Emergence of Postural Patterns as a Function of Vision and Translation Frequency

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Buchanan, John J. and Fay B. Horak. Emergence of postural patterns as a function of vision and translation frequency. J. Neurophysiol. 81: 2325–2339, 1999. We examined the frequency characteristics of human postural coordination and the role of visual information in this coordination. Eight healthy adults maintained balance in stance during sinusoidal support surface translations (12 cm peak to peak) in the anterior–posterior direction at six different frequencies. Changes in kinematic and dynamic measures revealed that both sensory and biomechanical constraints limit postural coordination patterns as a function of translation frequency. At slow frequencies (0.1 and 0.25 Hz), subjects ride the platform (with the eyes open or closed). For fast frequencies (1.0 and 1.25 Hz) with the eyes open, subjects fix their head and upper trunk in space. With the eyes closed, large-amplitude, slow-sway motion of the head and trunk occurred for fast frequencies above 0.5 Hz. Visual information stabilized posture by reducing the variability of the head’s position in space and the position of the center of mass (CoM) within the support surface defined by the feet for all but the slowest translation frequencies. When subjects rode the platform, there was little oscillatory joint motion, with muscle activity limited mostly to the ankles. To support the head fixed in space and slow-sway postural patterns, subjects produced stable interjoint hip and ankle joint coordination patterns. This increase in joint motion of the lower body dissipated the energy input by fast translation frequencies and facilitated the control of upper body motion. CoM amplitude decreased with increasing translation frequency, whereas the center of pressure amplitude increased with increasing translation frequency. Our results suggest that visual information was important to maintaining a fixed position of the head and trunk in space, whereas proprioceptive information was sufficient to produce stable coordinative patterns between the support surface and legs. The CNS organizes postural patterns in this balance task as a function of available sensory information, biomechanical constraints, and translation frequency.

INTRODUCTION

The CNS must coordinate many joints and muscles and regulate sensory information from the visual, somatosensory, and vestibular systems to maintain balance and postural orientation during standing, walking, and running. To better understand how the CNS adapts to different environmental conditions, it is important to study how postural coordination and the role of the senses change as a function of different task constraints. Tasks that translate the body at different frequencies require changes in the coordinative patterns of the head, trunk, and legs to accommodate the different forces acting on the body. Translating the body at different frequencies also moves the sensory systems within and outside of their optimal operating ranges. To maintain balance, it is important to control the position of the trunk for two reasons: 1) most of the body’s center of mass (CoM) is located in the trunk and 2) the trunk serves as a platform for the visual and vestibular sensory organs. How does the CNS coordinate the legs and trunk to control postural stability, i.e., the position of the CoM over the base of support, as a function of translation frequency? What is the role of visual information in the control and coordination of postural orientation and equilibrium?

Although several studies have investigated postural responses to sinusoidal surface perturbations, they have been limited either in the range of frequencies studied or in their kinematic and dynamic analysis. Over a small range of anterior–posterior sinusoidal translations frequencies (0.25–0.5 Hz), Dietz et al. (1993) and Berger et al. (1995) observed a change in body inclination and some damping of head and CoM motion as translation frequency increased. Neither study observed any significant changes in interjoint coordination or affects of visual information on body inclination and CoM. In contrast, others have reported large increases in body sway with the eyes closed for lateral and anterior–posterior oscillatory tilt (or pitch) rotations of the surface (Gurfinkel et al. 1975; Walsh 1973). This suggests that visual information may be important for controlling the position of the head and trunk in space. By studying tilting oscillations at higher frequencies, Walsh (1973) also observed a change in postural strategy from moving in phase with the platform at low frequencies to relative stabilization of the head in space at high frequencies (0.66 Hz) (see also Gantchev et al. 1972; Gurfinkel et al. 1975).

A possible explanation for the reported differences in results is that sinusoidal rotational tilting may perturb the head and CoM more than sinusoidal anterior–posterior translation for the same frequency of motion. During rotational tilting, when the body moves with the platform, the CoM moves close to the support surface boundary at the points of maximal tilt within each cycle. Without vision, this movement of the CoM is accentuated as seen in an increase in upper body sway (Walsh 1973). In contrast, during anterior–posterior surface translations, when the body moves with the platform, the CoM may not approach the support surface boundary at any time during a cycle of translation, and posture remains quite stable. If the CoM does not approach the support surface boundary, vision may be less critical to maintaining stable posture. However, Dietz et al. (1993) may not have driven the system to fast-enough translation frequencies to tease out this interaction between CoM motion and the role of visual information in stabilizing posture as noted by Walsh (1973). Perhaps at faster...
anterior–posterior translation frequencies, vision may play a more important role at keeping the CoM away from the support surface boundary.

It is generally believed that vision plays its largest role in posture at low frequencies of motion. Postural sway can be driven by linear motion of a moving room (Lee and Lishman 1975) or visual scene (Lestienne et al. 1977). Frequency analysis of sinusoidal movement of the visual scene has shown the strongest effects to be <0.4 Hz (Berthoz et al. 1979; van Asten et al. 1988). However, the influence of moving visual fields on postural stability depends not only on the characteristics of the visual environment but also on the characteristics of the support surface. For example, when the surface is compliant, the sway induced by sinusoidal visual motion is four times as large as when the surface is fixed (Peterka and Benolken 1995). Thus vision may play a more important role in postural control when the support surface moves compared with when the surface is fixed, especially when both the surface and visual scene oscillate at high frequencies that typically do not drive postural sway in studies of visual motion with subjects standing on a fixed surface. To further examine the role of vision in controlling head and trunk position in space, we extend the work of Dietz et al. (1993) by translating subjects across a larger frequency range (0.1–1.25 Hz) with their eyes open and closed.

Visual, like vestibular information, may be more important in controlling the orientation of the trunk and head than coordinating lower leg responses to surface perturbations (Horak et al. 1994; Keshner et al. 1988). Humans and cats with profound loss of vestibular function show normally coordinated leg behavior, e.g., forward lean or knee bending, before platform motion. The feet were placed slightly less than shoulder width apart with the toes angled slightly outward. Foot position was marked on the platform to insure a consistent initial foot position within and across trial blocks. Fall prevention consisted of a shoulder and trunk harness worn by the subject and attached to a steel support track mounted in the ceiling. Subjects were read the following instructional set: 1) keep your arms folded across your chest at all times, 2) stand upright at the start of each trial, but once the trial starts you may flex and extend your hips, knees, and ankles in any manner to remain on the platform, but do not step except to prevent a fall, and 3) with your eyes open look straight ahead and not to the left, right, down, or up, and with your eyes closed face forward as if looking straight ahead.

Reflective markers attached to the subject and platform were recorded (60 Hz) with a motion analysis three-dimensional optical system consisting of three high-speed video cameras (742 × 560 pixel accuracy). Eight markers were attached to the following landmarks: 1) cathi of right eye, 2) right lateral mandibular joint, 3) seventh cervical vertebra, 4) right greater trocanter, 5) right lateral femoral condyle, 6) right lateral malleolus, 7) right heel, and 8) right fifth metatarsaphalangeal. A ninth marker was positioned posterior to the subject’s right heel on the translated surface. Computation of the marker’s x, y, and z trajectories was performed off-line on a SUN workstation. The x, y, and z trajectories were then low-pass filtered (Butterworth) with a cutoff frequency of 6 Hz. From the x and z trajectories of the markers, the ankle (markers 5, 6 vertex, 7), knee (markers 4, 5 vertex, 6), hip (markers 3, 4 vertex, 5), and head pitch (markers 1, 2 vertex, 3)\(^1\) angles in the sagittal plane were calculated. At rest, the head pitch angle measured from 200 to 230° across subjects, with an increase in pitch angle representing head pitch up and a decrease representing head pitch down. The xyz trajectories of the eight body markers and subject morphological measures were input into a three-segment model (legs, trunk, head) to estimate total body CoM position in the anterior–posterior (x), lateral (y), and vertical (z) directions. CoM positions (x, y, z) were calculated as a weighted summation of individual segment CoM positions (Vaughan et al. 1991).

The platform’s two force plates allowed for standardized foot placement. Four strain gauges (sampled at 120 Hz) embedded in each plate (2 forward, \(F_1\) and \(F_2\), and 2 backward, \(F_3\) and \(F_4\)) measured the force exerted by the foot against the surface of the plate. Summation of the four strain gauge signals produced an estimate of vertical force, \(F = F_1 + F_2 + F_3 + F_4\), under each foot. With this measure of vertical force, the anterior–posterior CoP was calculated under each foot as

\[
\text{CoP}_i = \frac{(F_{1i} + F_{3i}) - (F_{2i} + F_{4i}) \times d}{F_{ci}}
\]

with \(i = 1, r\) for the left and right foot, respectively, and \(d = 17.5\) cm (the longitudinal distance between the plate’s center and the force transducers). From the individual foot CoPs, total body anterior–posterior CoP was computed

\(^1\) Correlations of A/P motion (x-axis) of markers 2 and 3 were >0.96 across subjects and trials, showing that the head and upper trunk moved as a unit in this task. Although head pitch angle is relative to upper trunk motion, there was no indication of a confounding of trunk inclination on head pitch angle.
The CoP<sub>A-P</sub> time series was low-pass filtered (Butterworth) with a cutoff frequency of 10 Hz.

EMG activity was recorded from eight muscles with pairs of 2.5 cm silver–silver chloride surface electrodes mounted over the muscle belly: left and right medial gastrocnemius, left and right tibialis anterior, right biceps femoris, right rectus femoris, and left and right erector spinae. EMG signals were preamplified, band-pass filtered (70–2,000 Hz), full-wave rectified before sampling (480 Hz), low-pass-filtered (100 Hz), and stored for off-line analysis.

**Data analysis**

Each translation frequency was associated with a different initial platform acceleration. The platform’s initial movement (firstquarter-cycle of motion) was always from the 0 position to −6 cm in the posterior direction. Any effect of the initial perturbation disappeared within the first one-half cycle of motion for the slowest translation frequency of 0.1 Hz. For the remainder of the translation frequencies (0.25–1.25 Hz), the initial perturbation effect lasted anywhere from one-half to three cycles of platform motion. We focus on how the human postural control system coordinates head and body motion to a continuously moving surface. Thus the perturbation associated with the platform’s initial backward motion was discarded as transient data. For the slowest frequency, the first one-half cycle of data was discarded, and for the other five frequencies the first two and one-fourth cycles were discarded. All the kinematic, force, and EMG data presented were computed from the following cycles: 0.1 Hz, from the 1st posterior peak of platform motion to the 6th posterior peak (5 cycles of motion); all other frequencies, from the 3rd posterior peak of platform motion to the 15th posterior peak (12 cycles of motion).

**BODY KINEMATICS.** To study the effects of translation frequency on anterior–posterior head (and trunk) and CoM motion, average measures of anterior–posterior head and CoM amplitude were derived. The head (marker 2, x-axis) and CoM anterior–posterior time series for each trial were mean centered and averaged across cycles within a trial. The posterior peaks of platform motion were used to define the cycles of head and CoM motion to average. From the averaged cycle trajectory for each trial, the maximum and minimum values were located, and the difference between them was taken as the average peak-to-valley amplitude for that trial. The head pitch angle was also divided into cycles and averaged within a trial. From the averaged cycle trajectory for each trial, the maximum and minimum values were found, and the difference between them was taken as the average head pitch amplitude in the sagittal plane. The head and CoM amplitude measures were used to study damping of head and trunk motion in the anterior–posterior direction as a function of translation frequency, and head pitch amplitude was used to study head motion in the sagittal pitch plane.

SD for each point in the head’s average cycle trajectory was computed. From these SDs of the average cycle trajectory for each trial, a mean (H<sub>SD</sub>) was computed and treated as a measure of the variability of the head’s position in space. Position of the anterior–posterior CoM within the support surface was studied by measuring the distance from the CoM’s position to the heel (marker #7) at the platform’s posterior turnaround point. The distance (cm) from the CoM to the heel was measured at each posterior peak in the heel displacement series. For each trial, mean and SD of CoM-to-heel distance were derived. The SD of CoM-to-heel distance provided a measure of postural stability based on the movement of the CoM over the base of foot support.

**SURFACE FORCES.** To examine the relationship between surface forces and platform translation frequency, spectral analysis was performed to measure the amplitude and phase of anterior–posterior CoP motion. An analogue trace from the platform (sampled at 120 Hz) was taken as the translation signal. The CoP and platform time series were mean centered, and Welch’s average periodogram method was employed to compute the spectra. The anterior–posterior platform translation signal always had a single dominant peak (f<sub>1</sub>) in its spectra, and the amplitude and phase of anterior–posterior CoP motion were calculated at the corresponding peak in the CoP spectra. CoP amplitude was defined as CoP<sub>PA</sub> = CoP x F<sub>PA</sub> / F<sub>PP</sub> <sup>1/2</sup>, with F<sub>PP</sub> <sup>1/2</sup> the magnitude of the platform signal and CoP x F<sub>PA</sub> the magnitude of the CoP signal. The phase of anterior–posterior CoP motion was defined as the phase of the coefficient in the CoP spectra associated with the value f<sub>1</sub>. Values of CoP phase in the interval 0° < Φ<sub>CoP</sub> < 180° are interpreted as maximum tosues under CoP leading the posterior turning point of the platform.

**JOINT ANGLE KINEMATICS.** To study joint–platform coordination, a cycle-to-cycle point estimate of relative phase between platform translation and ankle joint angular motion was computed; to study interjoint coordination, a point estimate of relative phase between ankle and hip joint angular motion was computed. Balance had to be maintained across a wide range of translation frequencies, and oscillatory motion about an individual joint was not observed at all frequencies. The anterior–posterior platform time series (marker #9, x-axis) and ankle, knee, and hip joint angular time series for each trial were mean centered, and the spectra were computed with Welch’s average periodogram method (see footnote 1). A single frequency peak, f<sub>1</sub>, was always found in the platform spectrum of each trial, and when the largest peak in the spectrum of an angular time series was at the value of f<sub>1</sub>, i.e., joint motion was frequency entrained to platform motion, that joint was considered active in that trial. To compute relative phase measures, a peak-picking algorithm was used to locate the cycle peaks of maximum ankle flexion, hip extension and the platform’s posterior turnaround point within a trial. In the platform–ankle phase, platform motion was taken as the reference event, r<sub>i</sub>, with platform cycle duration defined as the time between successive reference events, r<sub>i</sub> and r<sub>i+1</sub>. The platform–ankle phase (Φ<sub>PA</sub>) was computed as the ratio of the time of a target event t<sub>1</sub> (maximum ankle flexion) within the reference cycle of platform motion, Φ<sub>PA</sub> = (r<sub>i</sub> - t<sub>1</sub>) / (r<sub>i+1</sub> - r<sub>i</sub>) × 2π. The phase in radians was converted to degrees. If 0° < Φ<sub>PA</sub> < 180°, then this positive value of the platform–ankle phase indicates that maximum ankle flexion occurred before the platform’s posterior turnaround point within a reference cycle. The ankle was taken as the reference event and hip extension was taken as the target event in computing the ankle–hip phase (Φ<sub>AH</sub>) between ankle flexion and hip extension. Positive values of the ankle–hip phase indicate that hip extension leads ankle flexion within a cycle of motion. In each trial in which a phase was computed, ~12 cycle phase values were derived, and from these values a mean phase and phase SD for the platform–ankle (Φ<sub>PA</sub>) and ankle–hip (Φ<sub>AH</sub>) relative phases were computed.

**EMGS.** A variety of muscle activity patterns was used to stabilize posture in this task. To study muscle activation patterns, individual EMG time series within a trial were averaged across cycles when a 1:1 relationship between muscle bursts and platform motion was observed. Each muscle EMG was normalized to the maximum value for that muscle within a trial. A peak picking routine located the posterior and anterior platform signal peaks, which were used to define 12 cycle

<sup>1</sup>The Welch procedure decomposes a signal into overlapping segments of equal length and averages the spectral estimates of the segments to reduce the variance of the spectral estimate of the signal. Because our trials were of varying length, the segment lengths and number of overlapping segments were different for each frequency, ranging from 3.4 cycles/segment (2 overlapping segments) at 0.1 Hz to 5.2 cycles/segment (5 overlapping segments) at 1.25 Hz, with each segment length equal to an integer power of two. Each segment overlap was one-half the length of the entire segment.

<sup>2</sup>This initial restriction limited the analysis of EMG bursting activity to translation frequencies of >0.1 Hz.
intervals in the EMG and joint angle time series. The maximum value in the averaged EMG signal was located; searching backward from this point, the onset was defined as the first point that was 10% of the maximum value with the average signal remaining above this 10% value for the next 50 ms. To characterize the timing of burst onset in the average signal across different translation frequencies, the onset was expressed as a percentage of the one-half cycle duration of platform motion. For the gastrocnemius and tibialis anterior, the time difference \( t_d \) between burst onset (On) and the platform’s anterior turnaround point (ATP) was computed. \( t_d = \text{ATP-On} \). This temporal measure was then expressed as a percentage \( (\text{HC}_p) \) of the one-half cycle duration \( (\text{HC}) \) of platform motion, \( \text{HC}_p = t_d/\text{HC} \). A negative value of \( t_d \) indicates onset before the ATP, and a positive value indicates onset after the ATP for gastroc and tibialis. For b. femoris, r. femoris, and e. spinae, the value of \( t_d \) was defined as the difference between On and time of maximum hip flexion, and \( \text{HC}_p \) was defined with respect to the one-half cycle time from maximum hip flexion to maximum hip extension in the averaged hip signal (when the hip was classified as active). A positive value of this temporal measure indicates burst onset after maximum hip flexion, and a negative value indicates burst onset before maximum hip flexion for b. femoris, r. femoris, and e. spinae. Both the positive and negative burst onset values were binned in 50% intervals to create four one-fourth cycle intervals of muscle onset.

**STATISTICAL ANALYSIS.** The trial values of the head amplitude measure \( (\text{H}_{\text{A/P}}) \), the head position variation measure \( (\text{H}_{\text{v}}) \), the CoM-to-heel variation data, and the platform–CoP phase measure \((\Phi_{\text{CoP}})\) were averaged across trials by subject as a function of vision and translation frequency and analyzed in 2 \( \times \) 6 ANOVAs with vision (eyes open or closed) and platform frequency (6 frequencies) as independent variables. Because the platform-ankle \( (\Phi_{\text{PA}}) \) and ankle-hip \( (\Phi_{\text{AH}}) \) phase values were not computed at all frequency plateaus and all trials, the individual trial means and SDs were analyzed in 2 \( \times \) 5 (5 frequencies, 0.25–1.25 Hz) and 2 \( \times \) 4 (4 frequencies, 0.5–1.25 Hz) ANOVAs, respectively, with vision and translation frequency as independent variables. Although we randomized across frequencies within a block, plots of the trial values of CoM amplitude and CoP amplitude for individual subjects revealed a strong trial \( \times \) translation frequency trend. The individual subject trial means of CoM amplitude and CoP amplitude were analyzed in 2 \( \times \) 6 \( \times \) 3 repeated-measures ANOVAs, with vision, platform frequency, and trial as independent variables.

The next section characterizes frequency-dependent postural coordination patterns through the analysis of body kinematics (head and CoM) and surface forces (CoP). Implementation of these postural patterns is described with reference to interjoint coordination and muscle activation patterns.

**RESULTS**

*Postural patterns emerged as a function of platform frequency and available sensory information*

Frequency-dependent postural patterns emerged with or without vision in this task. For slow translation frequencies of 0.1 and 0.25 Hz, subjects rode the platform with little damping of head and trunk anterior–posterior motion (Fig. 1, A and B); for fast frequencies of 1.0 and 1.25 Hz, subjects damped head and trunk motion extensively at the translation frequency (Fig. 1, C and D). Both patterns were evident for intermediate frequencies within a block, plots of the trial values of CoM amplitude and CoP amplitude for individual subjects revealed a strong trial \( \times \) translation frequency trend. The individual subject trial means of CoM amplitude and CoP amplitude were analyzed in 2 \( \times \) 6 \( \times \) 3 repeated-measures ANOVAs, with vision, platform frequency, and trial as independent variables.
Three of eight subjects (in a total of 9 trials) responded with an out-of-phase pattern between head and platform motion when first encountering a fast translation frequency ($0.75 \text{ Hz}$) with the eyes open. The trial displayed in Fig. 1E was the first exposure of one subject to the translation frequency of $1.0 \text{ Hz}$ with the eyes open. Even with this out-of-phase pattern available, the behavior of these three subjects converged to the head fixed in space pattern with repeated exposure to the same translation frequency.

A clear decrease in head amplitude (increased damping of head motion) emerged with increasing translation frequency, with little or no damping of head motion at the slowest frequency of $0.1 \text{ Hz}$ and extensive damping for the fast translation frequencies of $0.75–1.25 \text{ Hz}$ (Fig. 2A). Head anterior–posterior motion was damped more with vision than without vision, $F(1,84) = 147.9, P < 0.01$, and damping increased with increasing translation frequency from 0.1 to 0.75 Hz with no change from 0.75 to 1.25 Hz, $F(5,84) = 32.8, P < 0.01$ (Fig. 2A). A small but significant difference was found between the visual conditions as a function of translation frequency, $F(5,84) = 2.66, P < 0.5$. This interaction was limited to translation frequencies of $\leq 0.5 \text{ Hz}$ ($P < 0.05$), with eyes open amplitude less than eyes closed (Fig. 2A). The head amplitude results suggest a frequency-dependent change in postural pattern with only a small difference in vision across translation frequencies.

Does such damping of head anterior–posterior motion for the fast translation frequencies represent fixing the head in space (as shown in Fig. 1, C and D) relative to the moving platform? In many trials with the eyes closed and translation frequency of $\geq 0.75 \text{ Hz}$, head position in space drifted, even with significant damping of head motion at the translation frequency (Fig. 3A). In some trials, higher-order frequency ratios between head and platform motion were observed. The example in Fig. 3B clearly shows a 2:1 ratio between platform and head motion. More importantly, the amplitude of oscillation grows across cycles to a maximum of 13 cm. Table 1 portrays the number of specific frequency ratios between the head and platform as a function of translation frequency with the eyes closed. Frequencies ratios of 4:1, 3:1, and 2:1 were seen most often for the translation frequency of $0.5 \text{ Hz}$, whereas slow-sway motion as shown in Fig. 3A was found only for frequencies of $\geq 0.75 \text{ Hz}$.

Although vision had only a small effect on damping of head motion at the translation frequency, it had a large effect on maintaining a fixed position of the head in space. For example, compare the large amount of drift (variability in the head's position) with the eyes closed to the minimal drift with the eyes open (Fig. 3A).

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mean position, $H_o = 4.5$ cm) in Fig. 3A with the eyes closed with Fig. 1C with the eyes open ($H_o = 0.82$ cm). The group means of the average cycle variability have been plotted in Fig. 2B as a function of visual condition and translation frequency. The head’s variability in space differed as a function of vision, $F(1,84) = 9.7, P < 0.01$, and varied significantly with translation frequency, $F(5,84) = 118.9, P < 0.01$. Most importantly, the vision × frequency interaction was significant, $F(5,84) = 6.79, P < 0.01$, with the head’s variability in space significantly larger ($P < 0.05$) with the eyes closed than with the eyes open for translation frequencies of $\geq 0.75$ Hz (Fig. 2B). Thus vision plays an important role in controlling the head’s position in space, especially for the fastest translation frequencies.

**Head pitch angle remains constant across translation frequencies**

Motion of the head in the pitch plane, whether discrete or oscillatory, was minimal in seven of eight subjects. In only a few instances was oscillatory motion of the head in the pitch plane observed, for example, when producing the antiphase pattern as in Fig. 1E or with the eyes closed as in Fig. 3B. The subject portrayed in Fig. 3B was the only subject to consistently produce oscillatory motion of the head in the pitch plane, with the eyes open or closed, that was frequency entrained to platform motion. For the other seven subjects, head motion in the pitch plane was consistent with the averaged cycles shown in Fig. 1, A–D, or the head angle trace shown in Fig. 3A. The group mean of head pitch amplitude was $< 2^\circ$ across visual conditions [$F(1,84) = 0.9, P > 0.3$] and translation frequencies [$F(5,84) = 0.9, P > 0.4$]. Thus, except in the case of one subject, when the head was fixed in space with the eyes open in the A/P direction, it was also fixed in space with respect to pitch plane rotation. With the eyes closed, even if large drift in head and trunk motion was observed (Fig. 3A), there was little rotational motion of the head around c1 in seven of eight subjects.

**CoM amplitude and position over the support surface vary with translation frequency and vision**

Damping of head and trunk motion at the fast translation frequencies was associated with a reduction in the displacement of CoM in the anterior–posterior direction. Representative examples of CoM position within the support surface boundary have been plotted in Fig. 4, A and B. At slow translation frequencies, anterior–posterior CoM displacement was approximately equal to the platform displacement with the eyes open or closed (Fig. 4A), whereas at fast translation frequencies, CoM anterior–posterior motion at the translation frequency was damped extensively with the eyes open or closed (Fig. 4B). CoM amplitude decreased as translation frequency increased, $F(5,35) = 152.3, P < 0.01$, and varied as a function of trial, $F(2,14) = 8.5, P < 0.01$. From 0.1 (11.5 cm) to 1.25 Hz (2.4 cm), CoM peak-to-valley amplitude decreased with a significant difference ($P < 0.05$) between each translation frequency, except 1.0 and 1.25 Hz. CoM amplitude was ~10% larger on trial 1 than trials 2 and 3 ($P < 0.05$) and was larger with the eyes closed than with the eyes open, $F(1,7) = 39.2, P < 0.01$. The visual condition × frequency interaction was also significant, $F(5,35) = 4.1, P < 0.01$. CoM amplitude was ~10% larger without vision for slow translation frequencies: 0.1 Hz (closed = 12.1 cm, open = 10.9 cm), 0.25 Hz (closed = 10.3, open = 8.4), and 0.5 Hz (closed = 7.2 cm, open = 6.1 cm). Thus CoM amplitude was large (little damp-

**TABLE 1.** Head–platform frequency pattern as a function of translation frequency for eyes closed

<table>
<thead>
<tr>
<th>Frequency (Hz)</th>
<th>1:1, ride</th>
<th>Head Fixed</th>
<th>2:1</th>
<th>3:1</th>
<th>4:1</th>
<th>Slow Sway</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5</td>
<td>11</td>
<td>1</td>
<td>6</td>
<td>2</td>
<td>4</td>
<td>—</td>
</tr>
<tr>
<td>0.75</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>15</td>
</tr>
<tr>
<td>1.0</td>
<td>—</td>
<td>3</td>
<td>—</td>
<td>—</td>
<td>2</td>
<td>19</td>
</tr>
<tr>
<td>1.25</td>
<td>—</td>
<td>2</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>21</td>
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</table>

![Fig. 4](http://jn.physiology.org/)

FIG. 4. Four examples of anterior–posterior center of mass (CoM) (——) position over the support surface defined by the heel and toe of the right foot (– – –). The examples in A are from the same subject as are those in B. A: translation frequency of 0.1 Hz (ride postural pattern) with the eyes open (top) and closed (bottom). B: translation frequency of 1.25 Hz with the eyes open (top, head fixed in space) and closed (bottom, slow sway). Vertical lines represent the CoM-to-heel distance at the platform’s posterior turnaround point. C: group means of the CoM-to-heel distance variability at the platform’s posterior turn around point.
ing) for the ride pattern at slow translation frequencies and was extensively damped for the head fixed in space and slow-sway patterns at high frequencies, with only a small effect of vision on CoM amplitude at slow frequencies.

Although vision has only a small effect on CoM damping at slow translation frequencies, does that also mean that vision has little effect on postural stability, i.e., the movement of the CoM within the support surface? At slow frequencies, vision has little effect on CoM position that moved little within the support surface (Fig. 4A), whereas at fast frequencies vision limits the movement of CoM within the support surface (compare Fig. 4B, top and bottom). The variability of CoM-to-heel distance was constant across frequencies with the eyes open, although the actual distance of the CoM from the heel increased with faster frequencies (compare Fig. 4, A and B, top). Without vision, CoM-to-heel distance variability increased with each increase in translation frequency (Fig. 4C). CoM-to-heel distance variability was significantly different as a function of vision, $F(1,180) = 184.4$, $P < 0.01$, and platform frequency, $F(5,180) = 17.9$, $P < 0.01$. The visual condition × frequency interaction was also significant, $F(5,180) = 10.6$, $P < 0.01$. Contrast tests ($P < 0.05$) of the interaction revealed that the variability in CoM-to-heel distance was larger without vision for all platform frequencies of >0.1 Hz. These results converge with the analysis of head position in space (Fig. 2B) in showing the importance of visual information in stabilizing balance by reducing variability of both head (and trunk) and CoM motion in space. Thus fixing the position of the head and trunk in space corresponds to minimal motion of the CoM within the support surface defined by the feet, establishing a direct link of head and trunk control in space to stability at the support surface.

**CoP amplitude increased with increasing translation frequency and was modulated across trials**

As the CoM amplitude decreased, CoP amplitude increased with each increase in translation frequency, but with only a small difference as a function of vision. The time series in Fig. 5 show the frequency-dependent differences in CoP amplitude that correspond with the ride postural pattern at low frequencies (Fig. 5A), head fixed in space pattern (Fig. 5B, top, eyes open), and slow-sway pattern (Fig. 5B, bottom, eyes closed) at high frequencies. The group mean CoP amplitudes have been plotted in Fig. 5C as a function of platform frequency and trial. CoP amplitude increased with increasing translation frequency, $F(5,35) = 51.6$, $P < 0.01$, and varied with trial presentation, $F(2,14) = 12.8$, $P < 0.01$. The trial × frequency interaction was also significant, $F(10,70) = 10.92$, $P < 0.01$ (Fig. 5C). The trial effect arose from differences at 0.75, 1.0, and 1.25 Hz, with CoP amplitude larger in trial 1 than trials 2 and 3 for all three frequencies and larger in trial 2 than trial 3 at 1.25 Hz.
CoP amplitude was ~10% larger with the eyes closed, \( F(1,17) = 10.5, P < 0.05 \), and from 10% (0.75 Hz) to 30% (1.25 Hz) larger with the eyes closed at the fastest translation frequencies, \( F(5,35) = 5.6, P < 0.01 \). The increase in CoP amplitude corresponds directly with the change in behavior from the ride pattern at slow frequencies (\( \leq 0.25 \) Hz) to head fixed in space or slow-sway pattern at fast frequencies (\( \geq 0.75 \) Hz). The CNS increased CoP amplitude to counter the increase in forces associated with increasing translation frequency, with a clear adaptation with repeated exposure even when the frequencies were randomly presented.

The phase of anterior–posterior CoP was more consistent within a given subject than across subjects as a function of translation frequency and vision. Positive values of CoP phase indicate that the maximum forward position of CoP under the translation frequency and vision. Positive values of CoP phase within a given subject than across subjects as a function of

\[ P(0.75) \]

\[ F(1,17) = 10.5, P < 0.05 \]

The group mean SDs for the ankle–platform and ankle–hip phase relationships were less variable with vision, the stability of interjoint coordination increased (i.e., became less variable) with increasing platform frequency with and without vision.

**Joint motion was coordinated to support frequency-dependent balance patterns**

To dissipate the larger forces associated with increasing translation frequency, fixed patterns of oscillatory joint motion emerged among the hip, knee, and ankle, with somewhat more variability in the joint coordinative patterns with the eyes closed. Figure 6 shows representative examples of the relationship between ankle–hip and ankle–knee for the ride pattern (column 1), head fixed in space pattern with the eyes open (columns 2 and 3), and slow-sway pattern with the eyes closed (column 4). When subjects rode the platform, there was little oscillatory joint motion, whereas at faster frequencies there were clear relationships between hip and ankle motion. Five of eight subjects continually produced oscillatory knee motion (Fig. 6, columns 2 and 4), and three of eight subjects consistently fixed their knees at a specific angle (column 3). Table 2 shows that more oscillatory motion occurred at the ankle and hip compared with the knee, and the number of trials with oscillatory joint motion increased as translation frequency increased. Oscillatory joint motion was not found at a platform frequency of 0.1 Hz.

The relative phase between ankle flexion and platform motion gradually changed across frequencies, whereas ankle–hip relative phase remained relatively constant with considerable intersubject variability. The group mean values of the ankle–platform (\( \Phi_{PA} \)) and ankle–hip (\( \Phi_{AH} \)) phases have been plotted in Fig. 6B. At slow frequencies, ankle flexion occurred in advance of the platform’s posterior turnaround point, and at fast frequencies maximum ankle flexion occurred simultaneously with the platform’s posterior turnaround point, \( F(4,201) = 21.0, P < 0.01 \). Post hoc tests (\( P < 0.05 \)) found that the mean relative phase at 0.25 Hz was larger than all other frequencies, and the mean relative phase at 0.5 Hz was larger than the phase at the two fastest frequencies (Fig. 6B). A small but significant difference was found in the ankle–platform phase relationship as a function of visual condition, \( F(1,201) = 4.4, P < 0.05 \) (eyes open, \( \Phi_{PA} = 7.9^\circ \); eyes closed \( \Phi_{PA} = 13.2^\circ \)). No significant effects were found in the ankle–hip phase \( \Phi_{AH} \) as a function of vision [\( F(1,154) = 1.7, P > 0.01 \)] or platform frequency [\( F(3,154) = 0.7, P > 0.05 \)] (Fig. 6B).

The variability in ankle–platform and ankle–hip relative phases decreased as translation frequency increased. The group mean SDs for the ankle–platform and ankle–hip phases have been plotted in Fig. 6C. Variability for both the ankle–platform \( [F(1,201) = 13.4, P < 0.01] \) and ankle–hip \( [F(1,154) = 5.7, P < 0.01] \) phase relationships decreased significantly with increasing platform frequency. Post hoc tests (\( P < 0.05 \)) revealed that the variability in the ankle–platform phase was largest at 0.25 and 0.5 Hz and that the variability in the ankle–hip phase decreased from 0.5 to 1.25 Hz. Both the ankle–platform \( [F(1,201) = 43.1, P < 0.01] \) and ankle–hip \( [F(1,154) = 39.1, P < 0.01] \) phase relationships were less variable with vision (\( \Phi_{PA} = 16.8^\circ; \Phi_{AH} = 24.3^\circ \)) than without vision (\( \Phi_{PA} = 28.1^\circ, \Phi_{AH} = 39.1^\circ \)). Although the joint coordination patterns were less variable with vision, the stability of interjoint coordination increased (i.e., became less variable) with increasing platform frequency with and without vision.

**Muscle activation was frequency dependent and functionally specific to the balance patterns**

More muscles were active at fast than slow translation frequencies, and a variety of muscle activation patterns was used to stabilize the upper body in the head fixed in space pattern. Table 3 shows the number of trials in which some type (tonic, rhythmic, and intermittent) of muscle activity (act column) occurred and those trials in which rhythmic muscle activity (rhy column) was observed. The numbers in parentheses are trials with the eyes open. In general, some form of gastroc activity was observed more than any other muscle at slow platform frequencies, whereas activity in other muscles increased with increasing translation frequency. More rhythmic activity was associated with faster translation frequencies for all muscles monitored, with somewhat more rhythmic activity with the eyes open.

Figure 7 portrays two different patterns of muscle activation associated with the head fixed in space posture at a fast translation frequency of 1.25 Hz. Gastroc and tibialis burst out of phase in both examples, with b. femoris bursting in-phase with gastroc in Fig. 7A, and r. femoris bursting in-phase with tibialis in Fig. 7B. Notice in Fig. 7A that the gastroc bursts before maximum ankle flexion; in Fig. 7B the gastroc bursts before maximum ankle extension and stays on as the ankle flexes. Similar differences arise in tibialis activity between the two trials. Gastroc was activated before maximum forward (toes) CoP, and tibialis activity was activated before maximum backward (heel) CoP in each example. In both trials, because the head and trunk were relatively fixed in space, hip extension and flexion resulted mainly from motion of the thigh as the platform moved from anterior to posterior. The onset of b.
femoris in Fig. 7A occurred as the hip extended, as did the onset of r. femoris in Fig. 7B, which remained active as the hip flexed. Table 4 summarizes the frequency of muscle onset in four one-quarter cycle intervals as a percentage of the one-half cycle duration: gastroc and tibialis in relation to the platform cycle and b. femoris, r. femoris, and e. spinae in relation to the hip cycle. The four one-quarter cycles are 1) early joint extension, maximum extension to mid extension; 2) late joint extension, midextension to maximum extension; 3) early joint flexion, maximum extension to mid flexion; and 4) late joint flexion, mid-flexion to maximum flexion. Gastroc activity was most often initiated during early flexion (Table 4, column 3) when it starts to lengthen as in Fig. 7A and next most likely during late extension similar to the example shown in Fig. 7B. Tibialis activity was most likely to be initiated in early extension as it started to lengthen as in Fig. 7A, with few burst onsets.
TABLE 2. Oscillatory joint motion as a function of translation frequency and visual condition

<table>
<thead>
<tr>
<th>F, Hz</th>
<th>Ankle</th>
<th></th>
<th>Knee</th>
<th></th>
<th>Hip</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Eyes Open</td>
<td>Eyes Closed</td>
<td>Eyes Open</td>
<td>Eyes Closed</td>
<td>Eyes Open</td>
</tr>
<tr>
<td>0.25</td>
<td>17</td>
<td>5</td>
<td>7</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>0.5</td>
<td>24</td>
<td>24</td>
<td>10</td>
<td>10</td>
<td>16</td>
</tr>
<tr>
<td>0.75</td>
<td>24</td>
<td>24</td>
<td>14</td>
<td>14</td>
<td>20</td>
</tr>
<tr>
<td>1.0</td>
<td>24</td>
<td>24</td>
<td>18</td>
<td>20</td>
<td>24</td>
</tr>
<tr>
<td>1.25</td>
<td>24</td>
<td>24</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Values in parentheses correspond to trials with the eyes open. act, muscle activity; rhy, rhythmic muscle activity.

occurring during early or late flexion as the example in Fig. 7B. Biceps femoris onset was observed more often in the late extension phase when the muscle was shortened as shown in Fig. 7A, whereas r. femoris onset occurred more often during the late flexion or early extension phases when it was shortened just before or after maximum hip flexion. Erector spinae was activated most often during the late extension and early flexion phases when the muscle was shortened, very similar to b. femoris and gastroc.

In some trials, rhythmic muscle activity disappeared without any obvious kinematic change, whereas in other trials muscle activity fluctuated in relation to slow-sway motion of the upper trunk. For example, Fig. 8A shows the sudden disappearance of frequency-entrained rhythmic muscle activity. Suppression of rhythmic muscle bursts was found with both the eyes open and closed and for all muscles. Figure 8B shows how muscles can be recruited and suppressed based on the slow drift in head and trunk anterior–posterior position. This trial corresponds to the trial in Fig. 3A. Just as the upper trunk and head reached their most posterior position (Fig. 8B, dotted line in 4th row), large bursts in tibialis occurred (while gastroc activity was suppressed considerably) that stopped the backward motion of the upper trunk and head. The tibialis bursts were followed by r. femoris and e. spinae bursts, which helped to control and maintain the upper trunk’s current position as well as help to move the upper trunk forward. Once the upper trunk and head reached a certain forward position, tibialis activity was suppressed, and gastroc activity was recruited. Most distal muscle activity was associated with ankle and platform motion, and most proximal muscle activity was associated with hip and upper trunk motion, although ankle muscle activity, as shown in Fig. 8B, was activated to help control the position of the upper trunk and head in space when they drifted near the limits of stability.

TABLE 3. Muscle activity as a function of translation frequency and visual condition

<table>
<thead>
<tr>
<th>F, Hz</th>
<th>Gastrocnemius</th>
<th>Tibialis Anterior</th>
<th>Biceps Femoris</th>
<th>Rectus Femoris</th>
<th>Erector Spinae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>act</td>
<td>rhy</td>
<td>act</td>
<td>rhy</td>
<td>act</td>
</tr>
<tr>
<td>0.1</td>
<td>42(19)</td>
<td>—</td>
<td>15(3)</td>
<td>—</td>
<td>21(8)</td>
</tr>
<tr>
<td>0.25</td>
<td>47(23)</td>
<td>20(13)</td>
<td>23(4)</td>
<td>1(1)</td>
<td>33(13)</td>
</tr>
<tr>
<td>0.5</td>
<td>47(23)</td>
<td>25(16)</td>
<td>34(10)</td>
<td>5(1)</td>
<td>38(8)</td>
</tr>
<tr>
<td>0.75</td>
<td>48(24)</td>
<td>32(17)</td>
<td>42(18)</td>
<td>20(7)</td>
<td>41(21)</td>
</tr>
<tr>
<td>1.0</td>
<td>48(24)</td>
<td>35(19)</td>
<td>44(20)</td>
<td>28(13)</td>
<td>43(20)</td>
</tr>
<tr>
<td>1.25</td>
<td>48(24)</td>
<td>38(21)</td>
<td>47(23)</td>
<td>29(15)</td>
<td>45(21)</td>
</tr>
</tbody>
</table>

Values in parentheses correspond to trials with the eyes open. act, muscle activity; rhy, rhythmic muscle activity.

DISCUSSION

Our results suggest that both sensory and biomechanical constraints limit postural coordination patterns at different translation frequencies. Control of the head and trunk in space appears to be a critical strategy for balance at all translation frequencies because the trunk has so much of the body’s mass and because it also serves as a platform for the visual and vestibular organs located in the head. Visual information is particularly important to control slow drift of the trunk and keep the CoM away from the limits of foot support at fast translation frequencies. Lower body joint motion is coordinated to dissipate the energy input of fast platform frequencies, in turn facilitating control of upper body motion. Muscle synergies are loosely assembled and functionally specific to the demands of limiting body CoM drift as well as modulating CoP amplitude.

Is postural coordination multistable?

We observed two distinct, stable postural patterns as a function of platform frequency. Subjects typically maintained an erect stance and rode the platform with or without vision for slow translation frequencies (0.1 and 0.25 Hz). These slow frequencies are within the range for normal sway frequency during quite stance (McCullum and Leen 1989) when most of the control is located around the ankles (Nashner 1976). For fast platform frequencies (1.0 and 1.25) with the eyes open, subjects fixed the head and trunk in space relative to the moving platform. Our observation of two distinct postural patterns as a function of platform frequency coincides with previous work on pitch and frontal plane sinusoidal tilting (Gurfinkel et al. 1975; Walsh 1973) and confirms and extends the findings of Dietz et al. (1993) on anterior–posterior sinusoidal translation. Fixation of the head and trunk in space over an oscillatory support surface is not due only to the inertial constraints of damping trunk motion at higher frequencies. Proximal muscle activity is added for the head fixed in space.
pattern and controlling trunk position in space, whereas distal muscle activity is related to CoP modulations under the feet for both postural patterns, in turn representing active neural control of these postural patterns.

Occasionally, an out-of-phase head-to-platform postural pattern was observed with the eyes open at fast frequencies, but with repeated exposure to a given frequency the out-of-phase pattern converged to the head fixed in space pattern. Without vision, slow-sway head and trunk motion emerged for fast frequencies (≥0.75 Hz) as did higher-order frequency ratios between head and platform movement. Walsh (1973) also reported such subharmonic ratios between head and platform motion during sinusoidal surface tilting at 0.66 Hz; however, it is not clear in Walsh’s study what ratios actually arose or how often. Our results show that higher-order frequency entrainment of head-to-platform motion occurs most often for the translation frequency of 0.5 Hz and consisted of low-order integer ratios (2:1, 3:1, and 4:1). In multijointed arm movements, such low-order frequency ratios (in this case 2:1) have been shown to be stable, reproducible, coordinative patterns between shoulder and elbow and shoulder and wrist motion during a spatial tracing task (Buchanan et al. 1997; deGuzman et al. 1997). A variety of bimanual coordination studies has also shown that low-order frequency ratios (2:1, 3:1, 3:2) between the hands are stable across several movement frequencies (e.g., Kelso and deGuzman 1988). With such short trials in this experiment, we cannot say conclusively whether the higher-order frequency ratios between head and platform and slow-sway motion are stable, reproducible patterns (as in arm movements, which are also multisegmented tasks) or just long

<table>
<thead>
<tr>
<th>Muscle</th>
<th>Early Extension</th>
<th>Late Extension</th>
<th>Early Flexion</th>
<th>Late Flexion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gastrocnemius</td>
<td>2</td>
<td>39</td>
<td>83</td>
<td>26</td>
</tr>
<tr>
<td>Tibialis</td>
<td>48</td>
<td>28</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Biceps femoris</td>
<td>9</td>
<td>42</td>
<td>11</td>
<td>9</td>
</tr>
<tr>
<td>Rectus femoris</td>
<td>22</td>
<td>7</td>
<td>10</td>
<td>21</td>
</tr>
<tr>
<td>Erector spinae</td>
<td>14</td>
<td>30</td>
<td>25</td>
<td>13</td>
</tr>
</tbody>
</table>

FIG. 7. Two examples of averaged normalized electromyograph time series and joint angular time series for a translation frequency of 1.25 Hz with the eyes open. A and B: ankle joint (—) and platform (---) traces plotted with gastrocnemius (row 1) and tibialis anterior (row 2). A: hip joint plotted with biceps femoris (row 3); B: hip joint plotted with rectus femoris (row 3).

A and B: CoP (———) and CoM (---) time series are plotted (row 4) with the CoP peaks and valleys labeled toes and heels, respectively. The vertical lines labeled On mark the average muscle onset. Reference point for gastrocnemius and tibialis is platform’s anterior turnaround point (ATP), and for r. femoris and b. femoris it is hip maximum flexion (HMF). One-half cycle duration is 400 ms for these examples. The onset based on the four one-quarter cycles are as follows: (A) gastroc, early ankle flexion; tibialis, early ankle extension; r. femoris, early hip extension; (B) gastroc, late ankle extension; tibialis, late ankle flexion; b. femoris, late hip extension.

FIG. 8. Examples of active muscle suppression (A) and muscle recruitment (B). Each muscle trace is plotted in microvolts, and the ankle and knee joints are scaled to hip motion in the third row. A: rhythmic bursting activity of gastrocnemius throughout the trial with suppression of muscle activity in tibialis (row 2), b. femoris (row 3), and e. spinae (row 4) for a translation frequency of 1.0 Hz with the eyes open. The knee (row 3) and hip (row 4) continue to oscillate after muscle suppression. B: recruitment and suppression of muscle activity for a translation frequency of 1.25 Hz with the eyes closed. The time series in this trial are from the same trial depicting slow-sway head motion in Fig. 4A (cycles 3–9). In row 4, the head (- - -) trajectory is plotted with the hip angle (———). See text for details.

TABLE 4. Muscle onset as a function of one-quarter cycle interval
transients as the system searches for a stable postural pattern. To explore this possibility, it is necessary to run trials with 24–36 cycles of motion without vision to see if the subjects establish the head fixed in space pattern or maintain a consistent 2:1-type pattern as seen in Fig. 3B. The observation of out-of-phase patterns, higher-order frequency patterns, head fixing, and slow sway are highly suggestive of multistability in the postural control system for this task. However, more experiments designed to study specific postural patterns as initial patterns, pattern switching between postural patterns, and fluctuation enhancement before a change in postural pattern are required to solidify the idea of multistability in the postural control system.

**Visual information stabilizes posture by helping to control the position of the head and trunk in space**

For the slowest translation frequency of 0.1 Hz, inertial forces acting on the head and trunk are minimal, and subjects ride the platform with or without vision. Each increase in translation frequency increases the forces acting on the body, and compensation arises in the form of damping head, trunk, and CoM anterior–posterior motion at the translation frequency. From 0.1 to 0.5 Hz, the increase in damping of head and CoM motion is approximately linear, and above 0.5 Hz motion of the head and CoM is damped. Such damping of head and CoM motion at the platform’s translation frequency is directly in line with the observations of Berger et al. (1995) (see also Berger et al. 1992; Dietz et al. 1993) for sinusoidal anterior–posterior translations. Berger et al. (1995) observed an increase in head and CoM damping as the translation frequency increased with or without vision, but they only tested postural responses to slow frequencies of 0.5 Hz. Our slow translation results are consistent with their results. Even for fast frequencies above >0.5 Hz, there is little difference in the extent of head and CoM damping at the translation frequency with or without vision.

Although vision plays a small role in damping head and CoM motion at the translation frequency, it plays a large role in controlling the position of the head and CoM in space, especially at high frequencies. The effects of vision are first seen at the translation frequency of 0.5 Hz, the cutoff frequency in the work of Dietz et al. (1993) and Berger et al. (1995), and the influence of vision increases as frequency increases. At fast translation frequencies, the availability of vision reduces the variation of the head’s position, and this reduced variability shows that the head is fixed in space with respect to the moving platform. Analysis of the head pitch angle revealed only a few examples of oscillatory head pitch motion, with most produced by a single subject. This result further confirms the head amplitude results in demonstrating the head fixed in space with the eyes open. Also of interest is the lack of any head pitch angle difference with the eyes open or closed, suggesting that the head is “strapped down” (e.g., Nashner 1985) to the trunk with the eyes closed. Across all translation frequencies, the availability of vision reduces the variation of the CoM’s position within the support surface, suggesting that fixing the head and trunk in space is functionally associated with stabilizing posture. Removal of visual input is associated with large-amplitude, slow-sway motion of the head and trunk, reflected in large motions of the CoM over the support surface. Thus head motion is not just damped at the translation frequency in this task; it is actually maintained in a fixed position in space when visual information is available. As a result, vision directly contributes to postural stability.

Our finding that vision is important at fast translation frequencies may at first appear contradictory with previous studies suggesting that vision plays a major role in posture at slow frequencies of body sway (Berthoz et al. 1979; Dijkstra et al. 1994a; Lee and Lishman 1975; Lestienne et al. 1977; van Asten et al. 1988). Studies of postural sway have shown that sway can be driven by slow visual field oscillations (both central and peripheral visual fields) between 0.1 to 0.3 Hz, whereas frequencies of 0.4 Hz may or may not induce coherent postural sway (e.g., Dijkstra et al. 1994b; van Asten et al. 1988). Dijkstra et al. (1994b) reported that visual scene oscillations of 0.5 Hz induced three types of postural sway behavior: 1) sway phase locked or coordinated with visual scene oscillation; 2) sway exhibiting intermittent behavior, i.e., phase locking interrupted by periods of no coordination between sway and visual scene oscillation; and 3) no coordination between sway and visual scene oscillation. This variety in postural sway coordination at 0.5 Hz observed by Dijkstra et al. (1994b) is directly in line with our postural coordination changes with respect to the positioning of the head in space. At 0.5 Hz, some subjects fix the head in space, whereas others continue to ride the platform. Both the ride and head-fixed pattern may be interpreted as postural behavior coordinated to surface translation. With the eyes closed, it is at 0.5 Hz that other postural patterns such as 2:1 platform to head motion is first observed and at 0.75 Hz that slow-sway emerges. This type of behavior is suggestive of either intermittent or no coordination as observed in the work of Dijkstra et al. (1994b) when sway is decoupled from visual motion. However, our trials are not long enough to clarify this issue, and more work consisting of trials lasting 1–2 min at the fastest frequencies is needed.

In our experiment, visual field oscillation results from moving the subject’s visual system through space on a moving platform, that is, we mechanically drive the body through a visual environment, and visual field oscillation studies drive body sway with sensory information. Movement of the body through space compared with movement of the visual field with the body standing on a fixed surface is different in three ways: 1) moving the body on a translating surface induces mechanical postural perturbations as well as visual field oscillations, 2) movement of the surface alters both proprioceptive as well as visual information, and 3) visual field perturbations can be ignored at fast frequencies, whereas the surface perturbations in our experiment cannot. Even with these differences in perturbation techniques to upright posture our findings are consistent with the work on visual field oscillations and point to the complex interaction among proprioceptive, visual, and vestibular information in the control and coordination of postural behavior. For slow surface translations with visual field oscillations below the critical frequency for decoupling visual information and postural sway (<0.5 Hz), subjects ride the platform and tolerate visual field oscillations induced by support surface translation. This demonstrates that the CNS actively suppresses visual information that has been shown to passively drive postural sway and selects proprioceptive and vestibular information to control and coordinate postural re-
responses in this task. For fast surface translations above the critical frequency for coupling postural information to visual sway, subjects fix the head in space and remove the large perturbing effects of fast visual field oscillations induced by the support surface translation. The slow drift observed with the eyes closed at fast frequencies, when combined with the head fixed in space with the eyes open, demonstrates that the CNS actively uses visual information to control the positioning of the head in this task. Although the body may act as a low-pass filter because of its inertia and stiffness, the passive component to damping of CoM, and head excursions in this task, without the active control of visual information there is more drift in CoM and head position that destabilizes posture at fast translation frequencies. Perturbation of both head–trunk and leg motion with the eyes open and closed at fast translation frequencies is one way to test this assumption and may clarify how the CNS coordinates sensory information with passive biomechanical constraints in controlling not just posture but movement in general.

Assuming the body acts as an inverted pendulum, the visually driven postural sway results suggest that visual information is filtered by a second-order, low-pass filter (Lestienne et al. 1977; van Asten et al. 1988) such that postural sway is not responsive to high-frequency visual information. As surface translation frequency increases to >0.5 Hz, postural sway switches from an inverted pendulum type of sway at slow frequencies to a multisegmented type of sway with significant motion about the hips and knees at fast frequencies. This change in postural pattern is consistent with biomechanical constraints on body sway. The human body swaying as an inverted pendulum has a maximum sway of ~0.5 Hz. To sway at faster frequencies, the body must break at the hips with the trunk and head oscillating out of phase with the legs (McCollum and Leen 1989). It is not clear from studies of visual field oscillation if subjects switch from an inverted pendulum to a multisegmented sway at higher frequencies or whether they ignore vision at high frequencies to avoid multisegmented sway on a fixed surface in which proprioceptive information is unvarying. Movement of the support surface may be interpreted as an unstable surface such that subjects rely on visual (and vestibular) information more than when standing on a fixed surface (Mergner et al. 1997). Thus subjects in our study may be using vision at higher frequencies compared with studies of visual scene oscillation because of the influence of surface perturbations on patterns of body sway and on sensory context.

This suggests that visual information about the velocity of optic flow may be important in establishing and maintaining a fixed position of the head in space when the CoM is perturbed by surface perturbations. When the eyes are open, fixing the head in space for translation frequencies of >0.5 Hz removes any visual field oscillation. The CNS, in this case, may use optical flow information in a feedforward manner to fix the head in space and in a feedback manner to help monitor head and upper trunk position once fixed. The neural strategy is one in which removal of sinusoidal optical flow immobilizes the head. Establishing a fixed position of the head and upper trunk in space achieves three things in this task: 1) stabilizes the visual field in terms of retinal image slip, 2) stabilizes CoM position within the support surface, and 3) minimizes external platform forces acting on the head and upper trunk. The loss of head and upper trunk fixation without vision supports the hypothesis of a top-down role for visual information in the control of head and upper trunk position in space, particularly on a moving surface.

**Stable intersegmental coordination produces a stable support base for the trunk and head**

Despite some small differences in phase relationship of hip-to-ankle motion among subjects, all subjects showed a decrease in the variability of the ankle–hip phase pattern with each increase in translation frequency of >0.5 Hz. Stable intersegmental coordination during fast surface oscillations (>0.5 Hz) suggests that oscillatory motion about the hips, ankles, and knees may be important for the efficient dissipation of external platform forces, in turn limiting the impact of these forces acting on the upper trunk and head. If stable joint coordination is representative of efficient dissipation of external forces, then any forces not dissipated by the lower body with the eyes open may be compensated for by small-amplitude motions of the pelvis and lower trunk. However, without vision, slow-sway upper trunk and head motion may reflect a resonance of any nondissipated forces from the legs to the upper body. Although these slow-sway movements in the upper trunk occur at fast translation frequencies, joint coordination patterns remain stable, strongly suggesting, although not conclusively, that stable joint coordination may help to efficiently dissipate most of the forces created by the translating surface. Such stable intersegmental coordination demonstrates the importance of a stable base of support in the production of global postural patterns with or without vision (i.e., head fixed in space or slow-sway motion). The lack of any real differences in vision and nonvision conditions in joint coordination supports a bottom-up control of leg coordination to support surface motion with proprioceptive information.

**Muscle synergies are flexibly assembled to stabilize CoM position and trunk orientation**

Changes in muscle activation patterns accompanying the changes in kinematic postural patterns suggest these postural patterns are neurally controlled and are not simply a function of biomechanical constraints. Proximal muscle activity increased as translation frequency increased, suggesting that proximal muscle activity (r. femoris, e. spinae, or b. femoris) is associated with the control of trunk orientation. These muscles typically burst during their shortening phase when platform motion would move the trunk in the opposite direction. For example, e. spinae fire as the platform and legs move backward at fast translation frequencies, thus helping to keep the trunk erect and not allowing it to flex at the hips. In contrast, gastrocnemius and tibialis muscles are predominantly active when stretched and clearly associated with CoP changes and regulation of CoM position within the base of support. Distal muscle activity also loads the front and back of the feet (CoP) in anticipation of the platform’s ATP and posterior turnaround point, respectively, helping to stabilize the system before the change in perturbation direction. Oscillatory activity of the distal muscles can also be recruited and suppressed to help control the motion of the
trunk in space when the CoM approaches the support surface boundaries when the eyes are closed. What sensory information triggers this recruitment-suppression effect of EMG burst activity? EMG activity associated with the slow drift in head and CoM motion (as seen in Fig. 8B) with the eyes closed suggests that either otolith or somatosensory information may trigger these muscle responses when the postural state reaches some critical position. In this case, the proximity of the CoM to the support surface boundary. The most interesting feature of this observation is that the CNS coordinates the responses of the same muscle to different parts of the body depending on the current state of the system. For example, in Fig. 8B, gastroc and tibialis activity are clearly related to ankle motion as well as motion of the head and trunk. Because there is little change in the nature of the ankle angle when the trunk and head slowly drift, the data are suggestive that the otolith organs may provide the necessary information enabling the CNS to switch the control of muscle activity from ankle to head and trunk motion. Amplitude of muscle bursts can also be modulated within a trial. For example, initial oscillatory proximal muscle activity disappeared in some trials without a change in kinematic posture, suggestive either of a passive balancing of the trunk or the recruitment of other muscles not recorded (Fig. 8B). While the recruitment—suppression of muscle activity seen when the head and trunk drift slowly are clearly sensory driven, the disappearance of rhythmic bursting with the eyes open and no kinematic modulations points to the active suppression of muscular activity by the CNS. Although a given muscle tended to be activated in a specific part of a translation cycle within a subject, quite a few differences in muscle activation patterns also occurred among subjects with very similar kinematic postural patterns.

Adaptation of postural control

Although frequency presentation was randomized, CoP amplitude significantly decreased with repeated exposure to frequencies of >0.5 Hz. On first exposure to a fast translation frequency, the nervous system responds with large CoP amplitudes to counter the platform forces and helps control the motion of the head and trunk in space. After repeated exposure to fast frequencies, the nervous system adapts and reduces CoP amplitude to accomplish the same goal. For translation frequencies of ≥0.75 Hz, CoP amplitude is always largest on trial 1 and decreases through trial 3. Such a decrease in CoP amplitude may represent a neural strategy of energy minimization. This modulation in CoP amplitude occurs during the production of the head fixed (eyes open) and large-amplitude, slow-sway patterns (eyes closed). Because this adaptation of CoP is consistent with the eyes open or closed, it suggests that this adaptation of CoP amplitude is independent of vision.

Conclusion

Results from this study suggest that the number of possible balance patterns is limited by biomechanical properties of the trunk and head, constraints on sensory information processes, and possible energy minimization requirements. However, the nervous system is not limited to a single solution and demonstrates flexibility of postural coordination in the form of a variety (head fixed in space, off-out-of-phase head to platform, slow-sway) of postural patterns at fast platform frequencies. Flexibility is also reflected in the motion and lack of motion in the knee as well as the recruitment and suppression of individual muscle activity that is task specific. The results also demonstrate the importance of vision in controlling the position of the head and trunk in space during high-frequency motion. To investigate the interaction of visual and vestibular information in this task, the same experiment is being repeated with bilateral vestibular loss subjects and aged-matched controls.

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