Exp Brain Res (1987) 65: 538–548

Experimental
Brain Research

Forward and backward axial synergies in man

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Summary. 1. Upper trunk and head forward and backward movements were analyzed in human subjects standing on a force platform. EMG of several flexor and extensor muscles was recorded together with the kinematics of the movement (EL.I.TE. system). 2. It was found that upper trunk movements are accompanied by movements of hip and knees in the opposite direction, resulting in a slight displacement of the center of gravity projection on the ground. 3. In fast movements, all the body segments were displaced at the same time, which suggests a feedforward control, whereas in slow movements, onset of displacement of the body segments was found to take place sequentially in a cranio-caudal direction. 4. EMG analysis during fast movements revealed two different types of control, utilized in forward and backward movements. With forward bending movements the action of two sets of muscles could be recognized: the prime mover (R. Abd.), the activation of which was not correlated with that of the other muscles and preceded the onset of movement with a fairly constant lead, and a group of postural muscles, the activation (VM, TA) and inhibition (Sol) of which were closely correlated. By contrast, with backward movements, the prime mover (Er.S.) and the postural leg muscles (Hamstrings, Sol) were activated simultaneously. In both cases, a feedforward type of control is evident. 5. Performance of the fast forward movements was accompanied by an initial forward displacement of the knee. The function of this phenomenon is discussed in term of a destabilizing action favouring the forward bending of the body or a prestretching of the knee extensor muscles increasing the strength of their subsequent contraction.

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Key words: Posture – Movement – Synergy – Coordination – Man

Introduction

The execution of voluntary movements by standing human subjects is always accompanied by adjustments of their postural attitude. In most cases, the muscles responsible for those postural changes are activated in advance of those acting as prime movers, indicating that a feedforward type of neural control is involved (see Massion 1984). Within the overall strategy underlying motor performance as a whole, postural adjustments are thought to minimize the disturbance of equilibirum brought about by voluntary movement, as first proposed by Belenkiy et al. (1967).

Indeed, most studies on coordination between posture and movement have been carried out on standing subjects performing voluntary arm movements (Belenkiy et al. 1967; Bouisset and Zattara 1981; Cordo and Nashner 1982; Clement et al. 1984; Friedli et al. 1984). In this case, the moving segments are not directly involved in the body support and their mass is relatively small. Postural adjustments of trunk and legs are therefore performed with only slight displacements of the corresponding joints.

The problem is quite different in the case of axial movements. Here, the segments participating in a movement are the same as those involved in body support; moreover, their mass is such that equilibrium maintenance could not be achieved without large displacements of axial segments other than those voluntary moved.

A qualitative analysis of these axial movements was previously conducted by Babinski (1899), who noted that backward and forward upper trunk and head movements are accompanied by displacements of hip and knee in the opposite direction. He interpreted the associated movements as preventing over-large displacements of the projection onto the ground of the center of gravity (CG), and called the whole set of upper trunk and associated limb movements "synergies".

The aim of the present investigation was to reanalyze these head and trunk movements together with the associated lower limb displacements, in order to answer the following questions:

1. To what extent is the CG projection regulated during axial movements?

2. Does the kinematic and EMG analysis indicate that the associated movements of hip and knee are controlled in a feedforward manner, as has been found to occur in the case of anticipatory postural responses to upper limb movements?

3. Do the pattern and timing of the head and trunk movements and the associated hip and knee movements vary with the movement speed?

4. How different are the axial "synergies" characterizing forward and backward upper trunk movement, in view of the anatomical constraints imposed by the knee joint, which can be flexed but not hyperextended?

It will be shown that the CG projection is very efficiently regulated during the axial movements examined and that the associated hip and knee movements are controlled in a feedforward manner, at least in fast bending movements. Two different modes of anticipatory control are utilized, however, in forward and backward movements.

Methods

The experiments were performed on 6 subjects (5 males and 1 female), aged between 20 and 25 years. As shown in Fig. 1, the subjects stood on a force platform equipped with piezoelectric transducers, giving the vertical (Rz) and horizontal (Rx) components of the ground reaction force.

The horizontal displacements of the center of pressure (CP) and the center of gravity (CG) were computed using the following formulae (see Cappozzo et al. 1976; Pedotti 1977):

$$CP = \frac{R_{z1} + R_{z2}}{\Sigma_i R_{zi}} \cdot d \qquad CG = \frac{1}{m} {}_0\!\int^t d\tau \, {}_0\!\int^t \Sigma_i R_{xi} \, d\tau$$

where CP = displacement of the center of pressure in the sagittal plane,

CG = horizontal displacement of the center of gravity in the sagittal plane (initial position and velocity are set at 0).

R_{zi}, R_{xi} (i = 1,...4) = the vertical and horizontal components, respectively of the ground reaction measured by the i-th transducer (i = 1 and i = 2 are the two anterior transducers).

d = distance between the anterior and posterior pair transducers.

m = mass of the subject;
t = current time;
dτ = time differential.

The kinematics of the movement were analyzed by means of an automatic TV-image processor (EL.I.TE. system) (Ferrigno and Pedotti 1985). Seven hemispherical retroreflective markers (5 mm in diameter) were placed on the main reference points on one side of the subject, as shown schematically in Fig. 1 (two markers on the head and the other five on the shoulder, the anterior superior iliac crest, the upper femoral trochanter, the knee and the ankle). The EL.I.TE. system is a dedicated computer which processes TV signals in real time, recognizes all markers on the basis of their shape, and computes simultaneously the coordinates of the centroid of all the markers. The sampling rate used was 50 Hz, so that during the execution of the bending movements, the position of each marker was detected every 20 ms. Accuracy of the system was one part in 2560. Under the present experimental conditions the field explored was 2 m × 2 m, and the accuracy was thus 0.78 mm.

The recorded positions were processed on line by a computer (Digital PDP 11/03). Digital filtering was performed by means of a Finite Impulse Response filter (FIR) with a centered window, in order to compute the velocity by a zero phase-shift differentiation (see Oppenheim and Shafer 1975). A linear interpolation was then performed and the onset of movement was calculated on this curve with an estimated error of ± 10 ms. In order to see whether with slow bending movements, the determination of the movement onset might include an additional error depending on the slow rise of the velocity curve and on the difference in the displacement amplitude between cranial and caudal body segments, control measurements were carried out on the acceleration curves obtained by further differentiation of the velocity signal. Due to the slight spontaneous oscillations occurring during standing, the onset of movement could be detected reliably on the acceleration curves in only 1/4 of the trials. In all these cases, however, the onset of displacement of the various body markers showed the same pattern as that previously observed in the velocity curves although there was a constant phase lead of 80–100 ms.

Electromyographic recordings were conducted by means of bipolar surface electrodes with an interelectrode distance of 2 cm and displayed by a mirror galvanometer recorder (band pass 0–1 kHz). Four pairs of antagonistic muscles were selected in each subject: neck extensor (upper portion of trapezius, extensor capitis, Ex.C.) and flexor (sternocleidomastoideus, Scm, which is also a neck extensor), trunk extensor (erectores spinae at L4 level, Er.S.) and flexor (rectus abdominalis, R. Abd.), knee extensor (vastus medialis, VM) and knee flexor (semimembranosus, Sm or biceps femoris, BF), ankle extensor (soleus, Sol or gastrocnemius medialis, GM) and ankle flexor (tibialis anterior, TA). The time elapsing between EMG activation or inhibition and the onset of movement was determined from the recorded data on the basis of the earliest detectable change with respect to the steady-state level. When latency determination was questionable because of background activity, an independent estimate was made by the experimenters and trials yielding conflicting measurements were discarded.

Experimental paradigm

The subjects were asked to stand quietly on the force platform and relax with their hands on their hips and their eyes open. At a given signal (tone) they were asked to bend both their head and trunk forward (or backward) until reaching a pre-estimated displacement of the head (marker 1) of about 30 cm in the sagittal plane, and to move back to the initial position.

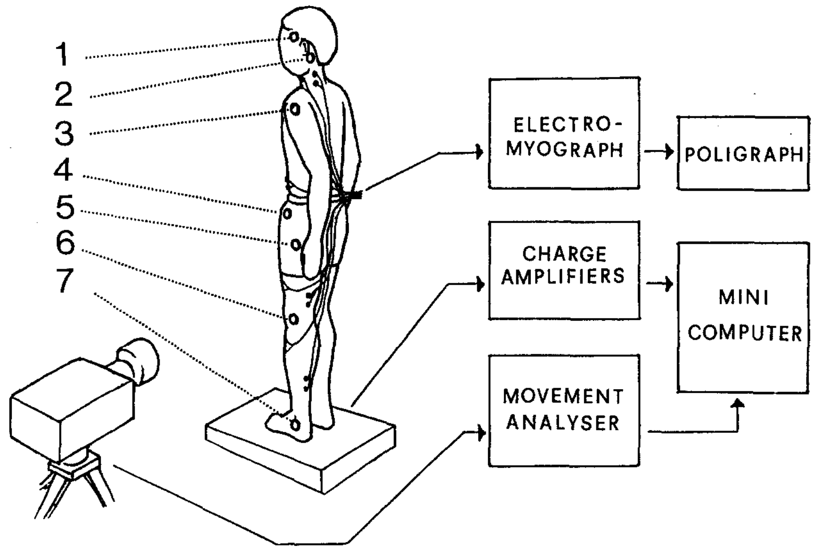

Fig. 1. Schematic diagram of the experimental arrangement used to study forward and backward movements of the upper trunk. The subject is standing on a force platform and is equipped with seven passive markers for movement detection and with surface electrodes for EMG recording from four pairs of antagonistic muscles. For further explanation see text

Three types of instructions were given:

1. The subject was required to perform the movement from upright to maximal bending within 1 s. He was allowed to train with a metronome. The movement performed within one second was considered by the subjects to be slow and quite within the range of their natural daily movements. This time allowance was 2.5 to 3 times longer than the minimal duration of a bending movement performed as fast as possible by the subject.
2. The subject was required to perform the same movement within 600 ms.
3. The subject was instructed to perform the movement as fast as possible.

Three to five trials were conducted with each of the above paradigms (instruction 1, 2 and 3) by each subject. In the presentation of the results, movements corresponding to paradigms 1, 2 and 3 will be referred to as slow, medium and fast, respectively.

Results

After the training period, in all the subjects examined the parameters of the bending movements were reproduced fairly consistently from trial to trial. Intersubject performances were also consistent.

As a general rule, forward and backward upper trunk movements were accompanied by hip and knee displacements in the opposite direction. This phenomenon is illustrated in Fig. 2. It can be seen that with forward movements the three upper markers (1, 2, 3) moved forward, whereas markers 4, 5 and 6 moved backward. The reverse was observed with backward movements in which the upper markers moved backward and the lower ones forward.

The excursion of the hip (markers 4 and 5) and knee (marker 6) was always lower than that of the upper body segments. With forward bending, it was 30–50% of that of the shoulder in the fast movements and 15–20% in the slow ones, although the overall movement amplitude was similar in both cases. Knee displacements were equal to or lower than hip ones.

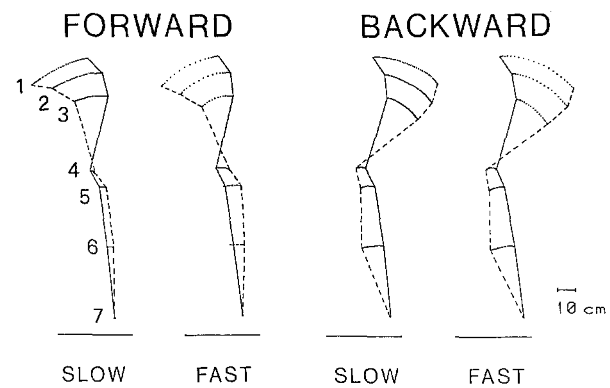

Fig. 2. Movement trajectories detected from changes in the position of the body markers, during forward and backward slow and fast upper trunk bending movements. Continuous and dashed lines joining the seven points represent the initial position and the maximal displacement, respectively. On the whole, the displacements of the lower markers (4, 5, 6) are in the opposite direction to those of the upper markers (1, 2, 3). Note that during fast forward bending the knee undergoes a temporary forward displacement in the same direction as the upper trunk. Traces from single trials performed by the same subject

With backward bending, the excursion of the hip was 30–50% that of the shoulders, being again slightly lower with the slow movements; however, at variance with forward bending, knee movements were always larger than those of the hip, and reached up to 75% of the shoulder displacements.

Forward upper trunk movements

Several parameters involved in forward upper trunk movements and in the associated hip and knee displacements were investigated.

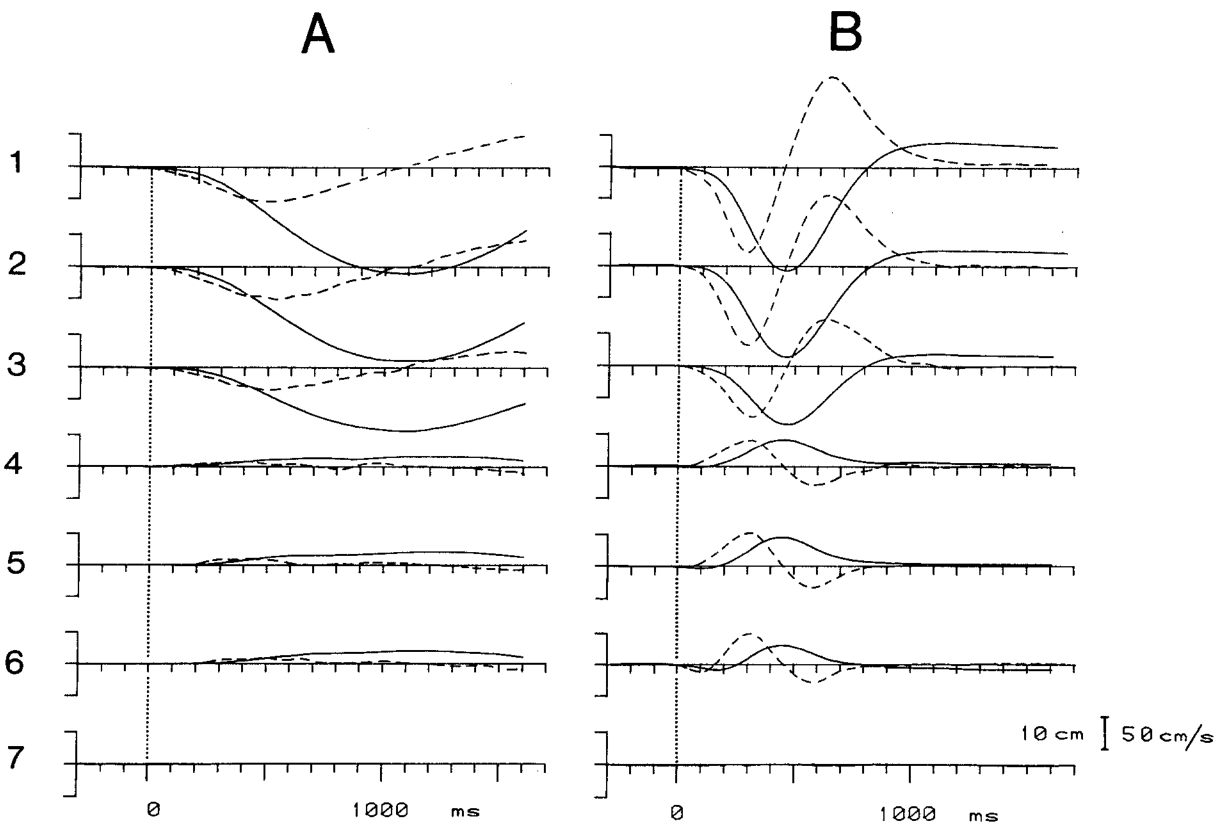

Fig. 3A, B. Forward upper trunk movement. Horizontal displacements of the seven markers (continuous lines) and their velocities (dashed lines) during slow (**A**) and fast (**B**) forward uppertrunk bending movements. In this and the following figures, downward and upward direction of the traces corresponds to forward and backward displacement of the markers, respectively. It can be noted that in **A** the upper trunk starts moving prior to the lower limb, while in **B** the movements of the upper and lower segments are simultaneous; note that in **B** a forward movement of the knee joint (marker 6) occurs before the backward displacement. Single trial performed by the same subject as in Fig. 2. The vertical dotted lines correspond to the onset of head movement as detected on the velocity curve of the first marker

First, the onset of movement of the various body segments was analysed from the velocity curves of the corresponding markers. Time values were computed in relation to the first displacement of the upper head marker (1), assumed to represent the actual onset of the bending movement (time 0). In this analysis the main finding was the fact that the timing and pattern of motion of the various body segments depended on the speed with which the movement was performed (Fig. 3).

In particular, with slow movements (deviation from the upright position to maximal bending from 800 to 1200 ms) (Fig. 3A), the upper head marker (1) started moving 233 ± 66 ms prior to the knee marker (6), indicating a sequential displacement of the upper and lower body segments. This result was confirmed in the trials where the movement onset could be detected on the acceleration curves.

With the fast movements (from 300 to 500 ms duration) (Fig. 3B), all the segments moved at roughly the same time. Moreover, a new pattern of displacement was observed, which was characterized by an early forward displacement of the knee (and sometimes of the trochanter). This behaviour seems unusual in that the knee did not move in the opposite direction with respect to head and shoulders, as usually observed with the lower limb segments; instead, its earliest movement was iso-directional with the upper trunk (see marker 6 in Fig. 3B). This phenomenon, which lasted some 250 ms, was followed by a backward knee and hip displacement, as observed with the slow movements. The new pattern, which was observed in all but one subject, might be related to a process of furthering forward movement, which will be discussed later.

Movements performed at medium velocity (from 500 to 650 ms duration) showed a pattern which was comparable to that of slow or the fast movements, and either or both of the behaviours could even be observed in the same subject in consecutive trials.

The position and velocity curves recorded with the EL.I.TE. system were compared with recordings

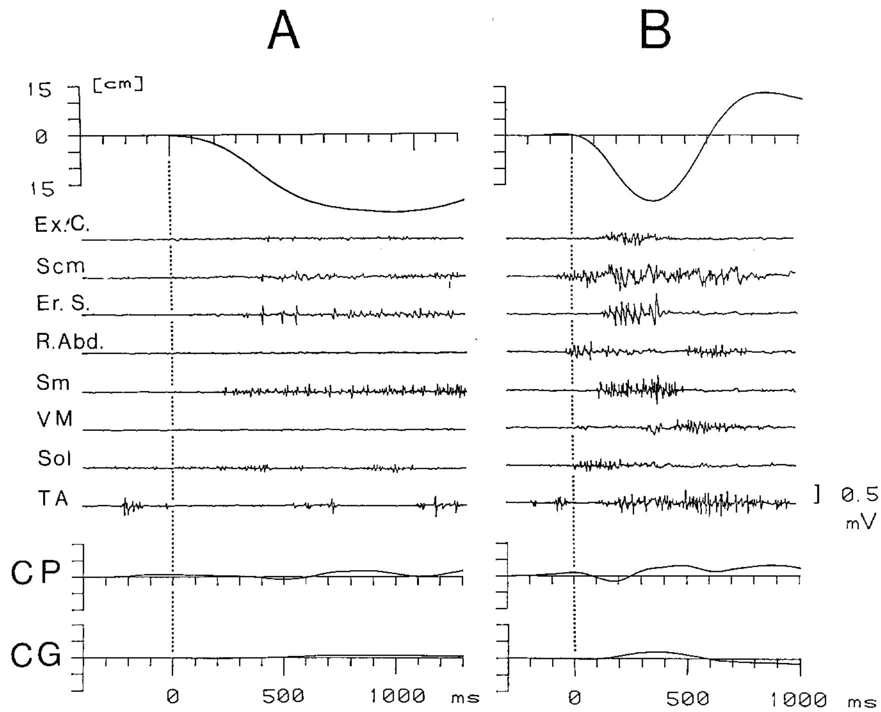

Fig. 4A, B. Electromyographic activity of four pairs of antagonistic muscles during a slow (**A**) and a fast (**B**) forward bending movement. Upper trace gives the horizontal displacement of the most cranial body marker (1). Horizontal displacements of Center of Pressure (CP) and Center of Gravity (CG) are also shown in the two traces at the bottom. Ex.C.: extensores capitis, Scm: sternocleidomastoideus, Er. S.: erectores spinae, R. Abd.: rectus abdominis, Sm: semimembranosus, VM: vastus medialis, Sol: soleus, TA: tibialis anterior. The vertical scale at the top is graded in cm, each gradation corresponding to 5 cm. The two bottom scales corresponding to CP and CG are also graded in cm, each graduation corresponding to 5 cm; upward deflexion corresponds to backward displacement of CP or CG. Note the early activation of the TA and the slight displacement of the CG

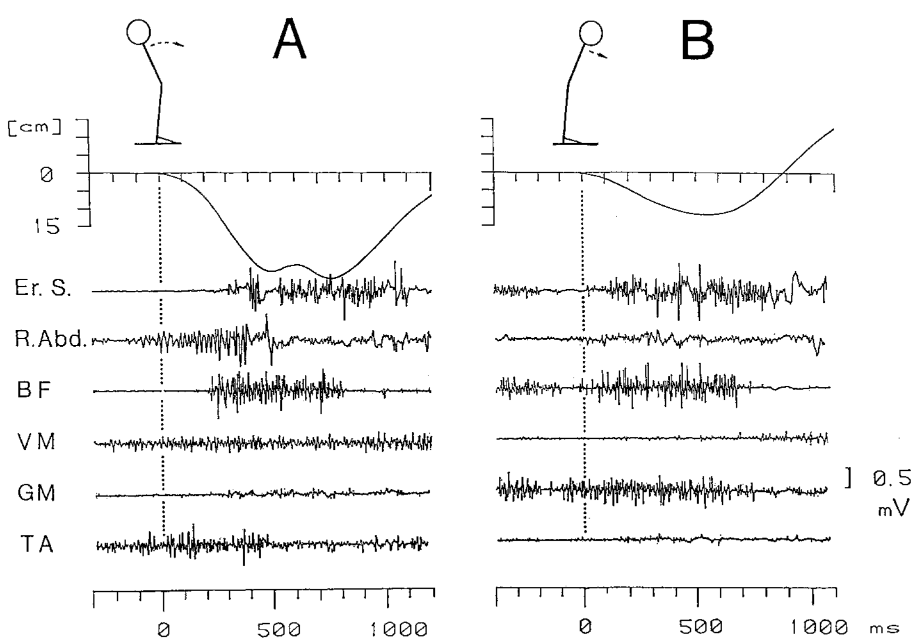

Fig. 5A, B. Effect of a change in the initial position on the EMG pattern observed during fast forward bending movements. The onset of the horizontal displacement of the head marker (1) is plotted as a time reference in the upper trace. Note that a flexor activation pattern (see R. Abd. and TA), observed when the subject starts moving from a slightly backward bending posture (**A**), turns into an extensor inhibition pattern (see Er. S., BF acting as a hip extensor, and GM), when the initial position is replaced by a forward leaning (**B**)

on the force platform (Fig. 4). Two dynamic parameters were examined: the horizontal displacements of the center of pressure (CP) and those of the center of gravity (CG), both in the sagittal plane. The changes observed were similar in movements with different velocities, and were sometimes very slight in the case of slow movements. As shown in Fig. 4, a backward displacement of the CP took place first, usually preceding by some 70–200 ms the earliest displacement of any body segment. Thereafter, the CP oscillated forward and backward. The displacement of the CG measured at the end of the forward movement was very small: 1.4 ± 1.2 cm, indicating the great efficiency of the stabilizing synergies.

For a rough analysis of this efficiency, we computed the displacement of the CG using a model in

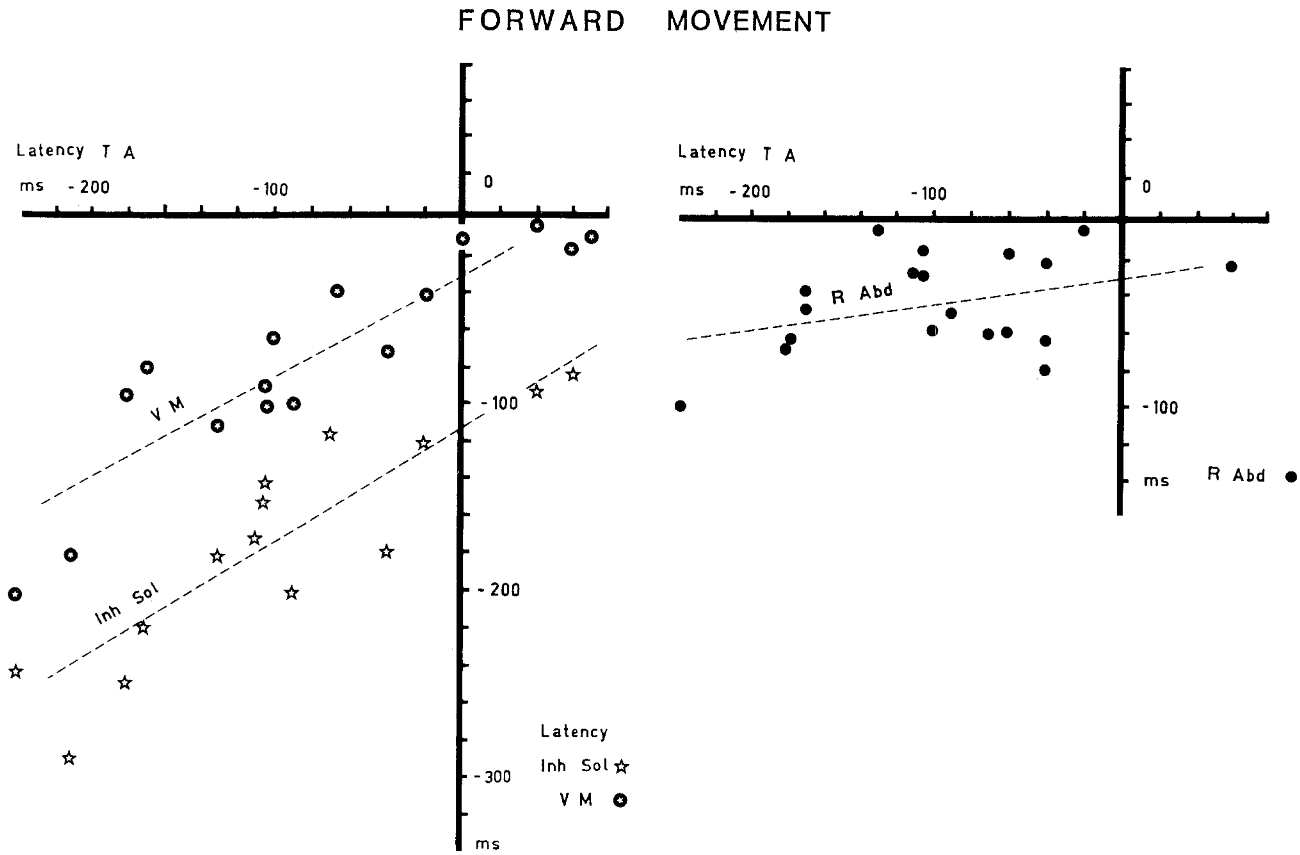

Fig. 6. Plotting of the latencies of Sol inhibition, VM activation and R. Abd. activation versus the latency of TA activation; data from all the subjects performing fast movements. Time 0 represents the onset of movement (first displacement of the upper head marker). Notice the sequential activation or inhibition of the muscles from the lower extremety to the trunk. The equations for the regression lines are $y = -114.1 + 0.62\ x$; $r = 0.89$ for the Sol. inhibition $y = -32.2 + 0.55\ x$; $r = 0.91$ for the VM and $y = -27.6 + 0.16\ x$; $r = 0.42$ for the R. Abd. The Spearman rank order correlation (Siegel, 1960) is significant ($p < 0.01$) for the regression lines of Sol and VM and non significant for R. Abd.

which the masses of the head, trunk, upper and lower limbs were respectively concentrated in their own barycenters. Body parameters were obtained by anthropometric tables (Drillis and Contini 1966). The results show that a trunk flexion of 30 cm in the sagittal plane will produce a displacement of the CG of approximately 12 cm in a subject 1.80 m tall, if no associated movements of the lower part of the body (pelvis and legs) have occurred.

The EMG pattern and timing associated with the above postural changes were also analysed in four pairs of antagonistic muscles of the neck, trunk and lower limb. It was found that in slow and medium speed movements (e.g. Fig. 4A), the onset of motion was preceeded by 150 to 350 ms either by activation of one or several of the following muscles: TA, VM, R. Abd. and Scm, all located in the frontal part of the body and displaying a common flexor function, or by inhibition of one or several of the following muscles: Sol, GM, BF, Sm and Er. S., all located in the dorsal part of the body, showing a common antigravitational extensor function. Figure 5 shows that a slight change in the initial position resulted in a shift of the EMG pattern from one extreme condition to the other. In fact, when the subject was initially in a backward bending position, in which R Abd, VM and TA are tonically active (Fig. 5A), the onset of movement was preceded by an increase in the activity of these same muscles. By contrast, when starting from a forward bending position, which requires the tonic contraction of Er S, BF and GM (Fig. 5B), the initiation of movement was preceded by inhibition of these same muscles. With fast movements, starting from the usual erect posture, the "flexion activation pattern" was usually associated with the inhibition of calf muscle activity according to the following sequence: Sol inhibition, TA, VM and R. Abd activation. The early inhibition of Sol together with the activation of TA might explain the previously described early knee flexion and backward shift of the CP.

In order to provide clues as to the neural events

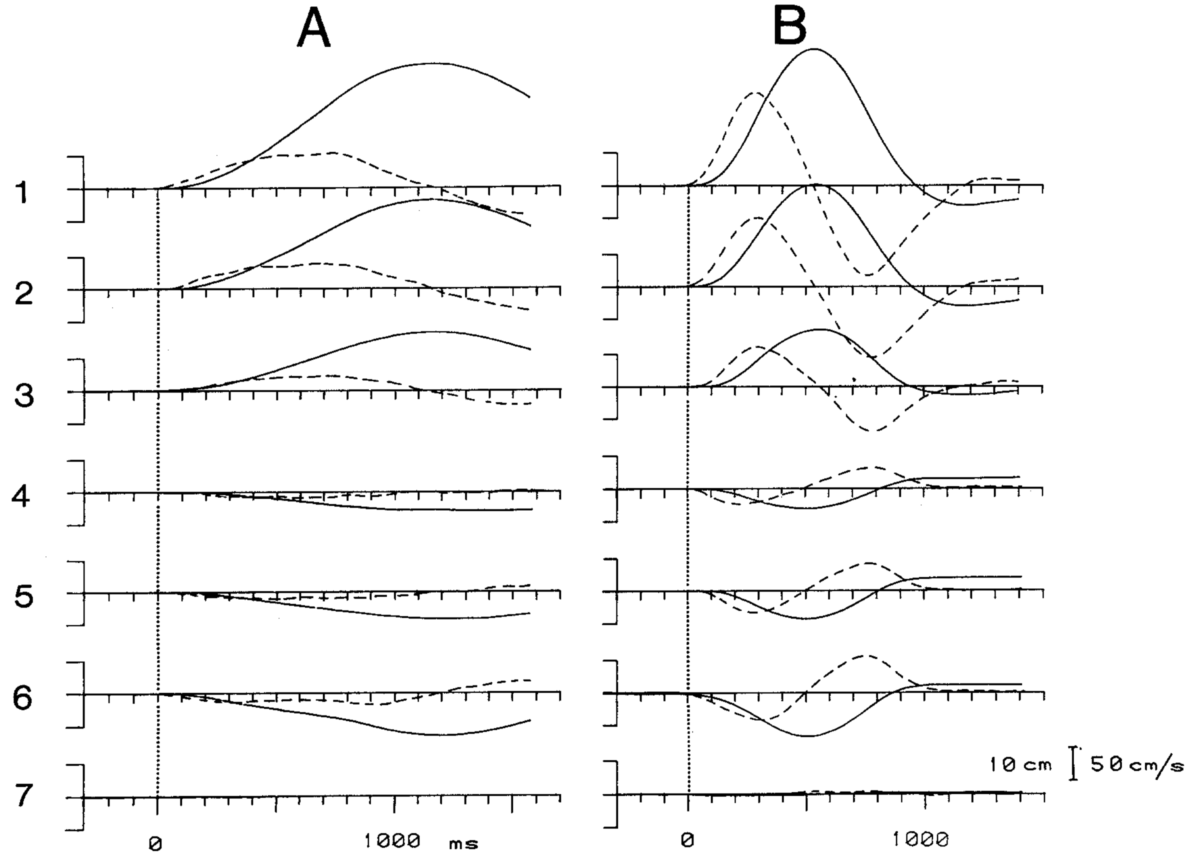

Fig. 7A, B. Backward upper trunk movement. Horizontal displacements of the seven body markers (continuous lines) and their velocities (dashed lines) during slow (**A**) and fast (**B**) backward bending movements. Same explanations as in Fig. 3

underlying the above postural changes, a more detailed analysis was performed on the timing of EMG recruitment. To this end, the values obtained from all the subjects during fast movements were pooled and the activation time of TA was plotted against the onset of inhibition of Sol (or GM) or activation of VM and R Abd. Figure 6 shows that the regression lines obtained between TA and Sol and between TA and VM are both highly significant ($R = 0.89$ and 0.91 respectively), indicating that these EMG events are closely time-related (this was confirmed by the Spearman rank order test, Siegel 1960). As a rule, inhibition of Sol started first, preceding the activation of TA and VM. At variance, the onset of activation of R Abd was not significantly correlated to that of TA ($R = 0.42$, Spearman test not significant, angular coefficient of the regression line not significantly different from 0). Rectus abdominis was activated before the movement onset, with a mean anticipation of 47.8 ± 31 ms ($n = 32$) and could thus be considered to be the prime mover. These results suggest a dual control of movement initiation, involving first the associated lower limb postural muscles, then the prime mover (R Abd).

Analysis of the EMG pattern at a point when the movement had reached its half amplitude showed that the head fixators (Ex C, Scm) together with trunk (Er S) and hip extensors (Sm, or BF), became active, as did the ankle extensors (Sol, GM) in most cases. This muscle activation pattern might subserve the braking of the forward movement and the return towards the upright position.

Backward upper trunk movement

As we have mentioned above, the backward movement of head and upper trunk was accompanied by a forward displacement of the hip and knee (Fig. 2 and 7).

Kinematic analysis revealed that with slow movements (950 to 1150 ms) (Fig. 7A), the onset of displacement of the head preceded that of the knee by a quite variable interval, 99 ± 84 ms, indicating a prevalently sequential displacement of the upper and lower body segments, as was found to be the case with forward movements. With fast movements (Fig. 7B), head, upper trunk and knee started mov-

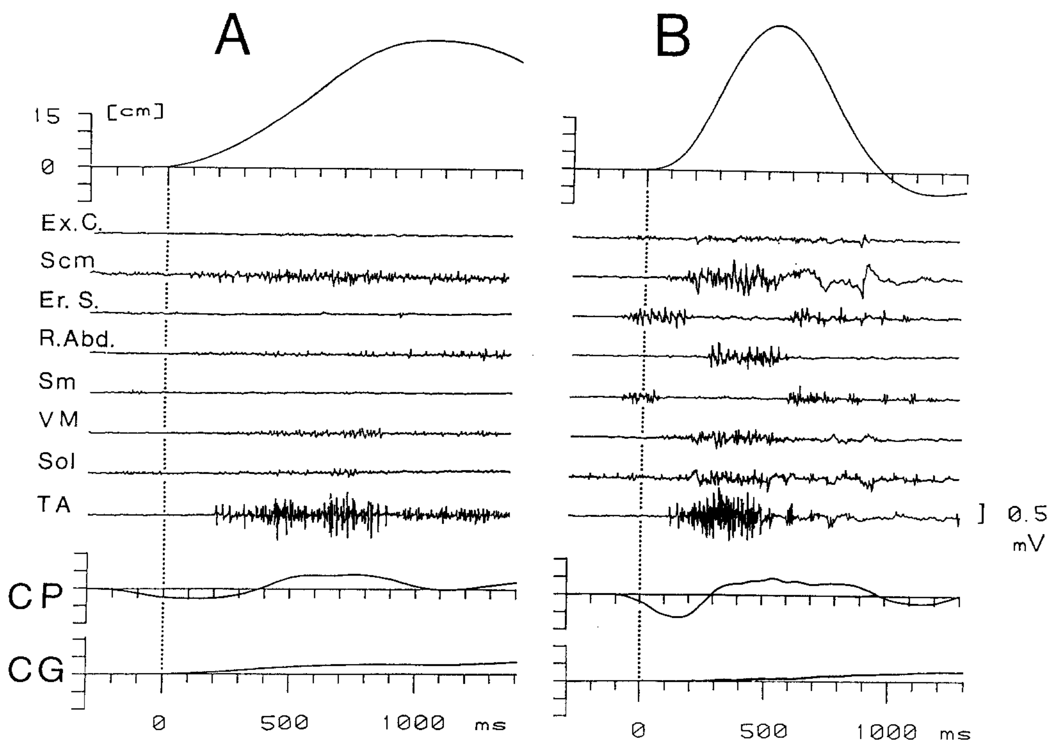

Fig. 8A, B. Electromyographic activity recorded from four pairs of antagonistic muscles during slow (**A**) and fast (**B**) backward bending movements. Horizontal displacement of the first marker (upper trace), Center of Pressure (CP) and Center of Gravity (CG) is shown. Note the simultaneous activation of Er. S. and Sm. during fast bending (**B**)

ing at about the same time, whereas the hip usually moved a little later. It is noteworthy that, in contrast with forward bending, no change in the direction of the early knee displacement took place; rather, knee and hip movements remained forward-directed in all three velocity ranges tested.

Analysis of changes in the CP and CG curves showed that the CP was first moved forward and then backward (Fig. 8). The early forward displacement preceded the earliest motion of any body segment by 50 to 100 ms, when the movement was performed at medium range and fast speeds. At both these velocities, displacement of the CG was very small, attaining a mean value of 1 ± 0.1 cm at the maximal amplitude of the backward movement. Paradoxically, with slow movements the CG underwent larger displacements (up to 2.5 cm).

EMG study revealed that with slow movements, a very slight activation of the Er S, Sm (or BF) and Sol (or GM) often occurred before the onset of movement, but the precise timing was difficult to measure, due to the tonic background activity and the very slow recruitment of the motor units. With medium range and fast backward movements (Fig. 8B), the same muscles, all located in the dorsal part of the body and acting as functional extensors, displayed a more intense EMG activity before the onset of movement. Measurement of the mean activation latency of each of them gave the following values which are not significantly different: Er s –59.6 ms ± 28 (n 22), Sm (and BF) –61.4 ± 31 (n 22), Sol (and GM) –53 ± 28 (n 16). As with forward movements, measurements carried out on all the subjects while performing fast bending movements were pooled and the time of onset of activation of one muscle (the Sm or BF) was plotted against the activation time of the others (Er S and Sol-GM respectively). This procedure was designed to highlight any possible correlation between these agonistic muscles. As shown in Fig. 9, the two regression lines are highly significant (r = 0.81 for Er S and 0.73 for Sol-GM; Spearman rank order correlation significant with $P < 0.01$), showing that these EMG events are closely coupled in time. The hypothesis of an equal activation time, as would be expected from a synchronous central control, was further tested on each pair of muscles. If the hypothesis is valid, the angular coefficient of the regression lines will be equal to 1 (y = x, slope = 45°). The hypothesis was confirmed in that the difference between the angular coefficients of the two experimental regression lines and the reference 45° slope proved to be non-

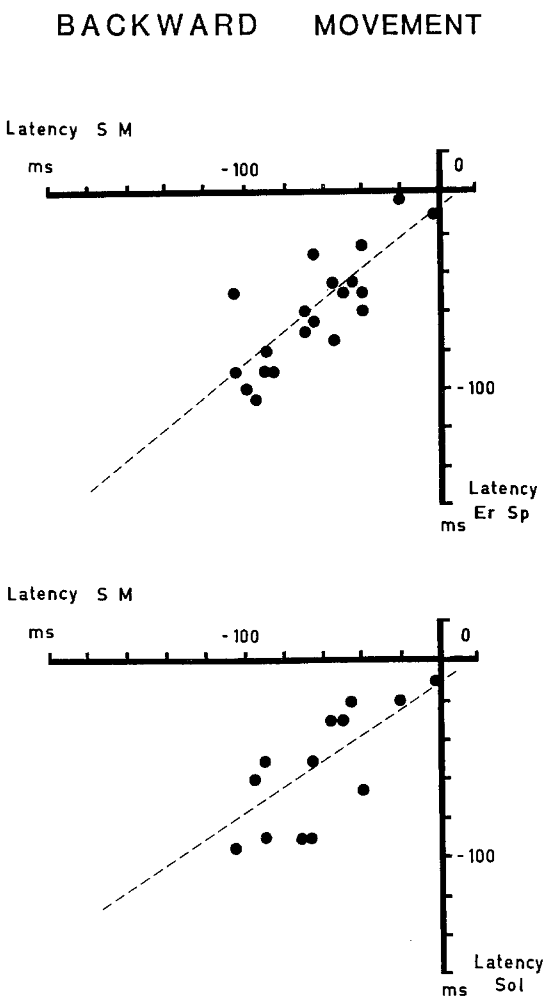

Fig. 9. Plot of the latency of Er. S. (upper graph) and Sol (pooled with GM, lower graph) both versus Sm (pooled with BF). Measurements on the subjects performing the fast movements. Note the simultaneous activation. Equation for regression lines are: $y = -7.2 + 0.81\,x$; $r = 0.81$ for Er. S. and $y = -9.6 + 0.71\,x$; $r = 0.73$ for Sol. The Spearman rank order correlation (Siegel 1960) is significant ($p < 0.01$) for both regression lines

significant ($P < 0.01$; Student's T test). The results are thus compatible with a synchronous recruitment of the three muscles examined.

A final remark concerns the onset of EMG activation in relation to the onset of CP displacement. In fact, CP often started moving before any EMG activation. This phenomenon might be explained either by the fact that no low level activation of one of the muscles investigated (such as Sol or GM) was detected, or by the early activation of some muscle which was not investigated.

After the early recruitment of Er S, Sm and Sol activation of the neck (Scm) and trunk flexors (R Abd), hip extensor (VM) and ankle dorsiflexor (TA) was found to be related to the braking of the backward movement and the initiation of return to the upright position.

Discussion

The present study was not specifically centered on the control of axial movements per se, as was the study by Thorstensson et al. (1985) but rather on the coordination between the axial movements and the associated hip and knee displacements.

Several interesting features were observed during forward and backward upper trunk movements.

The first point concerns the efficiency of the overall motor performance as regards the regulation of the CG position. In fact, we found that the sagittal displacement of the CG at the maximal amplitude of the bending movement was very small, about 1 cm, both during forward and fast backward movements. It is interesting to note by comparison that during quiet stance, posturographic recordings show extreme oscillations of the CP projection onto the ground of about 0.75 cm in the antero-posterior direction (see Gantchev et al. 1985). The effective compensation observed during axial movements appears to depend on the hip and knee movements in the opposite direction to that of the upper trunk, as suggested by the ten-times larger shift of the CG (12 cm) in the biomechanical model in which a comparable forward trunk flexion was produced without any associated movement of the lower body segments. Interestingly, Gurfinkel et al. (1971) have described the axial synergies during normal and forced respiratory movements, and noted that no rhythmic displacements of the CP are present in normal subjects. Here again, the postural adjustment is very efficient.

Insights into the type of control strategy underlying upper trunk bending can be provided by kinematic and EMG findings, especially during fast movements. In fact, analysis by the EL.I.TE. system showed that a motion of all the body segments during both fast forward and backward bending was synchronous. Such behaviour might be attributable to the fact that for purely mechanical reasons, the movement of the upper trunk in one direction should cause a simultaneous passive acceleration of the buttocks and lower limbs in the opposite direction (action-reaction principle) or else by the alternative possibility that a common central command is at work, setting in motion, the upper trunk and the lower limbs at the same time. Measurement of the timing of EMG activation provides strong evidence in favour of the latter hypothesis, suggesting that the "postural" muscles of the lower limbs are activated earlier than or simultaneously with the trunk and neck muscles, which are assumed to act as prime movers. A feedforward type of neural control appears therefore to subserve the fast axial movements.

Furthermore, a deeper analysis of the relative timing of activation of several synergistic muscles revealed that within this feedforward strategy two specific modalities can be adopted. The first was observed with fast backward bending and consists of a synchronous activation of the lower limb postural muscles (Hamstrings and Sol) and the prime mover (Er.S.). This modality implies the existence of a common central command reaching all the muscles involved in the motor act simultaneously. The second modality was observed with fast forward movements. Here, the postural muscles were activated in a sequence (Sol inhibition, TA activation and VM activation), in close temporal correlation, in most cases before the prime mover (R.Abd.). The latter exhibited a far less significant time correlation with the postural muscle group, being recruited at a fairly constant latency before the onset of motion. Such a strategy, implying a dual control of movement initiation involving on the one hand the postural muscles and on the other, the prime mover, is the same as that described in voluntary movements of the upper limb, where an anticipatory adjustment of leg muscles usually precedes the activation of the prime mover of the arm (see Massion, 1984). The lack of any close correlation between the onset of the postural muscles activation and that of the prime mover in our groups of subjects might be explained if each subject utilized a somewhat different strategy concerning early changes of posture, depending on his own mechanical constraints and his previous experience. The preliminary results of some further experiments favour this interpretation.

An additional difference between forward and backward upper trunk movements is the initial forward displacement of the knee consistently observed with fast forward movements, but not with backward bending. The functional meaning of this early knee flexion, which is probably induced by the EMG burst on TA and by the inhibition of Sol activity, is difficult to explain on the basis of the stabilizing role currently ascribed to the associated postural changes. In fact, the most likely outcome of the activation of TA is a shift of the CP in a posterior direction which in turn will result in a larger imbalance of the whole body structure. In this respect, this displacement of the knee should not be viewed as a compensation to equilibrium disturbance; rather, it might play a role in furthering voluntary movement, by yielding a geometrical configuration of the kinematic chain formed by the successive body segments, which accelerates, for purely mechanical reasons, a forward bending of the upper trunk. The action should therefore contribute towards speeding up the onset of movement or allowing it to be performed with less energy expenditure. A similar interpretation was proposed by Cook and Cozzens (1976) in connection with the initiation of human gait, which is also characterized by a forward bending of the body, until the swing leg starts the first stride. Here again, the EMG pattern may consist of a burst on TA and a simultaneous inhibition on calf muscles.

The early knee flexion observed with fast forward movements is likely to also cause a passive stretching of the knee extensors (VM) which might potentiate the force of their subsequent contraction. This mechanism has previously been suggested in connection with jumping and running by Cavagna et al. (1971).

A further question addressed in the present study was whether the pattern and timing of the head and trunk movements and the associated hip and knee movements varied with the movement speed. Comparison between bending movements performed at different velocities indicates that different kinematic patterns do indeed occur, and suggests a velocity-dependent control of the various movement parameters. In particular, the synchronous displacement of the body segments typical of fast movements was replaced by a sequential cranio-caudal displacement with the slow ones. This new sequential pattern is compatible with several types of neural organization. In fact, the delayed movements of the hip and knee might result from a reflex action starting after the onset of the upper trunk movement. Alternatively, a sequential control of upper and lower segments might be centrally preorganized. Again, a synchronous central control might take place, but the sequential displacement might be due to mechanical factors. At present, no definite answer can be proposed, since the EMG analysis did not provide clear evidence for either a sequential or a synchronous activation of the various muscles, due to the very slight and often undetectable changes in motor unit discharge, except during the braking phase.

The influence of the anatomical constraint imposed by the knee joint on the synergies described above deserves some final comment. Actually, we have seen that in forward and backward upper trunk movements, displacements of the hip and knee are in the opposite direction to those of the upper trunk. In both cases movement is performed about an axis of rotation situated somewhere at the lumbar level, but the ability to rotate is limited by the fact that the feet are fixed on the ground. Therefore, the displacement of the body can be represented at best by the analogy with an elastic beam which is hinged both at the ankle and at a point located at lumbar level. In fact, one main difference exists between forward and backward upper trunk movements, namely the ability of the knee to flex but not to hyperextend. As a result, with forward movement, the effect of the rotation is stopped at the level of the knees, and allows only a rather limited backward displacement of the legs. By contrast, with upper trunk backward bending, the effect of the rotation on the lower segments increases because of the flexion of the knees. This might explain why two different motor control modalities are adopted in fast forward and backward upper trunk and leg movements: sequential activation of the postural muscles and prime mover in forward movements and the simultaneous activation of both muscle groups in backward movements.

However, the observed differences might result from other factors, such as a more usual daily practice of forward axial movements.

The axial synergies thus constitute an interesting model for the study of postural control during movement performance and invite us to reanalyze current interpretations of the functional significance of these synergies in the light of biomechanical data and subject's practice.

Acknowledgements. The authors wish to thank A. Berthoz and C. Terzuolo for helpful discussions. This work was partially supported by the MPI 84.12.01 U, the CNR, CTS, PFTBS, and the CNRS AI n° 6943 grants.

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Received January 5, 1986 / Accepted October 6, 1986