Exp. Brain Res. 36, 463–476 (1979)

Experimental
Brain
Research


# Organization of Rapid Responses to Postural and Locomotor-like Perturbations of Standing Man

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**Summary.** This study has described the organization of EMG activities among the muscles of a standing subject's legs during rapid postural adjustments (95–120 ms latencies). Adjustments were elicited by the horizontal translation of both feet (causing antero-posterior sway), by the synchronous vertical displacement of both feet (causing changes in height) and by the reciprocal vertical displacement of the feet (causing a locomotor-like motion of the legs and lateral sway of the body). The resulting patterns of EMG activity were highly specific for each kind of displacement, and all subjects completely reorganized the pattern of activity from one form to another within the first trials, even immediately following unexpected stimulus changes.

The organization of EMG activities during reciprocal vertical displacements was qualitatively quite similar to those observed during the comparable swing and stance phases of the locomotor step cycle; flexor muscles of the ankle and knee (those being shortened by the displacement) contracted in the upwardly displaced leg while extensor muscles were active in the downwardly displaced leg. This pattern was in marked contrast to the activation of lengthening muscles during synchronous vertical and antero-posterior sway displacements. Finally, electrical cutaneous stimulation of the dorsum of one foot during reciprocal vertical displacements always enhanced the EMG activity of the agonist leg muscles, in-phase with the vertical movement.

**Key words:** Posture – Locomotion – Reflex adjustment – Coordination

In recent years a large number of experiments have supported the concept that sensorimotor systems express patterns of purposeful movement and adapt these patterns to the external conditions through hierarchically organized groups of specialized subsystems (e.g., Engberg and Lundberg, 1969; Kots et al., 1971; Gelfand et al., 1971). In fact, Bernstein (1967), arguing on theoretical grounds, anticipated that such organization was essential, since it would be difficult for the brain to independently regulate the vast number of motions of the many

0014–4819/79/0036/0463/$ 2.80

mechanical linkages and activities of associated muscle groups which collectively compose purposeful movement.

Additional evidence supporting the concept of hierarchical organization of movement control has come from treadmill experiments using spinal cats (Grillner, 1975; Wetzel and Stuart, 1976). These studies demonstrated that specialized subsystems within the spinal cord can produce stereotyped locomotor movements and need only a minimum of movement specific proprioceptive inputs or nonspecific activation of inputs from the brain for initiation. It was also demonstrated that subsystems within the spinal cord gate or reverse reflex activity during the stance and swing phases of locomotion so that activity of the appropriate muscles (flexors or extensors) is always enhanced for proper gait and stabilization. However, because the cat treadmill preparations were deprived of normal visual and vestibular input, the integration of balance and adaptive mechanisms into the locomotor activity could not be studied. Also, because procedures for establishing locomotor activity were rather qualitative, the many questions regarding the initiation of purposeful gait could not be studied.

While experimental limitations upon the human subject preclude a probe into the basic neural mechanisms of organization, the human is an excellent subject with which to study the more integrative processes involving the interactions of balance, adaptation, and movement. Previous human studies found that rapid postural adjustments executed by leg muscles during the perturbation of standing subjects (EMG latencies of 100–120 ms) were stereotypically organized in a functionally useful way (Nashner, 1977) and were progressively adapted to the external proprioceptive (Nashner, 1976) and visual (Nashner and Berthoz, 1978) conditions of the task. These results have motivated the hypothesis addressed here that rapid postural adjustments in humans are expressed by the same organizing neuronal machinery as are the stereotypical locomotor movements previously seen in cats. However, the previous observations were far too limited to confirm such a hypothesis, since locomotor activity entails reciprocal relations between the limbs and joints and vertical as well as horizontal and rotational motions. The object of this study has been to expand the description of rapid postural adjustments to include those elicited by more locomotor-like reciprocal movements of the limbs.

The significant advance made here is that stereotypical organization (similar to that found in the locomoting cat) has been elicited using transient locomotor-like motions and with standing human subjects who are awake and have all of their sensory, adaptive, and voluntary faculties intact. These results open the way for closer integration of studies involving balance, adaptation, and locomotion and also closer integration of animal and human motor studies.

## Methods

### *Stimulation and Recording*

The experimental paradigm described previously (Nashner, 1976, 1977), to perturb the posture of subjects standing upon a movable platform and to measure the resulting EMG activity of selected

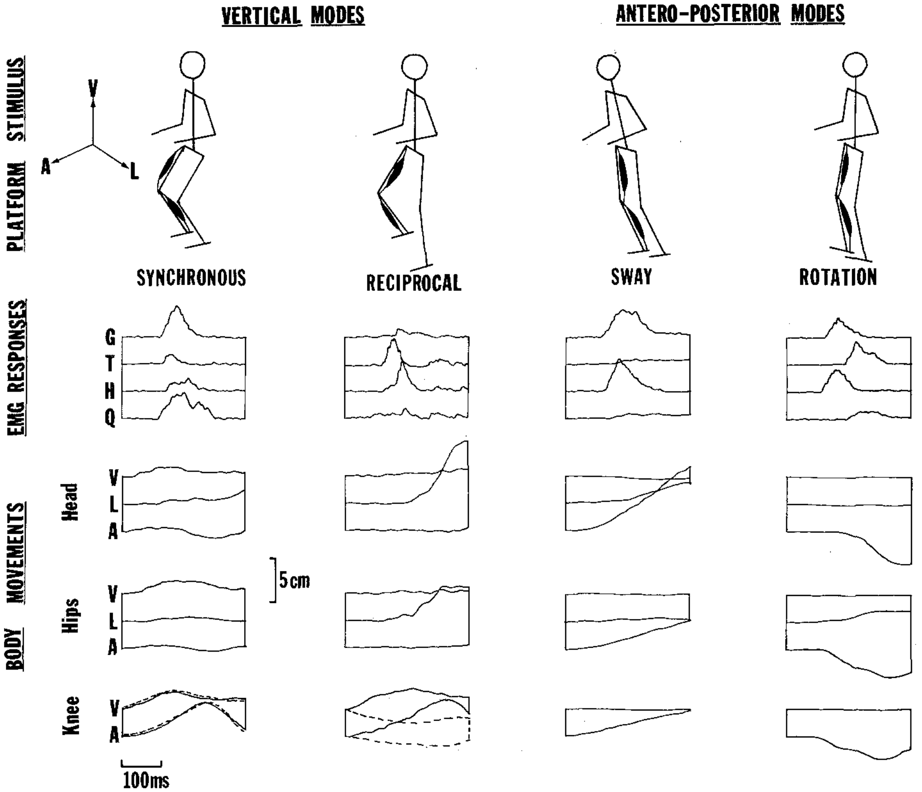


**Fig. 1.** Four stimulus motions of the platform and the resulting body motions and EMG responses: synchronous vertical displacement of both platforms, reciprocal vertical displacement, translation-induced sway displacement, and direct rotational displacement of the ankles. EMG responses of the gastrocnemius (G), tibialis anterior (T), hamstrings (H), and quadriceps (Q) muscles. Movements of the head, hips, and a knee joint in the vertical (V), lateral (L), and anterior (A) directions

leg muscles, has not been altered here. However, the original repertoire of two independent platform movements has been considerably expanded and the procedures for producing the platform movements somewhat refined. A new platform has been constructed which moves in six degrees-of-freedom, each degree of which is independently controlled by a separate hydraulic servomotor (0–8 Hz frequency response). Each foot of the standing subject rests upon a separate, adjacent platform which translates horizontally (range 30 cm), translates vertically (range 15 cm), and rotates about an axis colinear with the ankle joint (range ± 15 deg). Figure 1 illustrates the platform movements and resulting postural motions for two stimulus modes studied previously (anteroposterior sway about the ankle joints induced by horizontally translating the platforms, and direct rotation of the ankle joints) and for two new stimulus modes (synchronous vertical displacement of the two platforms and locomotor-like reciprocal, vertical displacement of the two platforms). Direct rotational motions were induced during some vertical displacements in order to interrupt the normal congruency between knee and ankle rotational motions. Such disruptions were used to test the relative importance of ankle and knee rotational inputs to the resulting vertical postural adjustments.

To minimize the possible extraneous inputs which would be associated with very abrupt platform motions, each perturbation (beginning with both platforms coplanar with the floor) was the first

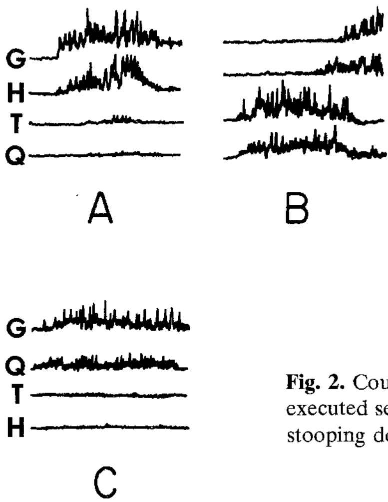


**Fig. 2.** Coupled patterns of EMG activity elicited during voluntarily executed sequences of forward sway (**A**), backward sway (**B**), and stooping downward (**C**)

one-quarter portion of a sinusoidal curve of 2 Hz (time to peak deflection, 125 ms). Following each perturbation the platforms were returned to the coplanar positions slowly over a 5-s interval. The amplitude of excursions used were 8 cm horizontal movements, 5 cm vertical movements, and 5 deg rotational movements.

In order to test the ways in which certain cutaneous reflexes were gated in-phase with reciprocal, vertical movements of the platforms, electrical stimuli were imposed between two surface electrodes (2.5 $cm^2$) spaced 3–5 cm apart upon the dorsum of one foot. During alternate trials a fixed level of current (Tektronix stimulus isolation unit) commenced at the onset of the movement stimulus and lasted for 5 ms. The current polarity was reversed in each stimulus presentation to guard against electrode polarization. The current was set at a level just below that which was subjectively perceptible to the subject. Typically, the current level was set somewhere within the 0.9 to 2.6 ma range.

Stereotypical patterns of activity among leg muscles and the relations between muscle activity and muscle length changes were analyzed by recording the EMG activity of four leg muscles which collectively play a role in the regulation of ankle, knee, and hip joint motions. Activity of the gastrocnemius (G), tibialis anterior (T), quadriceps (Q), and hamstrings (H) muscles (using 2.5 $cm^2$ surface electrodes spaced 2–4 cm apart) was processed by band-pass filtering (10 Hz to 10 kHz) full-wave rectification, and then low-pass filtering (0–40 Hz) to give a DC signal approximately in proportion to the amplitude of activation of the muscle. The gain of each EMG amplifier was set only once at the beginning of each session by equalizing the response amplitude of functionally related muscles during voluntarily executed sway and stooping movements (see Fig. 2). Although the processed EMG signals could not be calibrated as an absolute measure of muscle contractile strength, the fixation of gain for the duration of each session allowed a meaningful quantification of *relative* changes in activity among the muscles.

Motions of the head and hips in the anteroposterior, lateral, and vertical directions and of the knee joint in the anteroposterior and vertical directions were measured by attaching a separate rigid light rod to each of these three points with a belt. The other end of each rod was linked via a set of two rotary and one linear potentiometers to a rigid structure placed 70 cm to the side of the subject so that the belted end of the rod was free to move in all directions.

### *Analytic Techniques*

To quantify the pattern of EMG activity elicited by a platform displacement, the activation latency of each muscle was first determined by a visual inspection of the record. A relative number value for the amplitude of each muscular contraction was computed by numerically integrating its processed EMG signal over a 50 ms interval immediately following the time the first muscle in the group became active. A 50 ms interval was selected after findings here and in previous studies (Nashner, 1973, 1976; Nashner and Berthoz, 1978) showed that activities within the 100–150 ms interval always required proprioceptive inputs, while activities occurring after this interval may also involve the complex combination of vestibular and visual inputs as well.

The patterning of EMG activity during a response was analyzed by first computing three coupling ratios, each expressing the relation between the amplitude of activity of the responding lower leg muscle and: (1) the upper leg muscle on the same dorsal or ventral aspect of the leg, (2) the upper leg muscle on the opposite dorsal or ventral aspect of the leg, and (3) the antagonist lower leg muscle. The statistical significance of fixed EMG patterns was assessed by lumping the data of all subjects and averaging each of these three ratios among trials of like stimulus movements. However, in a few instances, parts of the data from particular subjects departed significantly from the norm. These few exceptions are always noted in the text and described separately.

Changes in rapid postural adjustments caused by electrically stimulating the dorsum of one foot (during alternate trials) were determined by measuring the differences in amplitude between these responses and the two adjacent trial responses (during which electrical stimuli were not given). This method (shown in Fig. 6) compensated in part for the significant shifts in baseline strength which occurred randomly over time.

*Protocol*

Each participating subject was asked to place one foot (bare) upon each of the adjacent platform bases and to maintain a comfortably erect posture while facing directly forward and folding the arms at the waist. In most sessions the subject wore earphones and listened to music in order to eliminate possible sensory cues from platform or other equipment noises.

In order to study the organization of EMG adjustments to locomotor-like platform motions, eight subjects were exposed on two occasions to the same 1-h session. The hour session was separated into three 15-min test periods and interposed 5-min rests. A test consisted of 40 trials (each 6 s long), which were interspaced randomly within 15–60 s to minimize a subject's anticipating the exact moments of stimulation. The same form of stimulus was always given in a sequence of four in order to observe completely any adaptive changes in the response characteristics. During the first test period the subject was exposed to four trials of each of the stimulus movement combinations. The second 15-min period consisted of similar but differently ordered movement combinations. The final 15-min period was used to isolate the effects of ankle and knee joint rotational inputs by interspersing sequences of combined reciprocal, vertical and rotational motions with sequences of pure reciprocal vertical motions.

Because subjects often began to modify their strategies of stance after experiencing the platform movements for 2 h, a naive group of four subjects was recruited to study the effects of cutaneous electrical stimulation on muscle response size and duration. In these experimental sessions only reciprocal vertical and AP sway sequences were used. These sequences were extended to include 10–16 trials of the same stimulus type.

To choose 12 subjects for the study, 25 candidates were screened using a brief test to select those who evidenced strong EMG responses at 100 ms latency. Candidates who tended to lean either forward or backwards about the ankles or the hips were excluded.

## Results

### *Postural Motions*

The synchronous, upward displacement of both platforms displaced both knee joints upward and forward, while having a relatively small effect upon the vertical positions of the trunk and head (Fig. 1). Computations based upon the measurements indicated that during the first 150 ms of a vertical displacement the coordinated (dorsi-) flexion of the ankles (approximately 5 deg), knees (approximately 12 deg), and hips (approximately 5 deg) absorbed most all of the upward movement of the feet. Similarly, synchronous, downward displacements of both platforms resulted primarily in a coordinated extension of the ankles (plantarflexion) knees, and hips.

During the first 150 ms of a reciprocal vertical displacement of the two platforms, each leg moved independently and its trajectory was approximately the same as that produced when the foot had been displaced by synchronous, vertical movement in the same direction. While reciprocal vertical displacements did not cause consistent vertical changes in height of the trunk and head, both of these body parts were shifted laterally to the side of the lowering leg. This lateral sway movement of the body began at latencies ranging between 100–120 ms at the hips and 130–175 ms at the head (observations from the eight subjects).

### *Latency and Direction of EMG Responses*

The *stretching* ankle muscle contracted first and with greater strength whenever the platform displacements *synchronously* rotated the ankle joints (AP sway and direct rotational stimuli) or *synchronously* displaced both of the feet vertically. In contrast, the *shortening* ankle muscle contracted first and with greater strength whenever the feet were reciprocally vertically displaced. The latency of earliest EMG activity was within 93–120 ms under all stimulus conditions, although activity elicited by reciprocal displacements (directionally reversed relative to the other modes of displacement) occurred on the average a small but significant fraction later than the other modal responses (110 ± 10 ms for reciprocally elicited activity versus 98 ± 5 ms for synchronously elicited activity). Figure 3 combines the latency and amplitude data of lower leg muscles from among the eight subjects to show the redistribution of contractile activity from the lengthening to the shortening muscles during reciprocal stimulation. This figure shows that the redistribution of activity was also observed in those instances (first reciprocal trials of a sequence) when the subject could not anticipate the occurrence or the direction of a reciprocal displacement.

### *Coupling Ratios*

Vertical displacements of the platform elicited EMG activities which were coupled between upper and lower leg muscles on the opposite dorsal and ventral aspects of the leg. Although the direction of response activities relative to the direction of stimulus displacements was reversed during reciprocal as compared to synchronous vertical displacements, the coupling patterns between upper and lower leg muscles were the same in both cases. Confirming previous results (Nashner, 1977), upper and lower leg muscles on the same dorsal or ventral aspect were coupled during AP sway and direct ankle rotational

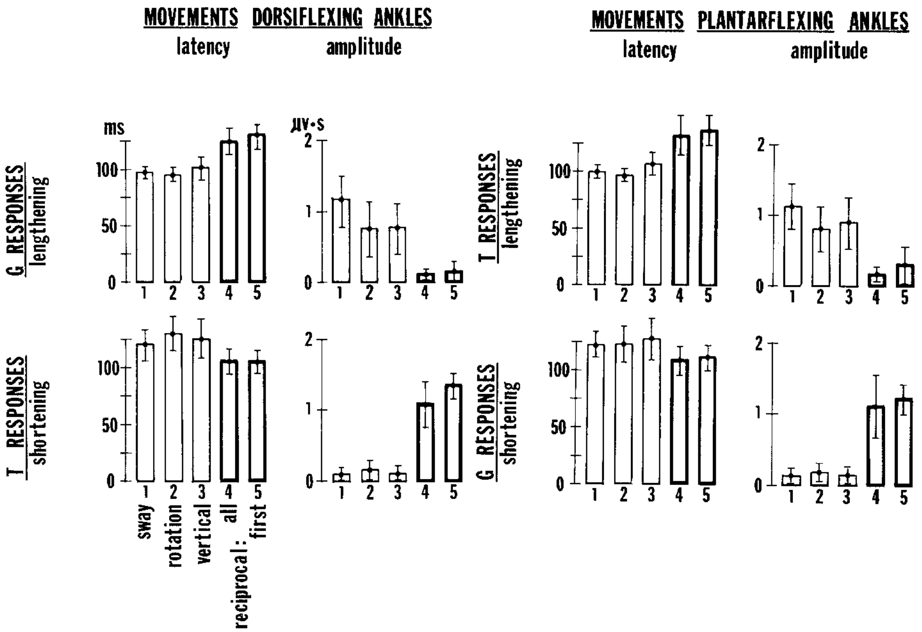


**Fig. 3.** The latency and amplitude of EMG responses of the lengthening and the shortening lower leg muscles during platform displacements which dorsiflexed (flexed) and plantarflexed (extended) the ankle joint: (1) translation-induced AP sway, (2) direct ankle rotation, (3) synchronous vertical displacement, (4) all reciprocal vertical displacements and (5) first reciprocal vertical displacements after an unexpected transition from another mode of stimulation

stimulation. Figure 4 illustrates these relations between the mode of platform stimulation and the pattern of coupling between lower and upper leg muscles.

Among the eight subjects tested to determine the coupling ratios among upper and lower leg muscles, three showed some minor deviations from the norms presented in Fig. 4. One subject, whose agonist coupling ratios followed the normal pattern, also evidenced significant co-contraction of both the lower and upper leg antagonist muscles (amplitudes approximately 25–40% of the agonists). Two other subjects showed preferentially large H activity during all modes of stimulation. Although all candidates were examined for obvious nonvertical postures, it became apparent that these two were leaning forward slightly above the hips, thereby tending to rotate the trunk forward about the hips during all modes of stimulation.

## *Isolation of Ankle and Knee Rotational Inputs*

Changes in the rotational motion of the ankle joint during reciprocal vertical displacements did not alter the pattern of EMG activity in which muscles were coupled on the opposite dorsal and ventral aspects of the leg and the contractile effort tended to move the leg up or down to follow the motion of the platform.

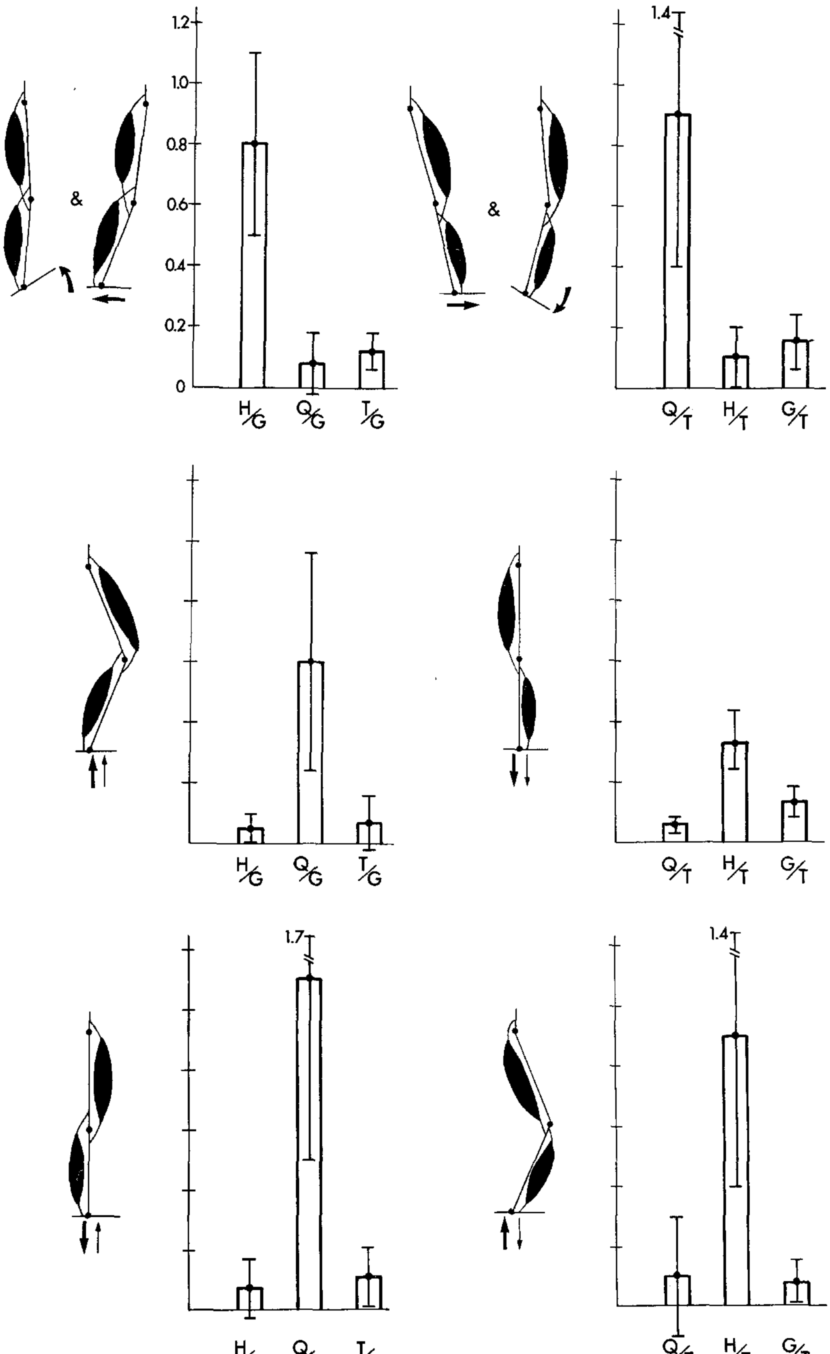


**Fig. 4.** Coupling ratios (average ±1 standard deviation) between the responding lower leg muscle (see Fig. 3) and the two functionally related upper leg muscles and the antagonist lower leg muscle. Leg figures at left illustrate the stimulus and response patterns. Heavy arrows show stimulus motions of the measured leg. Light arrows show the stimulus motion of the other leg. The responding muscles are shown in heavy black

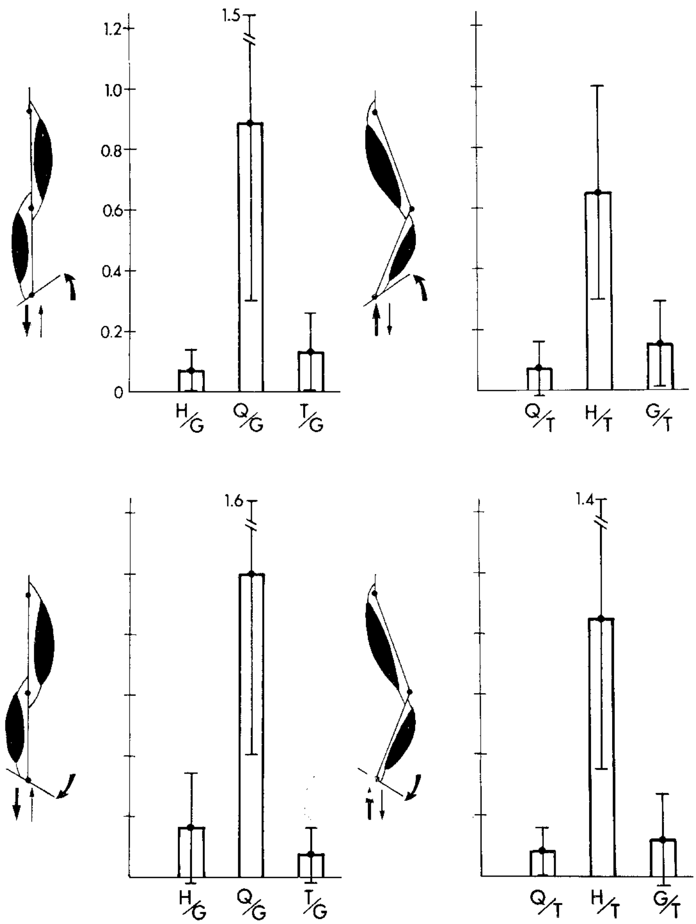


**Fig. 5.** Invariance of coupling ratios (average ±1 standard deviation) during reciprocal vertical motions with imposed ankle rotations. Data are presented in the same form as used in Fig. 4

Figure 5 shows no changes in the direction or coupling ratios of EMG responses, even when the rotational motion of the ankles was either doubled or reversed in direction relative to the motions of the other leg joints. This result is in contrast to previous observations which showed that unexpected, direct ankle rotational inputs by themselves elicited responses which resisted rather than followed the displacement of the ankle joint and which were coupled between upper and lower leg muscles on the same dorsal or ventral aspect of the leg (Nashner, 1977).

*Enhancement of Movement Specific EMG Patterns by Cutaneous Electrical Stimuli*

Stimulating the dorsum of the foot with brief electrical current pulses during platform displacements enhanced the amplitude of EMG activities of whichever

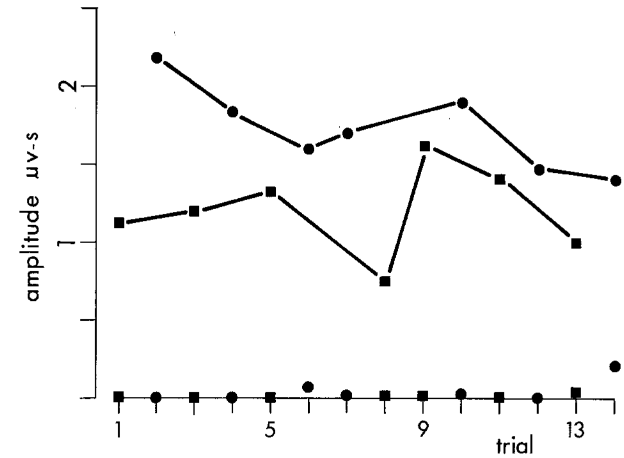


**Fig. 6.** Amplitude of T muscle EMG activity during reciprocal elevations of the measured leg. Cutaneous electrical stimuli (filled circles) imposed during alternate trials between those without electrical stimuli (filled squares). Filled circles and squares at the bottom of the graph without connection lines show the amplitude of G muscle EMG activity during this same sequence

muscles were normally activated by the displacement. Figure 6 shows a sequence in which electrical stimuli were imposed during alternate trails of reciprocal vertical displacements. The selective enhancement of those muscles normally activated by the movement was clearly evident in this sequence. The selective enhancement of muscle activities was evident during most all of the other sequences tested, although the effects were sometimes partially obscured by the normally significant trial-to-trial variations in response amplitudes and by a tendency (also evident in Fig. 6) for the stimulus effects to progressively diminish after repeated presentations. On the average, however, agonist muscle EMG responses were always enhanced during trials which combined electrical with platform displacement stimuli (as compared to trials with displacement stimuli alone), while the electrical stimuli had little effect upon the amplitude of antagonist muscle responses.

## Discussion

Moving the platforms upon which a subject stood in a given way specified the particular synergic arrangement of muscles which became active during the resulting rapid postural adjustment. While it is not possible to fully assess the neuronal mechanisms mediating these coordinated muscular activities or to analyze their precise functional significance without a complete knowledge of all the many sensory inputs and of the many other active muscles, the experimental observations suggest a number of organizational principles which are quite consistent with hierarchical principles of motor control: (1) Rapid postural adjustments are organized into a limited number of synergic patterns, each of which is movement specific and is expressed by relatively fixed relations among the EMG activities of functionally related leg muscles. (2) The organization of synergies during stance postural adjustments appears to be performed by local mechanisms, utilizing inputs primarily from the receptors of the leg muscles, joints, and skin surfaces. (3) Certain similarities in the organization of contractile activities of the leg muscles during reciprocal, vertical displacements and during phases of the locomotor step cycle suggest the possibility that some of the same neuronal mechanisms organize rapid postural adjustments and stereotyped locomotor behaviors.

### *Functional Properties of Fixed Synergic Patterns*

The activation of the lengthening lower leg muscle and the upper leg muscle on the same dorsal or ventral aspect of the leg during postural disturbances which primarily rotate the ankle joints (AP sway and direct ankle rotations) resists the ankle rotation and at the same time extends (or flexes) the hip joints in the same direction as the effort exerted about the ankles. This fixed pattern would be functionally useful to limit the antiphasically coupled motions of the ankles and hips which are a dynamical characteristic of the body of a standing subject during AP sway (Nashner, 1977). A vertical displacement of the foot, which extends (or flexes) the ankles, knees, and hips, organizes the activities of upper and lower leg muscles on opposite dorsal and ventral aspects, a contractile pattern which tends to flex the entire leg upward or extend it downward. This pattern of movement would be functionally useful in maintaining the vertical height of the body and in compensating for vertical loading changes. The functional significance of each of these two movement-specific patterns of activity is illustrated with examples of EMG activities recorded as a subject voluntarily performed isolated AP sway and vertical stooping maneuvers (Fig. 2).

Another significant organizational feature of rapid postural adjustments is that the direction of a muscular response effort relative to that of the direction of the stimulus motion is governed by the relative phasing of the two leg movements. While synchronous, vertical movements elicited activity which resisted the stimulus motion of each leg, reciprocal vertical leg movements elicited a similarly organized pattern of muscular activity which was, however, directionally reversed so that each leg tended to follow rather than resist the displacement imposed by the platform. Extending the leg downwards on the lowering platform and raising it upwards on the elevating platform would be functionally useful to help stabilize the lateral sway disturbance created by this platform displacement.

Observations also suggest that the local mechanisms not only fix the patterns of muscular activities composing the postural adjustment but also organize the sensory inputs to each muscular synergy as well. An earlier study already showed that unexpected, ankle rotations alone organized the complete pattern of activity appropriate to compensate AP sway, even though there could not have been any of the normal visual and vestibular sway inputs to the system within the 100 ms latency of the response (Fig. 1 shows the absence of head movements within the first 100 ms after a direct ankle rotation). In contrast, ankle rotational inputs had no apparent influence upon activities during responses to reciprocal, vertical displacements, a result which suggests that inputs other than from the ankles (perhaps knee and hip rotations and/or changes in loading upon the surfaces of the foot) were used exclusively during these adjustments.

### *The Local Organization of Synergies*

A consistent observation during all phases of the experiments was the ability of the posture control system to appropriately and fully reorganize the synergic arrangement of muscular activities within a *single trial,* even in those instances when the subject could not anticipate the exact moment of the disturbance or the particular kind of platform movement involved. Most significantly, the response activity of each leg was directionally reversed relative to its displacement following an unexpected transition from synchronous to reciprocal vertical displacements. These reversals could not have been caused by changes in the trajectory of each leg individually, as Fig. 1 showed that movements of each leg during the first 150 ms of stimulation depended only upon the direction of its own movement (and was independent of the movement of the other leg). The reversal also could not have been triggered by vestibular or visual inputs, since Fig. 1 shows that there were no significant changes in the lateral position of the head during the first 100 ms of either synchronous or reciprocal vertical stimulation. In marked contrast to the lack of executional errors in the organization of leg muscle activities immediately following transitions from one mode of stimulation to another, errors in amplitude and direction of responses occurred predictably for several trials after subjects were exposed unexpectedly to conflicts between ankle rotational and AP sway (vestibular and visual) inputs (Nashner, 1976). When exposed to unexpectedly alternating sequences of AP sway (body rotation principally about the ankles) and direct ankle rotations (unrelated to AP sway), subjects first responded to direct rotational displacements by resisting them, altering this inappropriate strategy only after three to five presentations.

One possible conclusion that can be drawn from these contrasting results is a functional distinction between the local and central components of the posture control system. The basic activity patterns for postural adjustments are organized by local mechanisms which rely principally upon somatosensory inputs from the muscles, joints, and skin surfaces of the legs. While acting within the latency of a rapid postural adjustment, these local mechanisms are limited to the control of *relative* body movements. Adaptive processes which modify the locally organized postural adjustments to suit the *external conditions* of the task and to maintain the equilibrium of the body must rely upon a combination of vestibular and visual as well as somatosensory inputs. These controls become apparent only at latencies signficantly longer than those required to generate a single rapid adjustment.

*Similarities Between Postural and Locomotor Activities*

The phasing of activity between the two legs during reciprocal vertical displacements is similar to the organization of activity of the two hindlimbs observed during locomotion. The period during and shortly after the toe-off phase of walking resembles that of the elevating leg during a reciprocal vertical displacement; the ankle joint begins to flex as the knee and hip joints continue to flex for an approximately 100 ms period (Herman et al., 1976). Just prior to and during heel-strike the ankle and knee and hip joints are all extending, a 100 ms period during which the movement resembles that of the downwardly displacing leg. Although complicated by the co-contractions of antagonists (providing extra stability), the pattern of EMG activities recorded during each of these locomotor phases is comparable to that observed during a reciprocal vertical displacement; namely, the T reaches its peak of activity and the H maintains the highest level of contractile activity during the toe-off (upward flexion) phase, while the activity of these two muscles declines rapidly and the G and Q muscles become most highly active shortly after the heel-strike (downward extension) phase.

In order to establish similarities in the organization as well as the pattern of EMG activities during platform movements and locomotion, electrical stimuli were delivered to the dorsum of one foot during reciprocal vertical and synchronous sway platform displacements. Studies using intact, thalamic, and spinal cats (Duysens and Pearson, 1976; Forrsberg et al., 1975 and 1977) had already demonstrated a phase-dependent reflex-reversal, a spinally controlled phenomenon that gated responses between antagonist muscle groups to match the opposed phases of the step cycle. Lisin et al. (1973) had also attempted a similar experiment with human hemiplegic patients, applying (unfortunately painful and prolonged) surface stimuli to the sural nerve. They found that the flexor response (which occurred during quiet standing) was directionally reversed to an extensor response during locomotion (although the strength of the stimulus also interrupted the step cycle as well). Using subthreshold stimulus currents and brief durations comparable to those used by Forrsberg et al. (1977), we have demonstrated that flexor muscle responses are enhanced in the upward moving leg (activity comparable to swing phase) and extensor muscle responses are enhanced when the leg is moving downwards (activity comparable to the thrust applied at the onset of stance). The gating of activity during forward and backward AP sway adjustments as well as during reciprocal vertical ones suggests that similar neural mechanisms organize the sensory inputs during the transient postural and balance adjustments as well as the phasic locomotor activities.

In conclusion, our results are consistent with the hypothesis that individual limb movements and interlimb coordination are organized stereotypically by largely autonomous "movement generators", which utilize specific combinations of local somatosensory inputs from the limbs. The complete absence of executional errors in the formation of patterned activity among the leg muscles, even when subjects were exposed to unexpectedly changing patterns of postural and locomotor-like platform movements, suggests that the "movement generators" are fully active in order to rapidly organize postural and locomotor activities in the freely standing subject, and that ongoing locomotor behavior is not necessary to facilitate these mechanisms. The results also emphasize the significant functional differences between these locally organized control mechanisms and the more complex adaptive controls which utilize complex combinations of vestibular and visual, as well as somatosensory inputs, in order to modify each basic movement pattern to suit the external conditions of the task.

*Acknowledgments.* L. Nashner is supported by Grant NS 00148 from the NINCDS. The laboratory facilities and M. Woollacott are supported by Grant NS 12661, also from the NINCDS. G. Tuma is supported by a CETA Title VI project grant.

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Received August 28, 1978