Exp Brain Res (1988) 69: 469–480

Experimental
Brain Research

Postural adjustments associated with voluntary contraction of leg muscles in standing man

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Summary. The postural adjustments associated with a voluntary contraction of the postural muscles themselves have been studied in the legs of normal standing men. We focussed on the following questions. Do postural adjustments precede the focal movement as in the case of movements of the upper limb? Which muscle(s) are involved in the task of stabilizing posture? Can the same postural muscle be activated in postural stabilization and in voluntary movement at the same time, in spite of the opposite changes in activity possibly required by these conditions? Six subjects standing on a dynamometric platform were asked to rise onto the tips their toes by contracting their soleus muscles, or to rock on their heels by contracting their tibialis anterior muscles. The tasks were made in a reaction time (RT) situation or in a self-paced mode, standing either freely or holding onto a stable structure. Surface EMGs of leg and thigh muscles, and the foot-floor reaction forces were recorded. The following results were obtained in the RT mode, standing freely. 1. Rising onto toe tips: a striking silent period in soleus preceded its voluntary activation; during this silent period, a tibialis anterior burst could be observed in three subjects; these anticipatory activities induced a forward sway, as monitored by a change in the force exerted along the x axis of the platform. 2. Rocking on heels: an enhancement in tonic EMG of soleus was observed before tibialis anterior voluntary burst, at a mean latency from the go-signal similar to that of the silent period; this anticipatory activity induced a backward body sway. 3. Choice RT conditions showed that the above anticipatory patterns in muscle activity were pre-programmed, specific for the intended tasks, and closely associated with the focal movement. When both tasks were performed in a self-paced mode, all the above EMG and mechanical features were more pronounced and unfolded in time. If the subjects held onto the frame, the early features in the soleus or tibialis anterior EMG were absent, and the corresponding changes in the foot-floor reaction forces were lacking. The anticipatory phenomena observed are considered postural adjustments because they appear only in the free-standing situation, and induce a body sway in the appropriate direction to counteract the destabilizing thrust due to the voluntary contraction of soleus or tibialis anterior. The central organization and descending control of posture and movements are briefly discussed in the light of the short latency of the anticipatory phenomena and of their close association with the focal movement.

Key words: Posture – Anticipatory postural adjustments – Voluntary contraction – Leg muscles – Reaction times – Man

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Introduction

It is known that postural adjustments of the trunk or legs may be initiated prior to the onset of voluntary movements of the trunk (Oddsson and Thorstensson 1986) or upper limb (Bouisset and Zattara 1981; Gahery and Massion 1981; Cordo and Nashner 1982; Friedli et al. 1984; Massion 1984; Woollacott et al. 1984). These postural adjustments appear to be pre-programmed and specific for focal movement and postural set, having the aim of minimizing the equilibrium disturbances provoked by these movements (Arutyunyan et al. 1969).

This paper deals with the motor synergies put into play by the brain in a situation in which a voluntary contraction of the muscles of the legs is required. In this particular case, the induced movement would lead, in addition to a reduction of foot contact surface, to a displacement of the center of gravity of the body: a brisk soleus muscle contraction would result in a backward thrust, whereas a contraction of the tibialis anterior muscle would lead to a forward lean of the body. Since postural stabilization should also be required during these tasks, the following questions arise: 1. Do anticipatory postural adjustments take place in this case? 2. Do they occur in the leg muscles? 3. Is the postural pattern of muscle activity similar or different to the automatic postural adjustment reflexively induced by an externally applied postural disturbance, such as that elicited by support-surface movements? 4. Can anticipatory postural events occur even in the same future agonist muscle? If the latter is true, then the postural requirement would imply a fast change-over in muscle activity, of opposite sign with respect to that evoked by the voluntary command, which is actually the perturbing factor.

The results, part of which have been published in abstract form (Nardone et al. 1986), show that an affirmative answer can be given to the first three questions, as well as to the fourth, regarding the soleus muscle. In fact, in this muscle, anticipatory postural changes are present when the voluntary command impinges either onto the motoneurones of the soleus itself or of the tibialis anterior.

Methods

Definition of terms

The following terms have been used in the text. Focal or intended movement is that induced directly by the voluntary contraction of the agonist muscle(s); in this context, the triceps surae in the case of rising on toe tips, or the tibialis anterior in the case of rocking on the heels. Automatic postural adjustments are short-latency muscle responses to an externally applied postural disturbance. Preset responses refer to motor responses to a command signal per se, which depend on the subject knowing in advance the equilibrium disturbance produced in the intended task; preset responses might therefore be connected with a prior facilitation of neural circuits. By contrast, an anticipatory postural adjustment is an activation of postural musculature, occurring in advance of the focal movements, and issued in a feed-forward manner; it therefore only occurs in connection with the subsequent focal movement and is specific for minimizing its relative perturbation.

Experimental procedures

Six normal males, aged between 23 and 39 years, were studied. They stood on a dynamometric platform (Kistler) with their feet parallel and spaced about 20 cm apart. They were asked to stand with both arms by their sides, and to place equal weight on each foot.

Subjects, standing freely at ease without a support (unsupported condition), were instructed to rise on their toe tips by contracting the triceps surae muscle ("rising" task), or to rock on heels by contracting the tibialis anterior muscle ("rocking" task). These tasks had to be performed 1. as quickly as possible in response to a low-intensity acoustic "go" signal (a click generated by a square wave 1 ms in duration delivered to both ears through earphones, of an amplitude ten times that required to give a just perceptible sound), or else 2. in a self-paced mode. In both cases subjects were not asked to remain balanced on their toe tips, nor to care about returning to the exact initial position. In the same experimental session, and in both the reaction time (RT) condition or the self-paced mode, these tasks were also performed while the subject held (without exerting a forced grasp) onto two stable handles fixed at shoulder height on the wall in front of him (supported condition).

Each subject was studied in three or more sessions, during which the sequencing of the conditions and of the tasks was randomly changed. The interval between two successive performances was varied in a pseudorandom condition, being at least 20 s in duration. During the sessions, RTs to the onset or termination of voluntary EMG activity of Sol muscle in the seated situation were also collected. They were then compared with the onset times of the early changes in the Sol EMG (see Results section) appearing in standing conditions, prior to the focal movements.

In three of the six subjects, a further series of experiments systematically studied the effect of the triggering signal per se on the postural adjustments by using a visual go signal in a non-choice condition. To this aim a LED was used, mounted on the wall in front of the subject's eyes and lit by a square pulse of current lasting 1 ms.

The hypothesis that the subject could preset the excitability of the neural pathways responsible for the postural adjustments was tested by using a visual two-choice RT paradigm. In this case, two LEDs could be alternatively switched on in random fashion. The subjects had to rise on their toe tips at the appearance of a green light, or to rock on their heels at the appearance of a red light.

EMG recording

The EMG signals were recorded by surface electrodes spaced 2 cm apart, placed on the bellies of the following lower limb muscles: soleus (Sol), gastrocnemius medialis (GM), tibialis anterior (TA), quadriceps (Quad), and biceps femoris (BiFe). In the preliminary experiments the EMG activities of sacrospinalis, gluteus, dorsalis, trapezius and rectus abdominis muscles were also recorded during the acoustic RT conditions. In these muscles the recorded activities appeared later than the onset of the bursts in the lower limb muscles causing the intended focal movements; therefore they have not been systematically investigated in this paper.

The raw EMG signals were amplified, band-pass filtered (10–625 Hz), and displayed on a CRO screen. Latencies of onset of the EMG activity were visually measured relative to the onset of the go signal from a storage CRO screen. Since very little or no background activity was present at rest in the EMG records of TA, GM, Quad and BiFe, the beginning of the first discharges of the motor units was taken as the onset of the responses in the agonist muscles. The postural changes in the EMG of the Sol muscle featured a premotor silent period (PMSP) prior to the appearance of the full-blown voluntary burst in the rising task. The termination of the Sol tonic activity was easily measured since no or very little background activity was present during the PMSP. During the rocking task, an increase in the level of background EMG activity appeared frequently in the Sol; owing to its small amplitude, however, measurement of its onset could not be made systematically.

The EMG signals were also rectified and integrated (iEMG, time constant 10 ms). A computer average (Olivetti M24, DT2801

A/D board) of ten to twenty successive events was made, by triggering the acquisition with the rising front of the Sol iEMG (in the case of the rising task) or of the TA iEMG (in the case of the rocking task).

Mechanographic recording

The foot-floor reaction forces applied along the axes of the dynamometric platform were also recorded. The signals were fed into the control board (type 9861A) and then into the computer for averaging. Signal variations were positive when the force increased in a rostro-caudal, antero-posterior or right-to-left direction, in the z, x and y axes respectively; as for example, in a forward sway performed actively or induced passively the x axis output showed a positive change, because a force component directed backwards appeared along the x axis. Comparison of the time course of the changes in activity of the muscles with those in the foot-floor reaction forces was obtained by averaging the z and x axes output, triggering the acquisition as above.

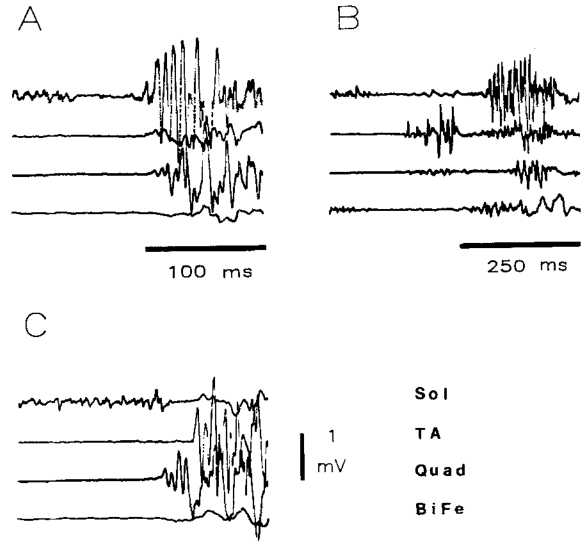

Fig. 1A–C. Electromyograms of lower limb muscles during the rising and rocking tasks, performed in acoustic reaction-time (RT) mode. The acoustic stimulus was delivered at the beginning of the sweeps. **A, B** Show two examples of the different pattern of activation of the lower limb muscles in two subjects during the rising task. In **A**, the premotor silent period (PMSP) in the Soleus EMG (Sol, upper trace) appears alone in the foreperiod; in **B**, the PMSP is accompanied by an early activation of the Tibialis Anterior (TA, second trace) and Quadriceps (Quad, third trace) muscles, and the focal Sol burst is delayed in relation to A (note the different time bases). In this subject the Biceps Femoris (BiFe, lower traces) exhibited tonic activity during the stance, interrupted by a PMSP prior to its activation, which occurred in advance to the focal Quad burst. **C** Shows the pattern of activity, common to all subjects, appearing when rocking on the heels. An early increase in the tonic EMG in the Sol muscle occurs prior to the focal bursts in the TA or Quad muscles

Results

Rising on toe tips, standing freely

Acoustic reaction time situation. During quiet stance without support, electromyographic (EMG) activity was clearly recordable only from the soleus (Sol) muscle; in one subject EMG activity of little amplitude was present also in the biceps femoris (BiFe) and in two subjects in the gastrocnemius medialis (GM) or lateralis.

When the subjects rose on their toe tips as quickly as possible in response to the acoustic go signal, the following events took place (Fig. 1A, B, Table 1):

1. The tonic background EMG in the Sol muscle (and in the GM, when present) underwent nearly in all trials a period of striking decrease in amplitude, featuring in most cases a complete silence. This period began very early following the go signal and was terminated by the onset of the voluntary burst of EMG activity leading to the elevation of the body; it will be referred to henceforth as the premovement silent period (PMSP). The onset of the PMSP was found to be on average 24.3 ms shorter than the termination of tonic activity in the Sol muscle, performed voluntarily in a RT mode while sitting (paired t-test, $P < 0.05$). Its duration was 60.5 ± 18.4 ms (grand mean and pooled standard deviation of all subjects). The regressions and correlations between the onset, and duration, of the PMSPs and the onset of the focal bursts (RTs) in the Sol muscle have been calculated for all subjects. It is shown in Fig. 2 that a strong association was present between the onset of the PMSPs and the RTs ($y = 0.88x - 23.8$; $P < 0.05$, $r = 0.78$), while no significant association was found between duration of PMSPs and RTs ($y = 0.12x + 23.8$; $P > 0.05$, $r = 0.17$).

2. The onset of the EMG burst in the GM anticipated that in the Sol in all the subjects (Fig. 3 left).

3. In three subjects, a burst of EMG activity of moderate amplitude was recordable from the tibialis anterior (TA) muscle, on 61% of the trials, during approximately the second half of the Sol PMSP; this activity terminated in all cases a few milliseconds prior to the Sol burst (Fig. 1B, Fig. 4 left), which was delayed in these subjects.

4. In these same subjects, an early and low-amplitude EMG activity in the quadriceps (Quad) muscle sometimes occurred in correspondence with the burst in the TA muscle (Fig. 1B).

5. In all the subjects, a burst of EMG activity in the Quad muscle occurred during the Sol burst.

6. In four subjects, a small, short-lasting burst of EMG activity sometimes occurred in the BiFe muscle in correspondence with the beginning of the Sol

Table 1. Lower limb muscles' EMGs during the rising task, performed in acoustic RT mode

	Standing freely						Standing and holding		
	Sol PMSP		TA burst		Quad	BiFe	Sol	Quad	BiFe
Subj	Onset	End	Onset	End	Onset	Onset	Onset	Onset	Onset
A.N.	77.6	168.2	113.0	152.7	181.8	145.0	131.1	161.9	118.0
	14.0	14.9	18.2	15.8	15.5	17.4	12.1	14.9	15.5
M.S.	86.3	126.7	–	–	136.8	–	115.7	142.9	159.4
	20.5	17.4	–	–	10.4	–	12.6	12.6	15.6
C.R.	76.4	148.3	102.1	130.0	164.5	121.9	112.3	160.8	111.0
	14.7	11.3	9.6	11.1	22.8	15.5	11.8	13.3	12.7
G.F.	95.8	143.7	–	–	153.0	–	111.5	127.5	–
	23.1	26.0	–	–	20.1	–	10.3	12.3	–
S.M.	71.7	131.8	89.9	113.2	128.5	141.7	97.6	110.8	105.8
	12.0	19.4	38.3	35.1	24.4	18.1	10.8	14.2	21.1
N.M.	77.9	130.5	–	–	167.5	128.7	110.1	147.6	98.6
	13.9	26.0	–	–	24.7	22.7	17.6	26.9	19.2
Mean	81.0	141.5	101.7	132.0	155.4	134.3	113.1	141.9	118.6
	16.4	19.2	22.0	20.7	19.7	18.4	12.5	15.7	16.8

Time in ms. Means ± standard deviations (n = 60) and grand mean ± pooled standard deviation

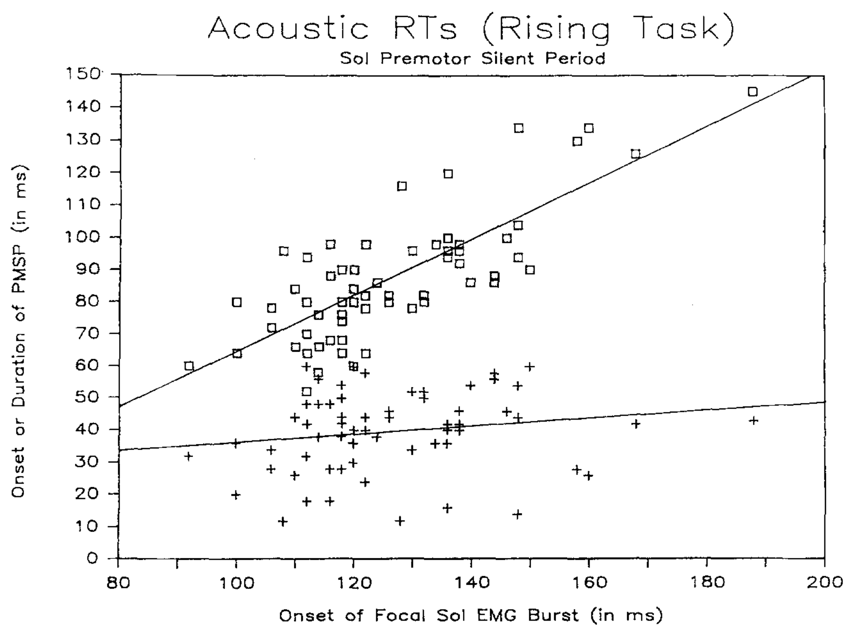

Fig. 2. Relationship between the onset (squares) or duration (crosses) of the Sol PMSP and the onset of the following focal Sol EMG burst, during the rising tasks performed in the acoustic RT Mode (data from one subject, behaving as in Fig. 1A). The regression lines show that the PMSP onset was delayed as a function of the delay in the RT, while the PMSP duration was instead rather constant, irrespectively of the RTs

burst, and was apparently terminated by the contraction of the Quad muscle (Fig. 1B). In one subject a small-amplitude tonic EMG activity was recorded from the BiFe; prior to its burst, a PMSP appeared on approximately half the trials.

During the task, the foot-floor reaction forces acting along the three axes of the dynamometric platform were recorded. Owing to the synchrony in the activation of the muscles of the two legs, no reproducible changes in the force along the y axis were observed in the foreperiod and in the earliest part of the tasks. The changes were very large in the case of the z axis and of a smaller extent in the case of the x axis. Both the z and the x axis force signals exhibited variations in advance of the onset of the triceps or Quad EMG bursts; these variations were correlated with the appearance of the PMSP in the Sol and/or with the burst in the TA muscle.

The results from two differently behaving subjects are depicted in the left panels of Figs. 3 and 4,

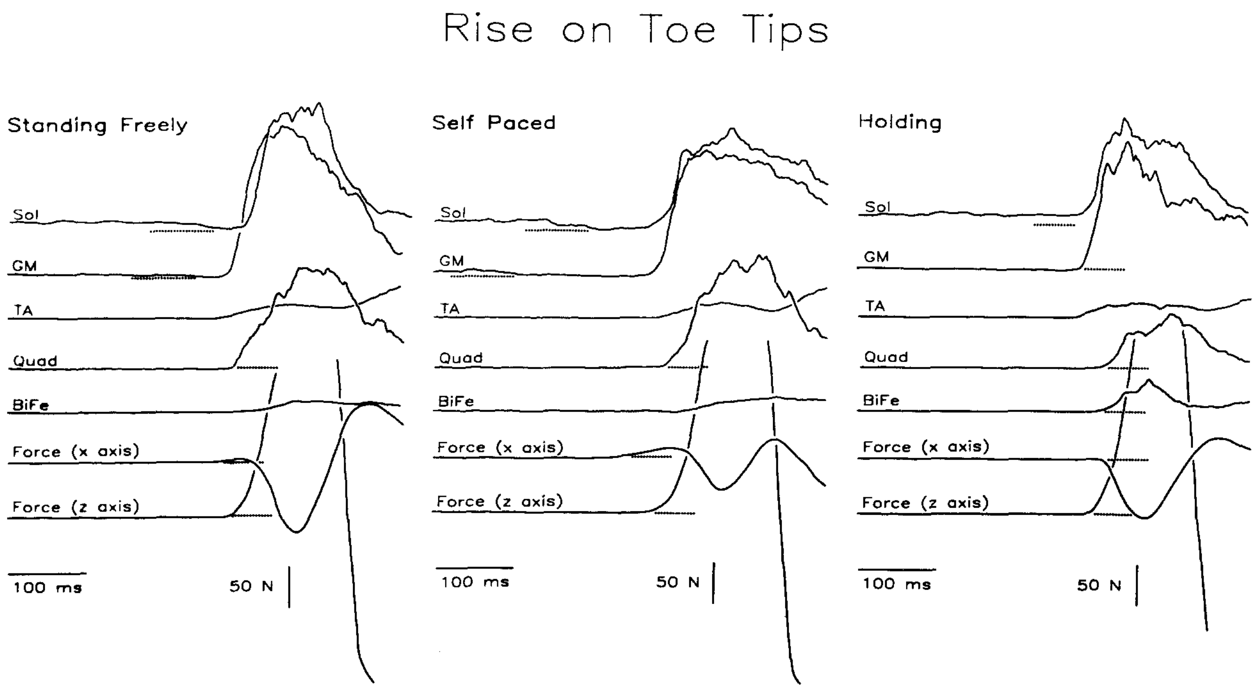

Fig. 3. EMGs and foot-floor reaction forces recorded during the rising task in a subject behaving as in Fig. 1A, in the conditions of acoustic RT standing freely (left panel), self-paced standing freely (centre) and acoustic RT holding onto a stable structure (right). Traces are computer averages (fifteen repetitions) of the rectified and integrated EMGs (iEMGs) of the indicated muscles and of the force changes along the antero-posterior (x) and vertical (z) axes of the supporting platform, triggered with the rising phase of the iEMG burst in the Sol muscle. It is shown that a PMSP in the Sol and GM muscles is present prior to the focal RT activation of the triceps surae (compare with Fig. 1A); the PMSP increases in duration in the self-paced performance, and disappears when posture is stabilized by holding onto a stable structure. PMSP is accompanied by an upward change (proportional to its duration) in the force exerted along the antero-posterior axis, in a direction opposite to that induced by the focal bursts; any such change is lacking when posture is stabilized

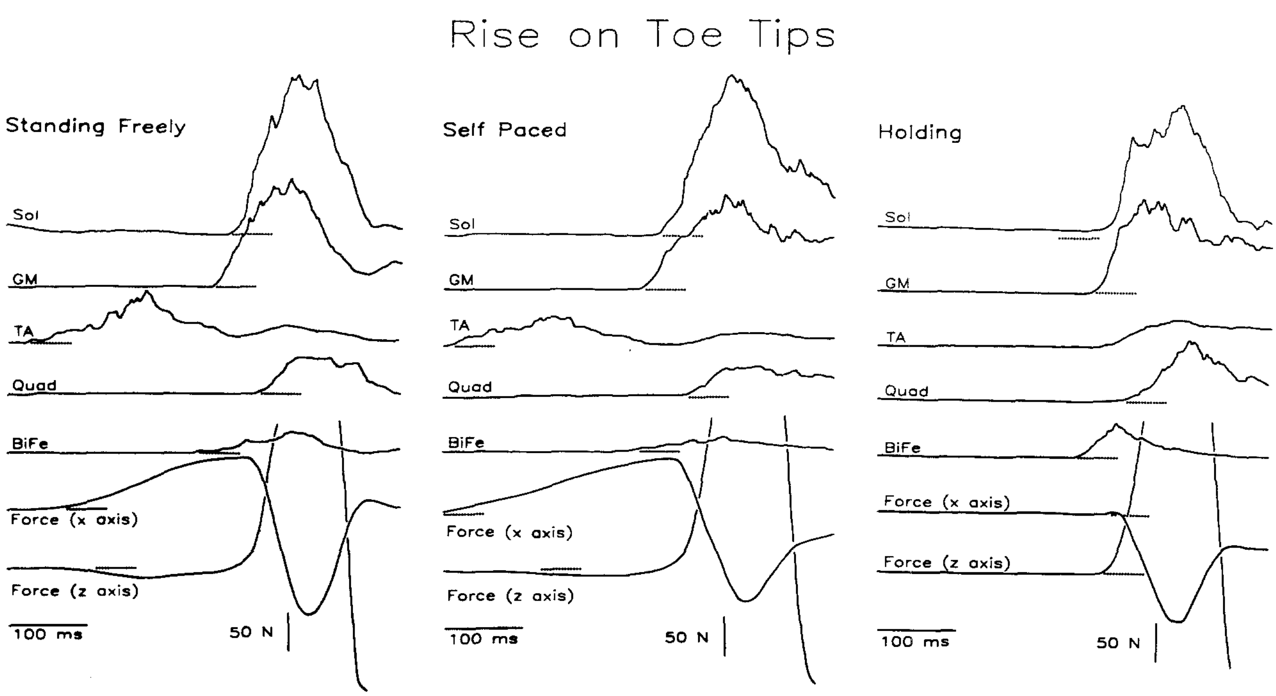

Fig. 4. As in Fig. 3, but in the case of a subject behaving like in Fig. 1B. The combined action of the long-duration PMSP (its onset is out of the averaged periods) and early TA burst leads to greater change in the force along the x axis, compared with that of Fig. 3. Note that in the stabilized, holding condition, PMSP, TA burst and force changes are absent

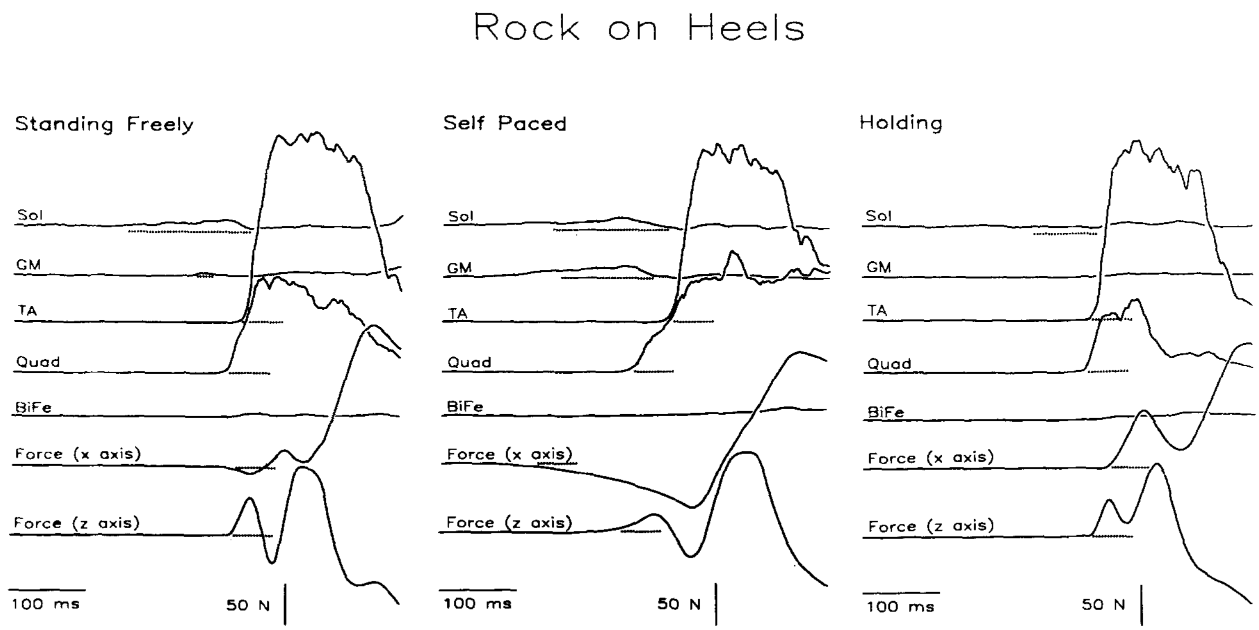

Fig. 5. As in Fig. 3, but during the task of rocking on one's heels. In this case, the averaging started with the rising phase of the TA iEMG. In the standing freely (left) and self-paced (centre) conditions, a clear-cut increase in the tonic background EMG in the Sol and GM muscles is present in the foreperiod, and is accompanied by a downward shift in the force along the x axis, the larger the longer its duration, in a direction opposite to that occurring during the focal TA and Quad bursts. No changes in the EMG level or in the force are present in the holding condition (right)

where it is shown that the Sol PMSP alone (Fig. 3) is able to induce a clear-cut increase in the reaction force along the x axis, in a direction opposite to that occurring during the elevation of the body as a result of triceps surae and Quad activation. In the subject of Fig. 4, this early change in the x axis output is much larger, and is accompanied by a small change in the force exerted along the z axis, owing to the simultaneous activation of the TA muscle.

Self-paced performance. When the task of rising on toe tips was performed in a self-paced mode, the pattern of activation (or inhibition) of the leg muscles observed in the case of RT performance was essentially similar with the following differences (see Figs. 3 and 4, centre):

1. The Sol and GM PMSPs were extended in time, while only minor changes were observed in their following bursts.
2. In the subjects displaying an early burst in the TA, the latter was also longer-lasting and of lower amplitude.
3. The early, low-amplitude activity in the Quad, in these same subjects, occurred more frequently.
4. In all subjects the changes in the force exerted along the x axis in the foreperiod began earlier than in the RT mode and were of larger extent.

Rocking on heels, standing freely

Acoustic reaction time situation. The same subjects, as reported above, underwent experimental sessions in which they were invited to contract their pretibial muscles as quickly as possible in response to the acoustic signal, in this way rocking on their heels. This task also induced a destabilization of the body, which tended to lean forward as the foot-platform contact surface was reduced in front of the projected point of the body's center of gravity.

In this condition the following events were observed in all the subjects (Figs. 1C and 5 left; Table 2):

1. An increase in the amplitude of the tonic EMG activity of the Sol muscle and an appearance of EMG in the GM muscle preceded and terminated in correspondence with the voluntary EMG burst in the TA. This phenomenon appeared in the Sol on 68% of all trials, and displayed a mean duration of 58.9 ms ± 20.3. Also in this case, the onset of this increase in amplitude of the EMG appeared significantly shorter (46.0 ms on average) than the onset of voluntary activation of the triceps surae muscles performed in a RT mode (paired t-test, $P < 0.05$).
2. The voluntary contraction of the TA was always accompanied by activation of the Quad,

Table 2. Lower limb muscles' EMGs during the rocking task, performed in acoustic RT mode

	Standing freely				Standing and holding		
	Sol EIA		TA	Quad	Sol	TA	Quad
Subj	Onset	End	Onset	Onset	End	Onset	Onset
A.N.	67.0	121.4	132.6	124.3	104.1	114.2	117.0
	20.3	12.6	13.7	17.0	18.5	17.4	19.8
M.S.	78.0	130.7	147.6	119.6	104.8	120.0	106.4
	13.9	15.7	12.2	9.3	13.8	8.5	7.1
C.R.	83.5	131.0	146.7	134.5	100.7	113.5	107.8
	14.6	14.0	16.3	15.2	12.1	9.3	8.9
G.F.	78.0	155.3	176.1	140.8	132.0	152.5	119.1
	13.6	15.4	16.3	15.6	17.6	18.0	12.9
S.M.	82.3	144.8	150.7	118.3	109.5	115.8	95.0
	17.7	17.4	20.7	20.9	10.2	11.0	9.9
N.M.	68.8	128.0	139.7	120.1	99.2	114.7	95.7
	16.2	21.9	22.5	24.3	21.2	18.9	20.3
Mean	76.3	135.2	148.9	126.3	108.4	121.8	106.8
	16.1	16.2	16.9	17.1	15.6	13.9	13.2

Time in ms. Means ± standard deviations (n = 60) and grand mean ± pooled standard deviation. EIA = early increase in activity

whose EMG burst actually preceded the onset of the EMG in the TA.

3. In no subject did the BiFe display EMG activity throughout the task.

During the rocking task the force along the x axis of the platform exhibited changes in advance of the onset of the focal movement. These changes were of smaller extent compared with those occurring prior to the movement of rising on toe tips, but were clearly of opposite sign with respect to those induced by the focal movement.

Self paced performance. Also in the condition where the subjects rocked on their heels, the pattern of muscle activation observed in the RT mode was reproduced, albeit in a more spread-out way, when the task was performed in a self paced mode (Fig. 5 centre). The main differences were:

1. A longer-lasting duration of the early increase in Sol EMG.
2. A large increment in the duration and amplitude of the early EMG activity in the GM.
3. These events led to a remarkable variation in the force exerted along the x axis of the platform in the foreperiod, of opposite direction with respect to that imposed by the focal movement.

Standing and holding onto a stable structure

Both tasks were also performed by all subjects in a supported condition, in which they held two handles which were fixed at shoulder height in front of them. Prior to all trials, body position and Sol tonic activity were checked and were like those observed while standing freely.

Both in the RT and in the self paced mode, the patterns of muscle activation in the two tasks were remarkably similar in all subjects to those observed in the standing freely condition, with the important exception that all changes in EMG activity in the foreperiod disappeared. In particular:

1. While rising on their toe tips, the PMSPs in Sol and GM muscles were abolished, and early activity in the TA muscle was no longer present in those subjects that displayed it in the unsupported condition (Figs. 3 and 4, right).
2. While rocking on the heels, the early increase in background EMG activity in the Sol and GM muscles was also absent (Fig. 5 right).
3. The forces exerted along the x and z axes did not exhibit any variation before the onset of the respective focal movements.
4. The onset RTs of the EMGs of the muscles involved in the performance of the focal movements were significantly reduced in respect with those recorded in the freely standing condition (two-tailed t-test, $P < 0.05$) (Tables 1 and 2).

Visual reaction times, standing freely

Non-choice condition. The visual modality was used in three subjects to test the hypothesis that the

Table 3. Lower limb muscles' EMGs during the rising task, performed in visual RT mode

	Non-choice condition						Choice condition					
	Sol PMSP		TA burst		Quad	BiFe	Sol PMSP		TA burst		Quad	BiFe
Subj	Onset	End	Onset	End	Onset	Onset	Onset	End	Onset	End	Onset	Onset
A.N.	134.2	224.6	169.0	210.3	244.9	210.3	196.7	342.2	251.4	304.0	357.0	312.1
	22.9	28.9	23.9	38.3	33.7	31.5	57.8	59.5	50.0	53.3	60.1	60.7
M.S.	120.6	170.3	–	–	180.2	218.3	202.4	285.0	177.7	217.1	297.6	303.5
	18.2	20.4	–	–	13.4	21.6	74.5	80.1	96.0	89.0	89.2	68.6
C.R.	115.0	161.2	–	–	193.8	149.9	215.2	316.2	249.5	303.8	360.0	300.8
	20.3	19.9	–	–	19.1	22.3	48.3	49.8	47.0	44.6	49.6	48.7
Mean	123.4	185.4			206.3	192.8	204.8	308.5	226.2	274.9	338.2	305.5
	20.5	23.1			22.1	25.1	60.2	63.1	64.3	62.3	66.3	59.3

Time in ms. Means ± standard deviations (n = 60) and grand mean ± pooled standard deviation

Table 4. Lower limb muscles' EMGs during the rocking task, performed in visual RT mode

	Non-choice condition				Choice condition			
	Sol EIA		TA	Quad	Sol EIA		TA	Quad
Subj	Onset	End	Onset	Onset	Onset	End	Onset	Onset
A.N.	125.0	166.7	187.7	178.5	216.5	230.3	295.4	285.5
	29.4	26.9	25.7	23.5	56.4	65.2	60.9	57.7
M.S.	110.0	172.9	185.4	165.7	227.5	250.8	277.0	250.1
	16.4	17.6	17.6	28.8	69.7	78.5	84.7	88.0
C.R.	110.0	177.2	194.8	167.5	250.9	269.2	304.6	264.3
	16.4	20.4	27.9	21.7	52.4	60.3	62.8	62.9
Mean	115.0	172.3	189.3	170.6	231.6	250.1	292.3	266.3
	20.7	21.6	23.7	24.7	59.5	68.0	69.5	69.5

Time in ms. Means ± standard deviations (n = 60) and grand mean ± pooled standard deviation. EIA = early increase in activity

quality of the go signal per se would not be relevant in triggering the above observed early EMG responses in the leg muscles. The results show that the patterns of change in EMG activity of the muscles involved in both tasks were reproduced in the condition of visual RT. The only difference was represented by a large (and statistically significant, $P < 0.05$) increase in latency both of the activation of the muscles inducing the focal movements and of the preceding EMG changes in the Sol or TA muscles (see Tables 3 and 4).

Choice condition. This experimental condition allowed us to distinguish between the two possible explanations of the early EMG changes appearing in the leg muscles, and not directly involved in the performance of the focal movements. In fact, these changes could be pre-set by the subject, on the basis of advance knowledge of the task to be performed and the consequent perturbation; in this case the go signal could itself "automatically" trigger the appropriate anticipatory pattern of muscle activity, upon which the voluntary command for the intended focal movement would be later superimposed. Alternatively, the anticipatory events might be an integral part of the voluntary command to execute the required task, and be generated by the brain together with, but prior to the command to perform the focal movements.

The results obtained in this condition show that both the PMSP in the triceps surae muscles or the anticipatory activity in the TA, and the early increase in basal EMGs of triceps surae muscles are still present during the two tasks of rising on toe tips or rocking on heels, respectively. It is remarkable that in this context, in the event that a wrong performance was issued in response to the visual stimulus, the pattern of the various muscles' activity was the same as that occurring when that particular focal movement was executed correctly. In comparison with the responses observed in the acoustic or visual non-choice RT conditions, the timing of the EMG

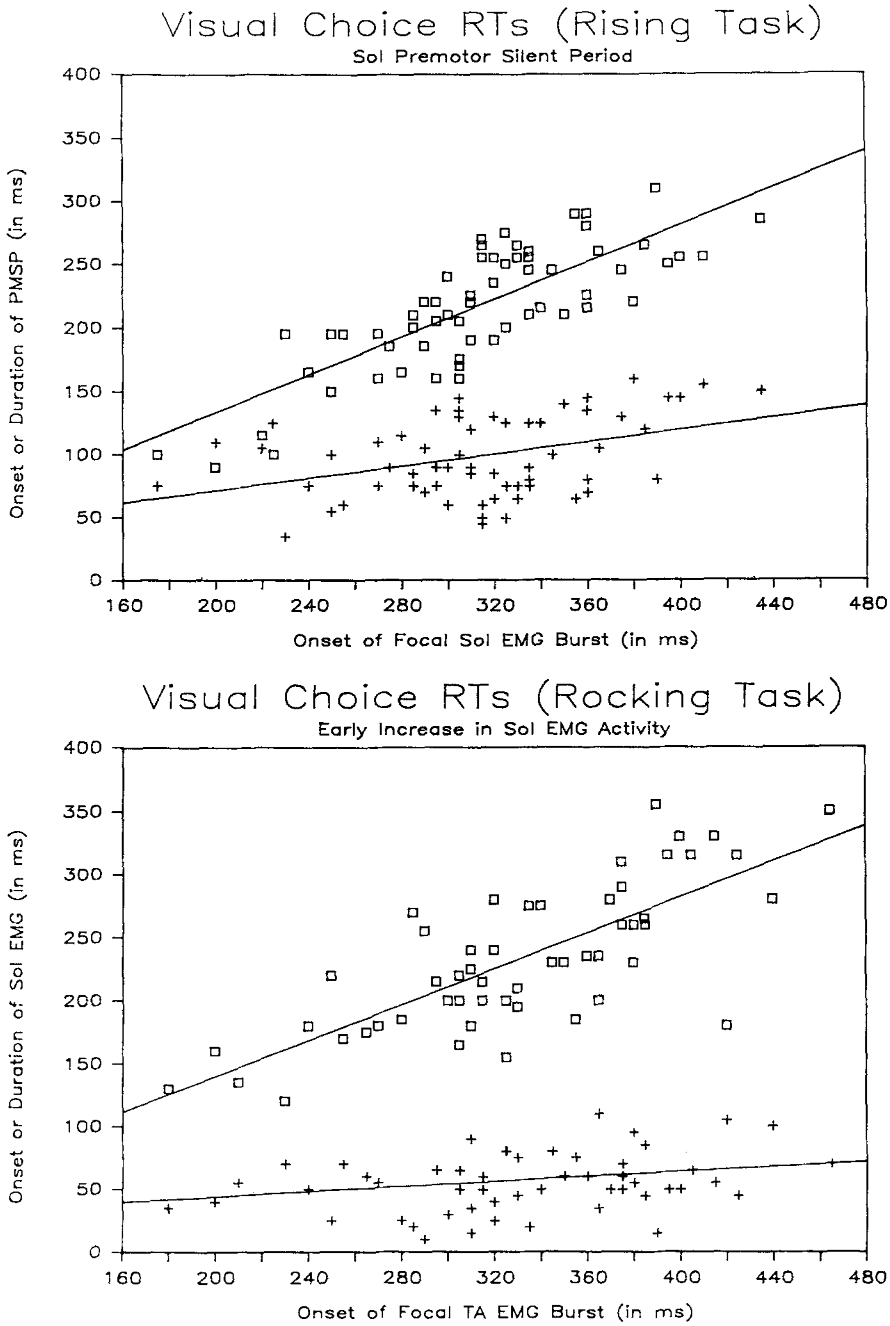

Fig. 6. Upper panel. Relationship between the onset (squares) or duration (crosses) of the Sol PMSP and the onset of the following focal Sol EMG burst, during the rising task performed in the visual choice RT mode (data from one subject, behaving as in Fig. 1A). Lower panel. Relationship between the onset (squares) or duration (crosses) of the early increase in tonic Sol EMG prior to the TA burst, during the rocking task performed in the condition as in A (data from three subjects have been pooled in this scattergram). The regression lines show that the onsets of PMSP or EMG increase were delayed as a function of the delay in the RT, in the rising or rocking tasks respectively, while the durations of the PMSP or EMG increase were instead rather constant, and not correlated with the RTs

activities appeared to be more spread-out, and approached that observed in the self-paced mode (Tables 3 and 4).

In order to ascertain whether the onset of the early changes in Sol EMG activity, observed in the rising or rocking tasks, were related to the onset of the focal movements, the regressions between their onset, or duration, and the onset of the focal EMG burst in either the Sol or TA muscles were calculated for the three subjects. The results in the case of the rising task are depicted in Fig. 6 (upper panel), where it can be seen that the regression and the correlation are much stronger for the onset ($y = 0.76x - 21.7$; $P < 0.05$, $r = 0.80$) than for the duration of the Sol PMSP ($y = 0.24x + 22.1$; $P < 0.05$, $r = 0.37$). The results for the rocking task are shown in Fig. 6 (lower panel); in this case the regression and the correlation were also stronger for the onset ($y = 0.71x - 2.0$; $P < 0.05$, $r = 0.76$) than for the duration ($y = 0.12x + 15.2$; $P > 0.05$, $r = 0.32$) of the increase in Sol EMG activity.

Discussion

We have described in this paper the EMG pattern and the changes in the foot-floor reaction forces occurring prior to two different voluntary motor tasks involving contraction of antagonistic leg muscles, namely triceps surae in the case of rising onto the toe tips and TA in the case of heel rocking (Houtz and Fischer 1961). The main results are 1. the occurrence of an early inhibition of the EMG activity of the triceps surae muscles in advance of their bursting activity leading to the intended focal movement, which may in some subjects be accompanied by a burst of short duration in the TA, and 2. the occurrence of an early increase in EMG activity in the triceps muscles before the voluntary activation of the TA.

These phenomena outline a complex pattern of activity, whereby a muscle's activity is decreased just prior to the fast activation of the same muscle, or is enhanced when the only intended command is the contraction of its antagonist. The TA muscle also underwent, in three subjects, an increase in activity just prior to the contraction of the antagonist, but could not show the inverse phenomenon (inhibition prior to its voluntary activation) since no background activity is present in normal stance in this muscle.

The early changes in activity, of opposite sign, in the triceps surae muscles showed approximately the same duration and latency, the latter being much shorter than for any voluntary contraction or release (Schieppati et al. 1986). They occur only when the subject is standing freely and not holding onto a support, in spite of the similarity in the amplitude and time course of the following voluntary bursts in the two conditions, and are able to cause clear-cut changes in the foot-floor reaction forces (Rossi et al. 1985) prior to those induced by the voluntary bursts. The early changes in the reaction forces are particularly evident along the antero-posterior axis, and are applied in the opposite direction in respect to those induced by the subsequent focal movements.

For these reasons we suggest that these phenomena are anticipatory postural adjustments, specific for that particular focal movement, and serve the purpose of minimizing the subsequent postural destabilization. This aim is achieved by initiating a forward lean of the body just prior to rising on toe tips, which by itself would give the body a thrust backwards, or by inducing a backward sway just prior to toe tips elevation, which gives rise to a forward destabilization. In three out of six subjects the Sol PMSP is accompanied by activation of the antagonist muscle, which is responsible for an increase in the forward anticipatory displacement of the body, as already described (Lipshits et al. 1981; Dichgans and Mauritz 1983; Clement et al. 1984). In this connection, it may be relevant to observe that under the circumstances studied by Lipshits et al. (1981), *all* subjects exhibited the TA contraction prior to rising on their toe tips. That task, however, posed stronger postural constraints on the subjects, who had to remain on their toe tips for an extended period of time. In fact, TA contraction disappeared when subjects were asked to perform the task starting from a forward inclined position, or to simply lift heels off and return to the initial position. Since the latter condition is comparable to ours, it is likely that our subjects displaying TA contraction would unconsciously try to perform the task without excessive destabilization, by selecting a more "reliable" strategy. This TA activation cannot be the result of a "voluntary" forward lean, not only for its short delay (see below), but also because voluntary leaning forward from the standing position should be accompanied by activation of triceps surae muscles to resist gravity (Portnoy and Morin 1956).

The very short latency of these responses could be due to a presetting of neural pathways by the subject knowing in advance the type of postural perturbations induced by the intended movement. We oppose this interpretation for the following reasons: 1. These events are absent in the supported condition, while they are present when the tasks are performed in an unsupported condition. 2. They are present in the absence of any external trigger, as in the self-paced mode. 3. In the event that the wrong performance is executed in the choice-RT mode, the anticipatory activities are appropriate to the actual focal movements. 4. The choice-RT condition allows us to exclude the possibility that these anticipatory postural adjustments may be connected to a particular change in body posture taken by the subjects (Diener et al. 1983) prior to a "go" signal of known significance. Therefore, we feel that the PMSP or the increase in EMG activity in the Sol and GM muscles are an integral part of the command to perform the intended movement, because their onset is strongly correlated with the onset of the following focal movements, both in the acoustic and visual (choice and non-choice) RT conditions, and because their duration is rather constant in the various conditions. This conclusion is supported by animal experiments describing the relationship between movements and anticipatory postural adjustments, and showing that the postural adjustment is not triggered reflexively by the disequilibrium induced by the movement but is a result of a central nervous command (Gahery and Nieoullon 1978; Coulmance et al. 1979; Pompeiano 1983).

Inhibition of muscle activity just prior to its voluntary activation has already been described in man, in the case of the Quad (Yabe 1976; Kawahats and Miyashita 1983), spinal and thigh muscles (Tanii 1984) and triceps brachii muscle (Conrad et al. 1983). This phenomenon, which has been considered to be part of the descending command, has been attributed a role of facilitation of the subsequent full-blown EMG discharge through better synchronization of motor unit activation. Our data also favour the hypothesis of its being issued from the brain together with the command to perform the focal movement, but its role appears to be chiefly postural. In fact, the Sol PMSP occurs in the free-standing but not in the holding condition, in spite of similar amplitude and duration of the muscle activity leading to the focal movement. The PMSP appears therefore to be the consequence of the sole possible effective interaction, at the level of the same motoneuronal pool, between the requirement of postural stabilization and the performance of the task.

There is some similarity between these anticipatory postural muscle activities and the reflexively-elicited activities observed when a standing subject is destabilized by shifting the supporting platform in antero-posterior direction (Nashner 1983). When the platform is displaced forward, the backward body sway is more commonly contrasted by a contraction of the TA and Quad muscles, a pattern described here in some subjects prior to the voluntary elevation of the body on the toe tips. When the platform is displaced backward, thrusting the body forward, a GM and hamstring contraction is initiated: an increase in tonic activity in the Sol and GM muscles occurs in all subjects prior to voluntary rocking on heels, i.e. prior to a forward destabilizing task. It is therefore likely that the descending command eventually leading to a postural destabilization is able to anticipate the same muscle synergies which are put into action by the passive body displacement, either by a functional stretch reflex or by a vestibular input (Nashner 1976, 1977). Such an hypothesis has been suggested by Cordo and Nashner (1982) in the case of lower limb muscle synergies anticipating voluntary contraction of biceps brachii in unsupported subjects.

An open question is that of the neural generators, and of the pathways and spinal circuits involved in the anticipatory postural command. It has been already shown that both automatic or associated postural adjustments always precede focal movements (Nashner and Cordo 1981). This priority could depend on two possibilities: 1. the postural command is generated before the focal command in the same or in a different generator, or 2. both the postural and the focal command share a common generator but the former travels through faster pathways. The close association between postural adjustment and focal movement, the accessibility to the complex pattern of muscle activation, both by command signals of different origin and by the "intention" to move, speak for a unique generator. This is also supported by the observation that the initiation of the command can be modulated in time, very much as in a voluntary movement which can be performed slowly or in a ballistic way. In fact, the same pattern of muscle activation can be very brief as in RT conditions, or last longer as in self-paced performances. On the other hand, when the subjects know in advance that the task will be not very destabilizing, because they are holding onto a stable frame, the postural adjustment disappears. The absence of the latter, however, does not lead to a corresponding anticipation of the focal movement, as if the whole command would be necessarily made up of two successive parts, the first of which can give way to a full-blown pattern of activity, or be cancelled, or concealed. As far as the pathways are concerned, they must have a very fast conduction velocity, be recruited in a very selective way, and have a very selective target, in order to yield an appropriate and specific stabilization. The hypothesis we favour is that a descending modulation, of opposite sign, of the degree of presynaptic inhibition of the Ia autogenetic afferences plays a major role. This can be brought about very quickly, at least as far as can be deduced by the very fast voluntary inhibition of Sol muscle activity observed in other experimental conditions (Schieppati et al. 1986). The presynaptic modulation would be appropriate for decreasing the level of discharge in the Sol motoneuronal pool, as indicated by the striking decrease in amplitude of the H-reflex elicited during the PMSP (Nardone et al. 1986), without impairing its excitability in response to a descending command (see Schieppati 1987). It can also explain the presence of an increase in EMG activity, as a consequence of removing the presynaptic inhibition in a period in which the Ia fibres are presumably firing, owing to the tonic alpha (and gamma) motoneuronal discharge to the Sol muscle in standing conditions. The recurrent inhibition might also contribute to the development of the PMSP observed prior to rising on toe tips, standing freely; in fact in standing man, without support, the Renshaw cells are more excitable than while standing supported by a wall (Pierrot-Deseilligny et al. 1977).

Acknowledgements. We thank Dr. Steve Forman for checking the English language. Supported by grants from MPI and Regione Lombardia.

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Received January 8, 1987 / Accepted September 21, 1987