

Central Programming of Postural Movements: Adaptation to Altered Support-Surface Configurations

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SUMMARY AND CONCLUSIONS

1. We studied the extent to which automatic postural actions in standing human subjects are organized by a limited repertoire of central motor programs. Subjects stood on support surfaces of various lengths, which forced them to adopt different postural movement strategies to compensate for the same external perturbations. We assessed whether a continuum or a limited set of muscle activation patterns was used to produce different movement patterns and the extent to which movement patterns were influenced by prior experience.

2. Exposing subjects standing on a normal support surface to brief forward and backward horizontal surface perturbations elicited relatively stereotyped patterns of leg and trunk muscle activation with 73- to 110-ms latencies. Activity began in the ankle joint muscles and then radiated in sequence to thigh and then trunk muscles on the same dorsal or ventral aspect of the body. This activation pattern exerted compensatory torques about the ankle joints, which restored equilibrium by moving the body center of mass forward or backward. This pattern has been termed the *ankle strategy* because it restores equilibrium by moving the body primarily around the ankle joints.

3. To successfully maintain balance while standing on a support surface short in relation to foot length, subjects activated leg and trunk muscles at similar latencies but organized the activity differently. The trunk and thigh muscles antagonistic to those used in the ankle strategy were activated in the opposite proximal-to-distal sequence, whereas the ankle

muscles were generally unresponsive. This activation pattern produced a compensatory horizontal shear force against the support surface but little, if any, ankle torque. This pattern has been termed the *hip strategy*, because the resulting motion is focused primarily about the hip joints.

4. Exposing subjects to horizontal surface perturbations while standing on support surfaces intermediate in length between the shortest and longest elicited more complex postural movements and associated muscle activation patterns that resembled ankle and hip strategies combined in different temporal relations. These complex postural movements were executed with combinations of torque and horizontal shear forces and motions of ankle and hip joints.

5. During the first 5–20 practice trials immediately following changes from one support surface length to another, response latencies were unchanged. The activation patterns, however, were complex and resembled the patterns observed during well-practiced stance on surfaces of intermediate lengths. During the course of practice, the relative amplitudes and timing of the ankle and hip strategy components changed progressively.

6. Our results have demonstrated that subjects can synthesize a continuum of different postural movements by combining two distinct strategies in different magnitudes and temporal relations. The combination of strategies used in a particular instance is influenced not only by the current support-surface conditions but also by the subject's recent experiences. These observations are consistent with the hypothesis that postural actions are orga-

nized by a limited repertoire of central programs selected in advance of movement.

INTRODUCTION

Do central motor programs simplify the execution of complex motor actions by fixing the interactions among functionally related muscle groups? It has been suggested that central programs reduce the motor behaviors of an organism from a potential continuum of muscle activation patterns and associated movement trajectories to a manageably smaller number of centrally organized strategies (2, 10, 12, 28). Organization of motor actions into central programs also simplifies the process of adapting movement to new environmental contexts. Because central programs incorporate knowledge of prior results, they anticipate external events and reduce an organism's reliance on feedback-mediated reactions. The above hypothesis is consistent with previous animal and human movement control experiments describing muscle activation patterns organized stereotypically and relatively independent of ongoing feedback information (1, 3, 5, 9, 11, 13, 14, 29).

Prior reports of stereotyped motor behaviors in humans, however, were based upon experimental observations made under fixed mechanical conditions. While these observations are consistent with the concept of central programming, they do not demonstrate its validity when changes in mechanical conditions force subjects to change movement strategy.

If principles of central programming hold under varying mechanical conditions, then postural strategies and associated muscle activation patterns will not vary continuously when the context in which a movement is performed changes. Instead, changes in activation patterns will be constrained to reflect the structure of the available central programs. In addition, if the appropriate motor programs are selected in advance of movement based on prior experience, actions executed immediately after an unexpected change in mechanical conditions will reflect parameters consistent with not only the current but also the prior conditions. A typical example of the effect of prior experience on motor patterns is the extra step taken at the bottom of a staircase in expectation of another stair.

In the present study, alterations in the configuration of the support surface forced stand-

ing subjects to change the way they recovered equilibrium in response to identical sagittal plane perturbations. Progressively shortening the support surface in relation to the length of the foot forced subjects to rely less on shifting the center of vertical foot pressure (torque about the ankle joints) and more on exerting horizontal shear forces. The resulting postural movements and associated muscle activation patterns were described by measuring the trajectories of the ankle, knee, and hip joints and electromyographic activity (EMG) of six leg and lower trunk muscles. Using this approach, we have demonstrated that a continuum of different postural movement trajectories can be generated by one or a combination of two stereotyped muscle activation patterns, which are partly determined by prior experience. Preliminary results from the present study have been reported elsewhere (15, 18, 25).

METHODS

To observe the organization of postural actions in relation to properties of the support surface, techniques developed in previous studies of human postural adjustments have been reapplied with minor modification (21, 26).

Stimulation and recording

Subjects stood upon a platform surface movable in forward and backward directions under the control of a hydraulic servomotor. Sagittal plane balance was perturbed at random intervals by moving the platform forward or backward at a constant velocity, 13 cm/s, for 250 ms. These perturbations displaced the center of body mass in the opposite direction to the feet, i.e., backward platform movements produced forward body sway.

Imbedded within the platform were strain gauges that measured, independently for each foot, the forward or backward changes in position of the vertical force center (ankle torque) and the horizontal shear force. The angular trajectories of the ankle, knee, and hip joints were measured from single-frame analysis of videotaped recordings. Markers consisting of circular white patches (4 cm diam) with circular black centers (2 cm diam) were placed at the head of the 5th metatarsal (ball of foot), the external malleolus (ankle), the lateral condyle (knee), the greater trochanter (hip), and the lateral aspect of the humerus (shoulder). This method provided a temporal resolution of 33 ms and a spatial resolution of approximately $\pm 0.75^\circ$. While this level of temporal-spatial resolution was not high, it was sufficient to unambiguously identify changes in movement trajectory in relation to the support surface properties.

Patterns of muscular activation were analyzed by recording the EMG activity of six representative leg, thigh, and trunk muscles on the subjects' right side. Muscle activities of medial gastrocnemius, tibialis anterior, hamstrings (primarily biceps femoris), quadriceps (primarily rectus femoris), paraspinals at the level of the iliac crest (primarily L₄₋₅ erector spinae), and rectus abdominis at the level of the umbilicus were recorded using 2.5-cm surface electrodes spaced 2–4 cm apart. Signals were processed by band-pass filtering (50–5,000 Hz), full-wave rectifying, and then low-pass filtering (0–40 Hz) to produce voltages in approximate proportion to the level of muscle activation. Although no attempt was made to calibrate the six EMG signals on an absolute scale, gains of individual signals were fixed throughout a session to allow a meaningful quantification of relative changes within activation patterns.

Measures of ankle torque and shear were monitored to assure symmetry between left and right sides. Monitoring background EMG activity and visual inspection of strain gauge measurements also assured that subjects maintained approximately equal weight distribution and the same initial center of gravity position prior to each platform movement.

Analysis

The patterns of muscle activation elicited by forward and backward displacements of the platform were characterized by visual inspection of single

trials and groups of 5–20 ensemble-averaged trials. The absolute latency of response to platform displacement was defined in single trials by the earliest time one of the six muscles deviated from a baseline level established over the preceding 100-ms interval. The temporal organization of a postural action was characterized by the delays in activation of remaining muscles relative to the first, using for each muscle the same criteria for onset of activity. Statistically significant differences in latencies of muscle activation following onset of platform displacement were determined using the Student's *t* test.

Protocol

Participating in the study were 10 normal subjects (4 male, 6 female) between the ages of 20 and 40 yr. Each subject was tested a minimum of two 1-h sessions. The subject stood upon the movable platform with weight equally distributed between the two feet, and arms folded at the waist.

The first test sequence consisted of 20 forward or 20 backward displacements imposed at varying times (minimum intertrial interval, 5 s) with the platform surface long in relation to the length of the foot (normal surface). The length of the support surface was then reduced to 9 cm (short surface), and the subject was reexposed to the identical perturbations at varying times. Because the proficiency of individual subjects standing upon the short surface varied considerably, perturbations continued for at least 10 trials after the subject reached a stable

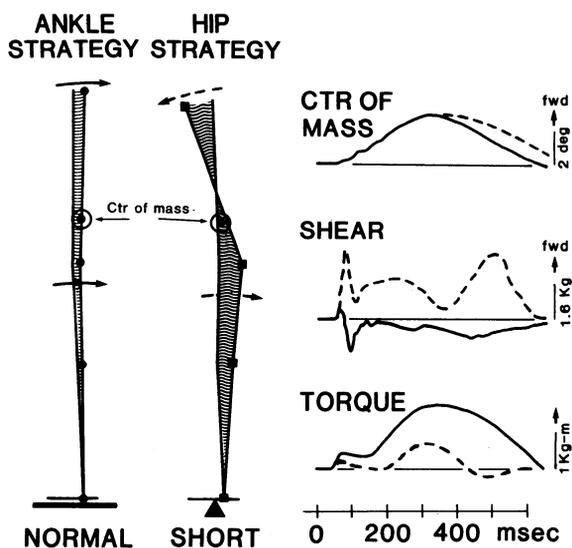


FIG. 1. Biomechanical compensation for forward sway with ankle strategy (solid lines) on normal surface and with hip strategy (dashed lines) on short surface. Ankle, knee, hip, and shoulder joint positions measured from video at the end of backward platform translation and following correction at position in equilibrium (solid circles and squares). Arrows indicate direction of segment active correction necessary to move center of mass back over center of support following backward platform translations.

plateau of performance; then the normal surface was replaced, and perturbations in the same direction continued until a new stable plateau was reached. Each session consisted of several alternations between long and short support surfaces and between forward and backward sway directions. In three subjects the process was repeated with surfaces of 5- and 13.5-cm lengths.

RESULTS

Well-practiced postural movement strategies

Displacement of the support surface in one direction moved the center of body mass in the opposite direction relative to the center of foot support. For a well-practiced subject standing on the normal-length surface, active ankle torque (forward or backward shift in the position of the vertical force center) opposing the body sway motion began within 60 ms fol-

lowing activity in the ankle joint muscles (Fig. 1). Forward-backward shear forces, in contrast, were small and in the wrong direction to compensate the sway. Maximum torsional resistance at the ankles coincided with acceleration of the body center of mass back toward the erect equilibrium position. During these corrective movements the body rotated as an approximately rigid mass about the ankle joints, hence its designation as the ankle strategy.

Although the initial displacements of the center of body mass caused by displacing normal and short support surfaces were comparable, the compensatory postural movements generated on the two surfaces were different. After practice on the short surface, a forward or backward sway displacement produced a large increase in sagittal shear force opposing the direction of the perturbation with little, if

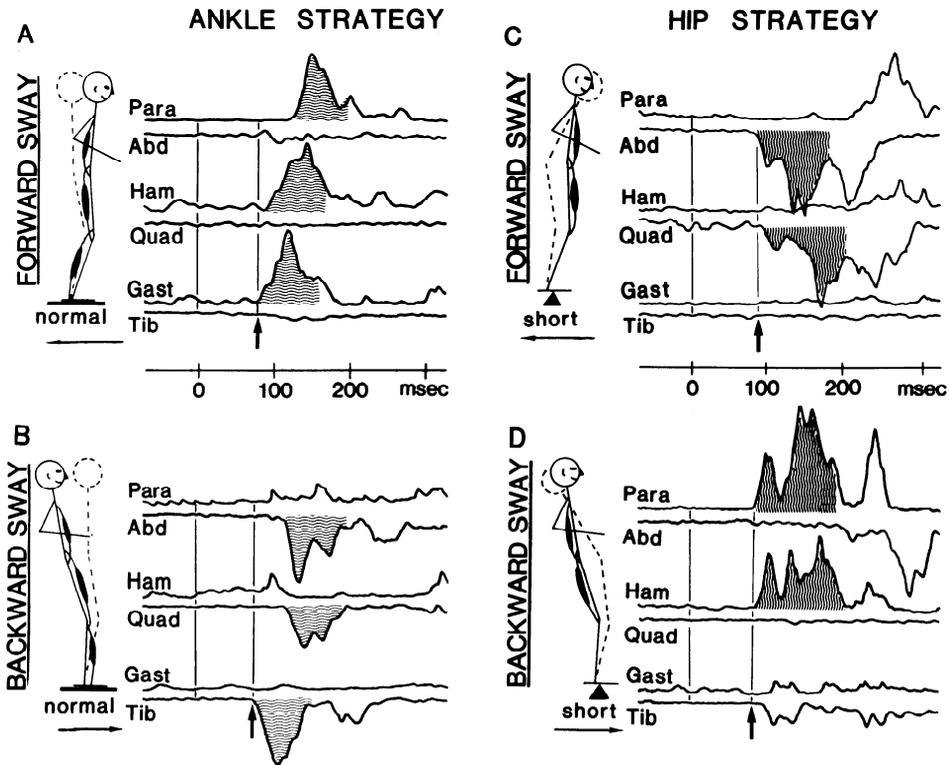


FIG. 2. Muscle response patterns to forward (*top*) and backward (*bottom*) sway perturbations: *A* and *B*: on normal surface, ankle strategy; *C* and *D*: on short surface, hip strategy. EMGs for 6 muscles are arranged in antagonist pairs with the dorsal muscle EMGs directed up and the ventral EMGs directed down. First 100-ms EMG response shaded in this and subsequent figures. *Dashed stick figures* represent corrected body position. Average of last 5 of 20 trials for subject *A* triggered 150 ms prior to platform perturbation (*solid line*, 0 ms). *Arrows* indicate latency of first EMG. Abbreviations for this and subsequent figures: Para, lumbar paraspinal muscles; Abd, rectus abdominis; Ham, hamstrings; Quad, rectus femoris; Gast, medial gastrocnemius; Tib, tibialis anterior.

any, ankle torque (Fig. 1). A large active rotation of the hip joint accompanied by smaller antiphase rotation of the ankles moved the trunk in the direction of the initial body displacement to a nonerect position, which was nevertheless in equilibrium with respect to gravity (see Fig. 7). Because the corrective shear force was generated by moving the hip joint, this method for moving the center of body mass anteroposteriorly is termed the hip strategy.

TABLE 1. *Intersegmental delays of EMG responses*

Subject	Normal-Surface Ankle Strategy		Short-Surface Hip Strategy
	G → H	H → P	A → Q
<i>Forward Sway/Backward Surface Translations</i>			
A	31	28	4
B	22	14	4
C	26	28	2
D	35	7	27
E	48	12	10
F	8	96	52
G	4	31	45
H	25	22	10
I	17	6	10
J	20	14	7
Means	23	27	19
± SD	± 12	± 27	± 18
	T → Q	Q → A	P → H
<i>Backward Sway/Forward Surface Translations</i>			
A	47	10	4
B	14	*	20
C	52	33	4
D	7	20	21
E	5	68	33
F	15	80	40
G	12	25	28
H	14	8	60
I	14	1	*
J	10	5	4
Means	18	28	14
± SD	± 17	± 30	± 13

Synergist muscle latencies measured as delays from each segment. Means (ms) of last 10 of 20 perturbation trails for 10 subjects. Individual SDs ranged from 4 to 30 ms and never exceeded their mean. Delay represents a statistically significant difference in mean muscle latencies measured from onset of platform perturbations for 10 subjects ($p < 0.025$, Student's t test). G, gastrocnemius; H, hamstrings; P, paraspinals; A, abdominals; Q, quadriceps. * No proximal muscle response detected.

Muscle activation patterns associated with well-practiced postural strategies

Activation patterns of ankle, thigh, and trunk muscles were stereotypical in all subjects following repeated exposure to perturbations on the normal support surface. Contractions commenced in the ankle joint muscle opposing the sway perturbation and then radiated in distal-to-proximal sequence to the thigh and then trunk muscles on the same dorsal or ventral aspect of the body. Figure 2, *A* and *B*, shows ensemble-averaged responses elicited by perturbing subject *A* in forward and backward directions, respectively. EMG traces are arranged in segmental groups with responses of the functional extensors directed upward and responses of the flexors downward.

Absolute response latencies averaged separately for each of the 10 subjects ranged from 74 to 102 ms during the forward sway perturbations (gastrocnemius) and from 73 to 110 ms during the backward sway perturbations (tibialis). For the group as a whole, mean absolute latencies were 88 ± 9 ms for forward sway and 91 ± 13 ms for backward sway. These absolute latencies are slightly shorter than the 95- to 110-ms latencies reported previously (20, 21, 26), possibly because repeated exposure to the same stimulus reduces automatic response latencies (31).

Temporal organization of postural responses on the normal surface was characterized by intersegmental delays in the onset of thigh and trunk muscle activations following ankle muscle activation. As shown in Table 1, intersegmental delays between ankle and thigh segments and thigh and trunk segments were statistically significant ($P < 0.025$) for the group as a whole, for both forward and backward responses. Although there was a tendency for distal-to-proximal muscle activation in all 10 subjects, the magnitudes of intersegmental delay varied from an insignificant 1-ms (thigh-trunk segment of subject *I*) to a large 80-ms delay (same segment of subject *F*). Activation of muscles in the opposite order, however, was not observed.

After a sufficient number of practice trials on the short 9.0-cm surface, subjects used different, but equally stereotypical, patterns of muscle activation to maintain their stability (Fig. 2, *C* and *D*). Perturbations activated the thigh and trunk muscles antagonistic to those activated on the normal support surface. Ab-

dominal and quadriceps muscles responded to forward sway perturbations; hamstrings and paraspinals responded to backward sway perturbations.

The absolute latencies of responses to perturbations while standing on the normal and short surface were comparable. On the short support surface, mean latencies for individual subjects ranged from 73 to 105 ms during forward sway perturbations (abdominals) and from 63 to 99 ms during backward sway perturbations (paraspinals). For the group as a whole, absolute latencies were 85 ± 11 ms for forward sway responses and 79 ± 12 ms for backward sway responses.

Compared with the temporal organization on the normal surface, the sequence of muscle activation on the short surface tended to be in the opposite proximal-to-distal order. Now, thigh muscle activation followed the lower trunk muscle activation for the group as a whole for both forward and backward directions ($P < 0.025$). Although there was a tendency for proximal-to-distal sequencing of mean latencies in all subjects, the intersegmental delays of several subjects were not sig-

nificant (Table 1). Activation of lower trunk and thigh muscles in the reversed distal-to-proximal order, however, was seldom seen on the short support surface.

After a period of practice sufficiently long for subjects to achieve a consistent level of performance on the short surface, ankle joint muscles were either silent (4 subjects), tonically active (2 subjects), or responded in a manner characteristic of the ankle strategy on the normal surface (4 subjects). In these latter four subjects, more complex patterns combined trunk and thigh muscle activation on one aspect of the body with ankle muscle activation on the opposite body aspect. These more complex patterns of activity are described in greater detail in the following section.

Complex movement strategies during practice

Immediately following changes in support surface length, subjects exerted both ankle torque and shear force against the surface while moving both the ankle and hip joints. Most subjects continued to use these complex movements for 5 to 15 trials (transitions to

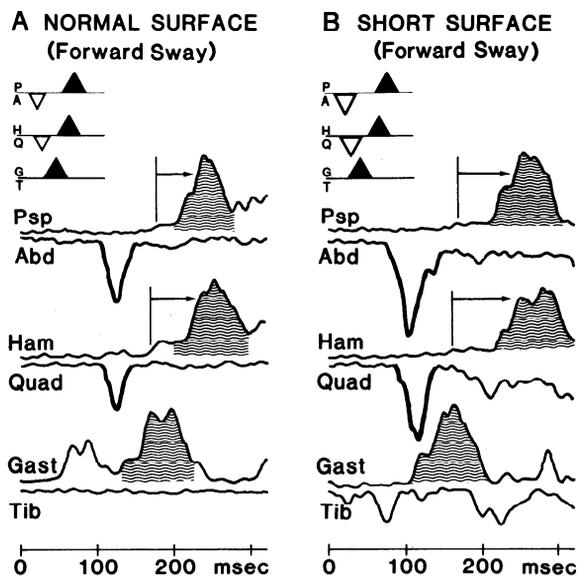


FIG. 3. Typical complex transition EMG patterns during practice trials on normal surface (A) and on 9-cm short surface (B). Ensemble average of first 5 trials, following change in surface, from subject C who later progressed to pure ankle and hip strategies with practice. Components of ankle strategy, *solid triangles* in schematic pattern and *shaded* EMG areas; components of hip strategy, *open triangles* in schematic and *outlined* EMG areas in this and subsequent figures. The latencies of Ham and Psp were proportional to the amplitude of activation of their respective antagonists, Quad and Abd (shown by *arrows*). Short-latency response in Gast while standing on the normal surface was seen only in this subject.

the short surface) or for 1 to 6 trials (transitions to the normal surface) before adopting the appropriate well-practiced strategy.

These initial practice movements were associated with complex patterns of muscle activation. The complex pattern observed most frequently (~75% of trials, 9 of 10 subjects) is illustrated in Fig. 3. Observed during initial practice on either the normal or short surface, this pattern included activation of gastrocnemius, rectus abdominis, and quadriceps, followed by hamstring and paraspinals. An unusual short-latency (55-ms) gastrocnemius response was also present when this subject stood on the normal but not on the short surface.

After practice sufficient to reach a consistent level of performance, 6 of the 10 subjects produced the pure ankle and hip strategy activation patterns shown in Fig. 2. In the remaining four subjects, activation patterns were almost always complex, even after 20–40 practice trials on the normal and short surfaces. In these four subjects, however, practice changed the relative magnitudes of individual muscle activations. After practice on the normal surface, muscles associated with the ankle strategy were proportionately more active, while muscles appropriate for the hip strategy became most active after practice on the short surface.

Neural origin of complex strategies

One possibility is that complex activation patterns are synthesized by combining patterns associated with the pure ankle and hip strategies. This is a parsimonious explanation because it assumes that two pattern generators produce both pure and complex strategies (18). It is supported by the observation that the complex activation patterns illustrated in Figs. 3 and 4 include all the essential elements of both the pure ankle and pure hip strategy patterns. In Fig. 3 ankle and hip strategy patterns are interdigitated, with some changes in the relative timing of distal and proximal elements. The complex activations in Fig. 4A resemble a pure hip strategy followed by a pure ankle strategy pattern. Combining pure strategies in the opposite order produces the complex activations illustrated in Fig. 4B. In these instances, relative timing among muscles of each strategy is not altered. The examples of complex patterns in Figs. 3 and 4 together ac-

count for the patterns seen in 94% of all trials. In the 6% of trials with patterns not conforming to one of the above examples, the most frequent variance was absent or tonic activity in one of the five muscles.

We tested the hypothesis that complex patterns of activation are synthesized from combinations of the pure strategy patterns by examining temporal and spatial properties of complex patterns during practice. Figure 5 illustrates two examples of typical progressive shifts between pure ankle and pure hip strategy following changes in surface length. During the second trial following a shift to the short

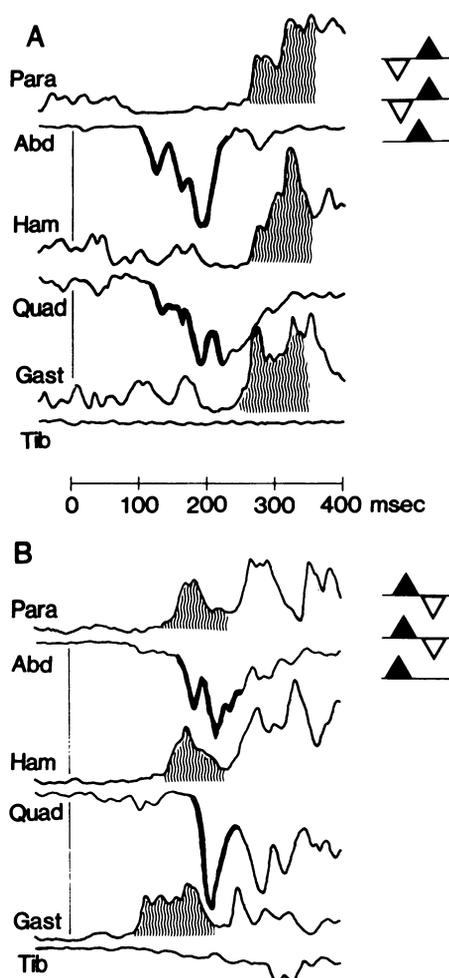


FIG. 4. Complex EMG response patterns to forward sway perturbations. *A*: pattern representative of hip followed by ankle strategy from subject *B* on 9-cm surface. *B*: pattern representative of ineffective ankle followed by hip strategy mixture from subject *I* on 9-cm surface.

surface (first line in Fig. 5A), an activation pattern consistent with the ankle strategy (hamstrings component shown) is followed closely by a second pattern consistent with the hip strategy (quadriceps component shown). During the third and fifth trials, the quadriceps component of the hip strategy pattern occurred both before and after the hamstring component of the ankle strategy. By the eighth trial, all traces of the hamstrings activation was gone, and a single quadriceps activation occurred 55 ms earlier than it did in the first two trials.

Following shift to the normal surfaces, the progression of activation pattern changes during transition from pure hip to pure ankle strategy following shift to the normal surface had a similar course (Fig. 5B). During the first, third, and fifth trials the quadriceps component of the hip strategy pattern became progressively smaller. By the eighth trial, all traces of hip strategy components were absent, and the hamstrings components of the ankle strat-

egy pattern occurred 60 ms earlier than it did during the first trial.

In general, we found that sequential practice trials involved gradual changes in EMG magnitude (18). Furthermore, the magnitudes of individual muscle components within a pure strategy pattern tended to change in proportion. In contrast, the relative timing of individual muscle responses within complex patterns tended to change abruptly between interdigitated and sequential combinations, constraining the complex patterns seen to a limited number of distinct combinations (see Figs. 3 and 4).

To illustrate the abrupt nature of timing changes, we measured the interval between gastrocnemius and hamstrings onset while exposing subject *B* to a long series of trials ($n = 81$) with support surface length varying in four increments between 4.5 cm and normal. Figure 6 shows a distinctly bimodal distribution of intersegmental delays between 0 and 200 ms. The two characterizations above the his-

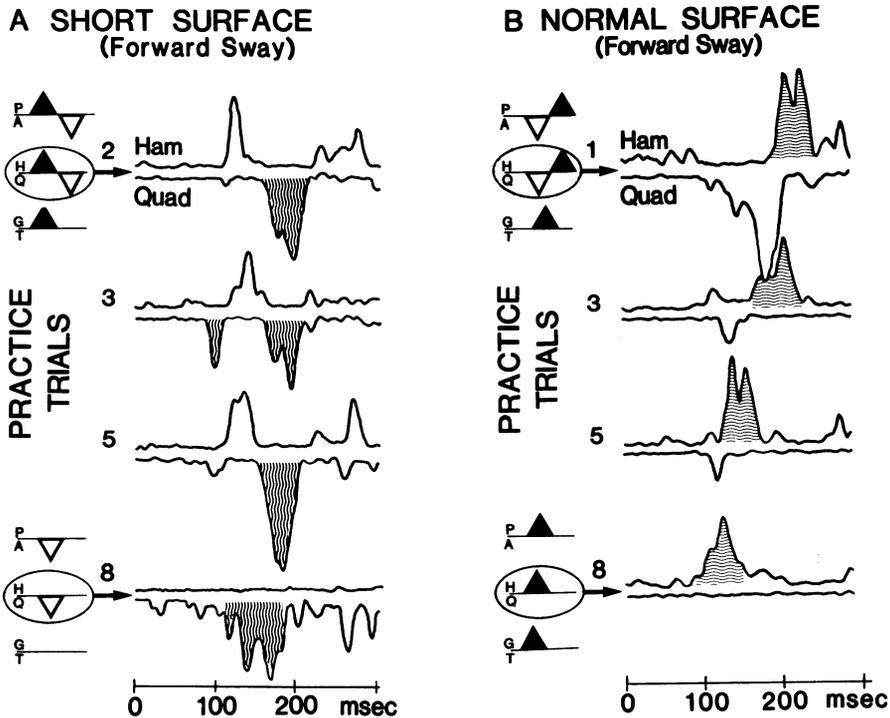


FIG. 5. Adaptation of muscle patterns during practice trials after change of support surface configuration. Hamstring and quadriceps EMG activity from individual responses to forward sway with schematic pattern of all recorded muscles at left from subject *A*. *A*: transition from complex ankle/hip strategy in early trials (2, 3, 5) on short surface to pure hip strategy (trial 8). *B*: transition from complex hip/ankle strategy in early trials (1-5) on normal length surface to pure ankle strategy (trial 8).

togram illustrate the distinct interdigitated and sequential combinations giving rise to the bimodal distribution. In both versions of the complex pattern, magnitudes of muscle components of the pure ankle and pure hip strategy patterns tended to vary as a unit.

Mechanics of pure and complex strategies

A continuum of different body movement trajectories can be generated by combining pure ankle and hip strategies. To illustrate this principle, movement trajectories associated with pure and complex strategies are analyzed in ankle (vertical axis) and hip (horizontal axis) position space (Fig. 7). The origin of the position space is the erect equilibrium position. The heavy diagonal line passing through the origin shows the locus of nonerect equilibrium positions of the body, i.e., those positions in which the center of body mass is vertically above the center of foot support.

The movement trajectories generated by pure ankle strategies (filled circles) curve slightly to the right while moving toward the origin on a path closely paralleling the ankle joint axis. Rightward curvature is caused by a subtle antiphase rotation of hip joints. Hip

joint rotations in trajectories associated with pure hip strategies (filled triangles) are approximately five times larger than ankle joint rotations. These hip strategy trajectories terminate at nonerect equilibrium positions remote from the origin. Despite the large differences in trajectory orientation and length, however, the transit times required to reach equilibrium positions using the two strategies were approximately the same (100–125 ms for the ankle and 105–145 ms for the hip).

Successful complex movements executed on normal and short support surfaces were confined to regions of position space bounded by the pure ankle and pure hip strategy trajectories. For example, the approximately equal combination of ankle and hip strategies (EMG records in Fig. 3) produced a trajectory (filled squares) comprised of hip rotation twice the amplitude of the ankle joint rotation. The nonerect equilibrium position reached in this instance was approximately one-third of the way between the origin and the position reached by the pure hip strategy movement. In other instances, complex patterns composed predominantly of one strategy produced

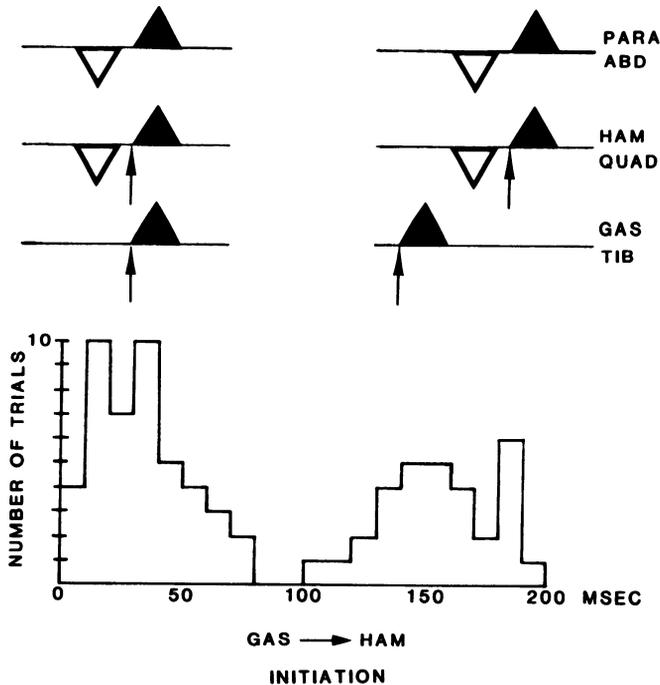


FIG. 6. Frequency histogram illustrating bimodal distribution of time delay between gastrocnemius and hamstrings EMG onsets from 81 trials in subject *B* on normal, 13.5-, 9-, and 4.5-cm surfaces.

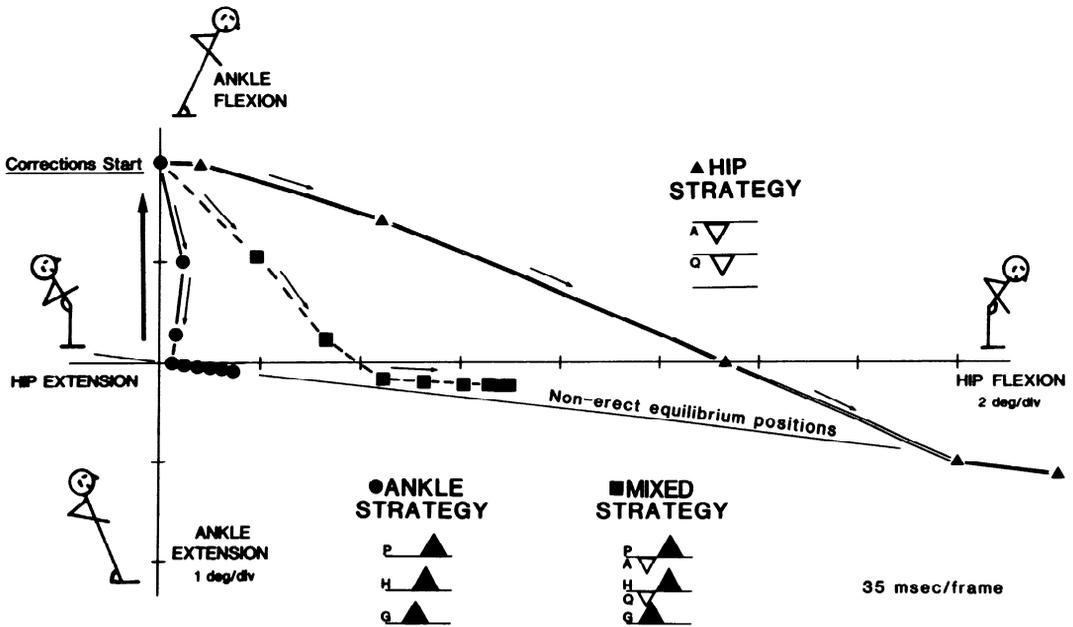


FIG. 7. Body movement trajectories in ankle (vertical axis) and hip (horizontal axis) position space produced by pure ankle strategy (circles), hip strategy (triangles), and mixture of hip and ankle strategies (squares). Measurements of ankle and hip joint angles every 33 ms from videotape of subject *B* on normal surface, 4.5-cm beam and 9-cm beam, respectively.

trajectories closer to those associated with that strategy.

Single-frame analysis of body joint angles revealed little, if any, change in angle of the knee joint during both pure and complex strategy movements. A small minority of responses of subject *10* were the exception. When hamstring activity preceded that of quadriceps during several initial practice trials on the short surface, the knee joint flexed. This subject, however, was seldom successful in maintaining equilibrium on the short surface.

Voluntary influences on movement strategies

In a final group of tests, we examined the ability of subjects to voluntarily change from ankle to hip strategy while standing on the normal support surface. Two of the subjects most proficient in producing pure hip strategy (*B* and *C*) were instructed to stand on the normal surface and as quickly as possible flex at the hips in response to forward sway translations. Following practice periods sufficient to reach consistent levels of performance, latencies of the gastrocnemius component of the ankle strategy (73–110 ms) were not significantly increased by the voluntary attempts to

change strategy. In contrast, muscle components of the hip strategy, rectus abdominis with quadriceps following, became active at 135 ± 22 ms ($n = 24$) in subject *B* and 132 ± 36 ($n = 20$) in subject *C*. Thus hip strategy movements produced voluntarily on the normal surface were ~ 50 ms slower than those generated automatically by the same subjects adapted to stance on a short support surface. These results are consistent with earlier findings that the appropriate automatic postural actions take precedence over intentional actions when the two movements compete (22).

DISCUSSION

Interactions among mechanical and neuromuscular substrates

A subject displaced forward or backward can return to an equilibrium position using, in theory, any one of a continuum of different postural movements and muscle activation patterns. In contrast to the continuum theory, the actual postural movements and muscle activation patterns of subjects perturbed while standing on surfaces of varying lengths were

limited to distinct ankle and hip strategies and combinations thereof.

The support surface forces produced by the two strategies are such that each is most effective under different conditions of the support. The ankle strategy works by repositioning the center of vertical force (ankle torque) and is therefore effective with long, rigid support surfaces and displacement distances short in relation to foot length. In contrast, the hip strategy works by exerting horizontal shear forces against the surface via hip motions and is therefore effective when the support surface is not slippery. In this study, we demonstrated that transitions from ankle to hip strategy occurred whenever the support surface length was short in relation to the forward and backward sway perturbations, thereby limiting the amount of ankle torque which could be exerted.

In other experiments, we are currently exploring the hypothesis that transitions from ankle to hip strategy also occur on a normal surface, when horizontal perturbations of the body center of mass exceed a particular distance or velocity boundary for effective use of the ankle strategy. Also, we are finding that biomechanical boundaries between the ankle and hip strategy can change as a result of pathology (16, 24). Most likely, there exists a third distinct postural strategy that is used when the distance or velocity boundary for effective use of the hip strategy is exceeded; i.e., a stepping or stumbling strategy (23, unpublished observations). Unlike the hip and ankle strategies, which correct equilibrium by returning the center of body mass over a fixed base of support, the stepping strategy reestablishes equilibrium by placing the base of support under the center of gravity.

The argument that the posture-control system synthesizes complex movement trajectories by combining a limited number of distinct strategies rests on two key assumptions: 1) the muscle activation patterns and associated movement trajectories elicited by perturbations while standing on surfaces differing in length represent a limited subset of the possible ankle, knee, and hip muscle activation and joint movement patterns, and 2) the complex movement strategies used during adaptation to new conditions are combinations of the pure strategies. A geometric analysis of muscle forces and body movement trajectories

which supports these key assumptions has been presented elsewhere (18, 25). In the present study, we have focused attention primarily upon the neural control aspects of these assumptions.

Are complex movements a synthesis of the pure strategies?

The synthesis of complex motor actions from interactions among a system of simpler behavioral units has been suggested by a number of investigators. Von Holst (30) suggested that walk, trot, and gallop patterns of gait might be produced by the same system of limb stepping generators, rather than by three separate processes. He reasoned that the different gait patterns would emerge following changes in the interactions among limb generators. Similar concepts were explored by, among others, Bernstein (2), Gallistel (10), and Greene (12).

Examples of complex behaviors believed to be synthesized from interactions among simple movement generators can be found in both the invertebrate and vertebrate experimental literature (4, 19, 28, 29). In these studies, complex muscle patterns were characterized as either sequential "switches" between two pure patterns or as "hybrid" blends of two patterns.

In our results and in these previous studies individual behavioral patterns maintained their internal consistency when blended into hybrids or executed in sequence. Furthermore, there were constraints placed on the blending process. Combinations of walking and running patterns were not seen in quadrupeds (13). Dorsal and ventral forms of the scratch reflex were not blended in turtles (29). In this study, mixtures of hip and ankle strategies that would produce knee bending were seldom seen and were less successful in restoring balance when they did occur.

Reciprocal activation of antagonists has also been a consistent feature for complex interactions among central pattern generators (1, 4, 8, 11, 13, 28, 29). In the functionally effective combinations of ankle and hip strategy patterns, there was a lack of simultaneous initiation of antagonist muscles at the same segment, even when addition of the distal-to-proximal activation of ankle components and the proximal-to-distal activation of hip components would have predicted coactivation

(18). Tonic activity and overlapping, but not simultaneously initiated bursts of antagonist trunk and thigh segment activities, occurred occasionally during the earliest unsuccessful attempts of some subjects to balance on the short surface (Fig. 4B). Reciprocal activation of antagonists for postural correction allows effective, directionally specific movement of the center of body mass back toward equilibrium (6).

In human experiments, the underlying neural processes controlling muscle activation patterns can only be inferred. Nevertheless, our ability to predict the existence of complex activation patterns and their mechanical antecedents by combining knowledge of the two pure strategies with simple rules governing their temporal interactions provides a parsimonious explanation of muscle coordination consistent with the available experimental evidence (18).

Strategies selected in advance

The rather long latencies (73–110 ms) of automatic responses and their dependence on recent experience suggest that the pattern of activation used in a given trial may be selected in advance. The idea that an organism's response to a given external stimulus depends on internal factors established in advance as well as on parameters of the stimulus is a well-established concept. In the field of movement control, Evarts and Tanji (7) demonstrated a possible neural mechanism by which an instructional set influences the motor reaction of an animal. The responses of both pyramidal tract neurons and prime mover arm muscles of trained monkeys exposed to perturbations of a manipulandum were influenced by the instructions given the animal prior to each trial. The phase-dependent gating of cutaneous reflexes in the locomoting cat is an example of a centrally programmed action influencing the form of response to external inputs (8).

Other studies already demonstrated that the organization of postural actions associated with voluntary movements is influenced by the configuration of support provided the subject (5, 20, 23). Results of the present study establish the fact that selection of two distinct postural movement strategies is influenced by prior experiences as well as by current feedback information. Specifically, changes in combination of ankle and hip strategies are progressive rather than instantaneous when

changes in configuration of support are caused by external events (Fig. 5). Furthermore, in trials prior to complete adaptation to a new surface condition, response patterns resemble those used under the previous condition. In contrast, changes in postural strategy anticipated the changes in configuration of support associated with stepping movements of the legs during locomotion (23).

Others have argued that more complex postural behaviors, such as standing on a shortened surface, inactivate the automatic mechanisms, and subjects rely instead on higher level learned mechanisms (27). In our experiment and the related study of postural movements during walking (23), alterations in movement strategy were not correlated with changes in response latency, suggesting that motor learning in this task takes place within the automatic posture-control system. Both studies also suggest that motor learning within the automatic posture-control system, rather than creating novel strategies, combines existing strategies in new ways.

Correcting perturbations by combining two distinct movement strategies permits a subject to respond quickly under a variety of different support surface configurations without increasing the complexity of coordinating the necessary muscular activations. If the changes in support-surface configuration can be anticipated, as during walking, the required changes in combination of strategies can be anticipated (23). If the support-surface configuration is relatively novel and unanticipated, balance can be attained within seconds because new complex strategies are created quickly by manipulating relatively few temporal and spatial parameters. This learning mechanism is in contrast to the possible hundreds of temporal and spatial parameter manipulations that would be required if the timing and amplitude of individual muscle contractions were controlled independently.

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