITTON, D. (1992). Control of eye-head coordination during orienting gaze shifts. *Trends in Neurosciences* **15**, 174–179.
- HOLLERBACH, J. M. (1982). Computers, brains and the control of movement. *Trends in Neurosciences* **6**, 189–192.
- IVANENKO, Y. P., GRASSO, R. & LACQUANITI, F. (2000). Neck muscle vibration makes walking humans accelerate in the direction of gaze. *Journal of Physiology* **525**, 803–814.
- JOHNSON, J. L. & SHARPE, J. A. (1994). The initial vestibulo-ocular reflex and its visual enhancement and cancellation in humans. *Experimental Brain Research* **99**, 302–308.
- KAMINSKI, T. R., BOCK, C. & GENTILE, A. M. (1995). The coordination between trunk and arm motion during pointing movements. *Experimental Brain Research* **106**, 457–466.
- KELSO, J. A. S., TULLER, B., VATIKIOTIS-BATESON, E. & FOWLER, C. A. (1984). Functionally specific articulatory cooperation following jaw perturbations during speech: evidence for coordinative structures. *Journal of Experimental Psychology, Human Perception and Performance* **10**, 812–832.
- LACKNER, J. R. (1988). Some proprioceptive influences on the perceptual representation of body shape and orientation. *Brain* **111**, 281–297.
- LASHLEY, K. S. (1951). The problem of serial order in behavior. In *Cerebral Mechanisms in Behavior*, ed. JEFFRESS, L. A. Wiley, New York.
- LATASH, M. L. (1993). *Control of Human Movement*. Human Kinetics, Urbana, IL, USA.
- LATASH, M. L. & GOTTLIEB, G. L. (1991). An equilibrium-point model of dynamic regulation for fast single-joint movements: II. Similarity of isometric and isotonic programs. *Journal of Motor Behavior* **23**, 179–191.
- LESTIENNE, F. G., THULLIER, F., ARCHAMBAULT, P., LEVIN, M. F. & FELDMAN, A. G. (2000). Multi-muscle control of head movements in monkeys: The referent configuration hypothesis. *Neuroscience Letters* **283**, 65–68.
- LEVIN, M. F., LAMARRE, Y. & FELDMAN, A. G. (1995). Control variables and proprioceptive feedback in fast single-joint movement. *Canadian Journal of Physiology and Pharmacology* **73**, 316–330.
- LEVIN, M. F., SELLES, R. W., VERHEUL, M. H. G. & MEIJER, O. G. (2000). Deficits in the co-ordination of agonist and antagonist muscles in stroke patients: Implications for normal motor control. *Brain Research* **853**, 352–369.
- MA, S. & FELDMAN, A. G. (1995). Two functionally different synergies during arm reaching movements involving the trunk. *Journal of Neurophysiology* **73**, 2120–2122.
- MATTHEWS, P. B. C. (1959). The dependence of tension upon extension in the stretch reflex of the soleus muscle in the decerebrate cat. *Journal of Physiology* **147**, 521–546.
- PIGEON, P. & FELDMAN, A. G. (1998). Compensatory arm-trunk coordination in pointing movements is preserved in the absence of visual feedback. *Brain Research* **802**, 274–280.
- PIGEON, P., YAHIA, L. H., MITNITSKI, A. B. & FELDMAN, A. G. (2000). Superposition of independent units of coordination during pointing movements involving the trunk with and without visual feedback. *Experimental Brain Research* **131**, 336–349.
- POIZNER, H., FELDMAN, A. G., LEVIN, M. F., BERKINBLIT, M. B., HENING, W., PATEL, A., & ADAMOVICH, S. V. (2000). The timing of arm-trunk coordination is deficient and vision-dependent in Parkinson's patients during reaching movements. *Experimental Brain Research* **133**, 279–292.
- POIZNER, H., FOOKSON, O., BERKINBLIT, M. B., HENING, W., FELDMAN, A. G. & ADAMOVICH, S. V. (1998). Pointing to remembered targets in 3D space in Parkinson's disease. *Motor Control* **2**, 251–277.
- SALING, M., STELMACH, G. E., MESCHERIAKOV, S. & BERGER, M. (1996). Prehension with trunk assisted reaching. *Behavioral and Brain Research* **80**, 153–160.
- SCHOLZ, J. P. & SCHÖNER, G. (1999). The uncontrolled manifold concept: Identifying control variables for a functional tasks. *Experimental Brain Research* **126**, 289–306.
- SCHOLZ, J. P., SCHÖNER, G. & LATASH, M. (2000). Identifying the control structure of multijoint coordination during pistol shooting. *Experimental Brain Research* **135**, 382–404.

- SCHWEIGHOFER, N., ARBIB, M. A. & KAWATO, M. (1998). Role of cerebellum in reaching movements in humans. I. Distributed inverse dynamic control. *European Journal of Neuroscience* **10**, 86–94.
- SHADMEHR, R. & MUSSA-IVALDI, F. A. (1994). Adaptive representation of dynamics during learning of a motor task. *Journal of Neuroscience* **14**, 3208–3224.
- STERNAD, D., DEAN, W. J. & SCHAAL, S. (2001). Interaction of rhythmic and discrete pattern generators in single-joint movements. In *Bernsteins Traditions in Motor Control*, vol. 2, ed. LATASH, M. L. & STERNAD, D. (in the Press). Human Kinetics Publishers, Champaign, IL, USA.
- STERNAD, D., SALTZMAN, E. L. & TURVEY, M. T. (1998). Interlimb coupling in a simple serial behavior: A task dynamic approach. *Human Movement Science* **17**, 393–433.
- ST-ONGE, N., ADAMOVICH, S. V. & FELDMAN, A. G. (1997). Control processes underlying elbow flexion movements may be independent of kinematic and electromyographic patterns: experimental study and modelling. *Neuroscience* **79**, 295–316.
- VON HOLST, E. (1936). Von Dualismus der motorischen und der automatische-rhythmischen Function in Rückenmark und vom Wesen des automatischen Rhythmus. *Pflügers Archiv* **237**, 364–378.
- VON HOLST, E. & MITTELSTAEDT, H. (1950/1973). Das Reafferezzprincip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie, *Naturwissenschaft* **37**, 467–476, 1950. The reafference principle. In *The Behavioral Physiology of Animals and Man. The Collected Papers of Erich von Holst*, vol. 1, translator MARTIN, R., pp. 139–173, 1973. University of Miami Press, Coral Gables, FL, USA.
- WANG, J. & STELMACH, G. E. (1998). The coordination among body segments during reach-to-grasp action involving the trunk. *Experimental Brain Research* **123**, 346–350.
- WANG, J. & STELMACH, G. E. (2001). Spatial and temporal control of trunk-assisted prehensile actions. *Experimental Brain Research* **136**, 231–240.
- WOLPERT, D. M., GHARAMANI, Z. & JOARDAN, M. J. (1995). An internal model for sensorimotor integration. *Science* **269**, 1179–1182.
- WON, J. & HOGAN, N. (1995). Stability properties of human reaching movements. *Experimental Brain Research* **107**, 125–136.

### Acknowledgements

We wish to thank Drs Mindy Levin and Ramesh Balasubramaniam for helpful comments on the manuscript as well as Dr David Ostry for the discussions of different motor control theories, which is partly reflected in this paper. This work was supported by research grants from the CIHR and FCAR (Canada).