Visual Control of Posture During Walking: Functional Specificity

William H. Warren, Bruce A. Kay, and Emre H. Yilmaz
Brown University

Three experiments examined the functional specificity of visually controlled posture during locomotion by presenting large-screen displays to participants walking on a treadmill. Displays simulated locomotion down a stationary hallway, a hallway that traveled with the observer, or a front wall that traveled with the observer. A superimposed oscillation specified postural sway in 6 possible directions. With the wall, sway amplitude was isotropic and directionally specific in all conditions. However, with the hallways, sway was anisotropic (lateral > anterior–posterior [AP]), and diagonal responses were flattened into the lateral plane. When the treadmill was turned 90° to the hallway, both the anisotropy and flattening were reversed (AP > lateral), indicating that they are determined by the visual structure of the scene. The results can be explained by postural control laws based on both optical expansion and motion parallax, yielding biases in planar environments that truncate parallax.

It is often supposed that the visual control of locomotion is based on optic flow patterns produced at the eye of a moving observer (Gibson, 1950; Lee, 1974; Warren, Morris, & Kalish, 1988). However, there is little direct evidence that human locomotion is actually regulated by such information. Here we report the first in a series of studies that examine how optic flow is used to control posture and gait. In this article, we examine postural responses to optical oscillations during walking. An unexpected pattern of biases in compensatory sway provides a window into the visual control laws for posture.

Laws of Control

The control of locomotion exemplifies the general problem of adaptive visual control. A standard view in psychology, artificial intelligence, and neuroscience has been that various types of information are used to construct a general-purpose three-dimensional (3D) representation of the environment, on the basis of which actions are planned. Although this model-based approach provides generality, its success has been limited by the computational problems of constructing a sufficiently accurate 3D model from visual data and using it to regulate a many-degrees-of-freedom system in real time.

Alternatively, a task-specific approach capitalizes on the regularities of a particular task, yielding special-purpose control relations between informational variables and the free parameters of an action system that is organized for the task (Gibson, 1958; Warren, 1988). Such control laws might take the form action = f(information | task), where the current task selects a mapping from information states to action parameter values. For example, steering through a field of obstacles could be controlled on the basis of optic flow information for heading and time to contact, without recovering metric 3D layout (Duchon & Warren, 1994). Recent work in behavior-based robotics and autonomous agents has moved in this direction (Aloimonos, 1993; Beer, 1990; Brooks, 1990), and there is physiological evidence for specialized visual–motor pathways that may support such control relations (Graziano, Yap, & Gross, 1994; Ingle, 1982; Milner & Goodale, 1993). This view predicts that manipulating task-specific information should produce corresponding "biases" in behavior, even when general 3D information is available. Such a result would imply that performance is not based on a general-purpose 3D model.

The aim of the present study was to investigate the preliminary question of whether optic flow is used to control posture during walking in an adaptive manner. We hypothesize that postural adjustments are functionally specific to optically specified disturbances, in particular, that we should find (a) selective responses to optic flow components specifying a postural disturbance, (b) directionally specific responses corresponding to the direction of the disturbance (e.g., anterior–posterior [AP] vs. lateral), (c) adaptation to rearrangement of the relation between stimulation and effectors, and (d) differential responses to different types of disturbances (e.g., translation vs. rotation). The present research examined the first three hypotheses; the fourth has been tested by Warren, Kay, and Hutchinson (1996). In the course of these experiments, we discovered a...
case that bears on the issue of model-based versus task-specific control.

Information for Postural Control

In principle, posture and balance could be regulated by visual, vestibular, or somatosensory information (i.e., by means of cutaneous, joint, and muscle receptors), but the evidence suggests that there is a division of labor (Howard, 1986; Warren, 1995). The visual and cutaneous systems are primarily effective in the low-frequency range of spontaneous postural sway, (Kay & Warren, in press; Lestienne, Soechting, & Berthoz, 1977; van Asten, Gielen, & van der Gon, 1988a, 1988b; Yoneda & Tokumasu, 1986), but vestibular responses and stretch reflexes are primarily elicited in a high-frequency range above 1 Hz, relevant to gaze stabilization and sudden perturbations (Diener, Dichgans, Bruzek, & Selinka, 1982; Diener, Dichgans, Guschlauer, & Mau, 1984; Grossman, Leigh, Bruce, Heubner, & Lanska, 1989; Melville-Jones & Young, 1978). In addition, the vestibular system is an order of magnitude less sensitive to the direction of self-motion than are the visual and somatosensory systems (Telford, Howard, & Ohmi, 1995). Here we focus on visual information.

As discovered by Gibson (1950; Warren, 1995), movement in a stationary environment generates an optic flow pattern 360° about the observer. Consider the case of standing posture, assuming pure translation of the eye with sway velocity $T$, as schematized in Figure 1a. The instantaneous angular optic flow for an environmental point $P$ is simply

$$\beta = \frac{T \sin \beta}{D},$$

where the point is a distance $D$ from the observer at a visual angle $\beta$ from the sway direction, and the flow vector is in the direction defined by $\beta$ (Gibson, Olum, & Rosenblatt, 1955; Nakayama & Loomis, 1974). The speed of sway $T$ is thus only specified if distance is known. Two aspects of the optic flow may be relevant to postural control. First, the flow pattern has a radial structure with a focus of expansion in the direction of sway, regardless of the 3D structure of the environment (Figure 1b). The rate or magnitude of expansion (the divergence) at a point on a surface is given by

$$\text{div} = -\frac{T_r}{D} \tan \delta \cos \gamma + 2\frac{T_r}{D},$$

where $T_r$ is the component of velocity along the line of sight to $P$, $T_l$ is the velocity perpendicular to the line of sight, $\delta$ is the slant angle between the surface normal and the line of sight, and $\gamma$ is the tilt angle about the line of sight (between $T_l$ and the direction of slant; Koenderink, 1986). Note that the magnitude of expansion goes to zero in the direction perpendicular to the direction of sway ($\beta = 90^\circ$, $T_r = 0$) for surfaces parallel to $T$ ($\gamma = 90^\circ$).

Second, in a 3D environment, there is also a pattern of motion parallax (Figure 1c). This can be defined locally as the relative motion between two points at different depths in the same visual direction ($\beta_1 = \beta_2 = \beta$), with its magnitude given by

$$\beta_1 - \beta_2 = T \sin \beta \left(\frac{1}{D_1} - \frac{1}{D_2}\right).$$

The parallax is thus zero in the direction of sway and increases to a maximum in the perpendicular direction, assuming that the depth structure is stochastically homogeneous in all directions, as in a forest or a field. Consequently, parallax tends to be greatest in those regions of the flow field in which expansion provides the least information about sway ($\beta = 90^\circ$), and vice versa ($\beta = 0^\circ$). This
equation can be generalized to describe parallax between neighboring elements, such as two elements at different depths along a ground surface. Finally, rotation of the observer yields still other flow patterns (Warren & Hannon, 1990; Warren, Mestre, Blackwell, & Morris, 1991). For example, lateral tilt about the ankles moves the eye on a circular path, adding a component of rotary flow.

The existing theory of postural control is based on the first variable, and proposes that the observer acts to minimize the suprathreshold optical expansion and contraction of a frontal surface, thereby anchoring the head to the visual surround with some phase delay (Lee & Lishman, 1975; Schoner, 1991; van Asten et al., 1988a; but see Dijkstra, Schöner-Giese, & Gielen, 1994). This model has the advantage that the amplitude of body sway is appropriately scaled without information for the distance of the surface, consistent with experimental evidence under closed-loop conditions (Dijkstra, Gielen, & Melis, 1992; Paulus, Straube, Krafczyk, & Brandt, 1989). In a 3D environment, the postural control system could also take advantage of the second variable, for minimizing suprathreshold motion parallax would similarly anchor the head to the surround. This would allow for adaptive responses when sampling different regions of the flow field, independent of perceived distance. However, bias would appear in degenerate cases when the depth structure is not homogeneous, such as planar environments that eliminate parallax in one direction. In summary, we can generalize the basic theory to propose that both optical expansion and motion parallax are used to regulate posture, yielding a robust system that would function adaptively with different samples of the flow field.

During walking, the optical transformations become more complex. In addition to postural disturbances, the flow pattern includes components produced by forward progression and by the stride cycle. The visual system is presumably able to use these components selectively to regulate locomotion and balance independently. For example, Cutting, Springer, Braren, and Johnson (1992) have shown that stride-related sinusoidal components do not interfere with perceptual judgments of heading. Below we test the converse: whether an oscillatory component corresponding to a postural disturbance can be used to control balance in the presence of a component corresponding to forward progression.

Postural Control During Standing and Walking

The biomechanics of balance are quite different during standing and walking (Winter, 1987; Yang, Winter, & Wells, 1990a, 1990b). Upright stance requires maintaining a so-called static equilibrium in which the body's center of gravity (cg) is kept above a fixed base of support. This places strict limits on the magnitude of sway, presumably specified by the locus of the center of pressure defined across the feet. In contrast, walking involves a dynamic equilibrium in which the cg is never directly above the base of support and continually changes with respect to the stance foot. The limits on postural sway are not as strict during walking, for there is more latitude for recovery by modulating foot placement from cycle to cycle (Townsend, 1985). In addition, somatosensory information from the feet and ankles is quite different, for during 80% of the stride cycle only one foot is on the ground.

Previous research on visual control has focused almost exclusively on standing posture. Body sway during stance can be induced by an oscillating visual display below 0.5 Hz, yielding maximum sway amplitudes of 3–4 cm at the eye (Andersen & Dyre, 1989; Lee & Aronson, 1974; Lee & Lishman, 1975; Lestienne et al., 1977; Soechting & Berthoz, 1979; Stoffregen, 1985; van Asten et al., 1988a, 1988b; Woollacott, Shumway-Cook, & Nashner, 1986). There is little evidence regarding the functional specificity of these postural adjustments. Directionally specific sway has been demonstrated along the AP axis (Delorme, Frigon, & Lagace, 1989; van Asten et al., 1988a), and isotropic responses have been reported with AP and lateral stimulation (Andersen & Dyre, 1989; Stoffregen, 1985, 1986).

There is almost no research on the visual control of posture during locomotion, largely due to the technical problem of manipulating optic flow for a moving observer. In a preliminary study of postural control during running, Lee, Young, Anderson, Warren, and McCrindle (described in Young, 1988) mounted a "tilting room" above a treadmill and observed directional sway in response to a 3° roll of the visual surround about the ankles. However, pitching the room fore or aft always evoked backward sway and a shortened flight time, suggesting a nonspecific response to increase stability. With a “moving hallway” above a stationary floor, sudden AP motion of the surround induced staggering or falling in walking children (Schmuckler & Gibson, 1989; Stoffregen, Schmuckler, & Gibson, 1987). A constant AP motion (0.6 m/s) led to reduced speed in adults when hallway motion was opposite the direction of walking, but no systematic adjustments when hall motion was in the same direction as walking (Konczak, 1994). Analogous results were reported using an apparatus that projected moving spots of light on a stationary floor (Ferrandez & Pallhous, 1986; Fluckiger, 1986).

The following experiments investigate the functional specificity of postural control by presenting large-screen displays to an observer walking on a treadmill. The displays were manipulated to test directional specificity, selective responses to postural components of flow, and adaptation to rearrangement, and to explore the information that is used to regulate postural sway.

**Experiment 1: Stationary Hallway**

In the first experiment, open-loop displays simulated locomotion down a stationary hallway (Figure 2), with a superimposed oscillatory component corresponding to postural sway. The oscillatory "driver" specified either a

---

2 That is, the displays were not updated on the basis of feedback about the position of the observer.
that overall postural sway be significantly correlated with the oscillatory visual display before a participant's data were analyzed in more detail. Obviously, this approach limits our generalizations to those who sway in response to visual stimulation.

**Method**

**Participants**

The 9 participants included 7 graduate students and 2 faculty members at Brown University, ages 22 to 37; they included William H. Warren, who was the only one informed about the purpose of the experiment. Students were paid for their participation.

**Apparatus and Displays**

The experimental setup is sketched in Figure 3. A flat rear-projection screen (3.0 m horizontal [H] × 2.2 m vertical [V]) was centered in front of a treadmill, the bottom edge 0.35 m above the belt and 1 m from the observer. The Quinton Q-55 treadmill had a 0.5 × 1.3 m belt and was set at a constant speed of 1 m/s. Raster displays simulating motion down the random-patch hallway were generated on a Silicon Graphics Iris 4D/210 GTX workstation at a frame rate of 30 Hz and projected on the screen with a Barco Graphics 800 RGB video projector with a 60 Hz refresh rate. Image resolution was 1,280 H × 1,024 V pixels, subtending a visual angle of approximately 112° H × 95° V. The participant's field of view was restricted to the hallway.

Independent variables were transformation type (translation or rotation), driver direction α, and driver frequency f. In control displays, the simulated hallway translated toward the participant along the AP axis at the same speed as the treadmill, yielding a flow pattern corresponding to forward progression at a constant speed. For test displays, oscillatory motions corresponding to translation of the head in the horizontal plane corresponding to a weaving gait or a rotation about the ankles corresponding to body tilt, at .25 or .40 Hz. To examine directional specificity, the oscillations specified body sway in six possible directions in the horizontal plane, including the AP axis (0°), four diagonal axes (±30° and ±60°), and the lateral axis (90°). Body sway was measured using a 3D motion analysis system with a marker on the neck. Assuming that the eye is stabilized with respect to the visual surround (Guitton, Kearney, Wereley, & Peterson, 1986), a neck marker would capture most of this response while avoiding extraneous head movements.

Given that the purpose of the experiment was to determine whether optic flow is used to regulate posture adaptively, participants were explicitly instructed to try to remain oriented to the hallway. The question of whether they do so spontaneously or unconsciously is difficult to assess experimentally, because even without instructions participants may adopt conscious strategies to guide their responses. We thus decided to specify the task explicitly. However, participants were not informed about the display transformations nor about our interest in directional responses. Given that display presentation was randomized, adaptive responses could not be due to task demands alone but must be based on the optical information in the display.

Finally, an unwritten observation among researchers on standing posture is that purely visual stimulation elicits significant sway in only one half to two thirds of participants (e.g., Dijkstra, 1994). This is not surprising, given that these are conflict conditions, and it might be due to contrary somatosensory information, insufficiently compelling visual displays, or attentional factors. However, our interest was not the proportion of people who respond to visual stimulation, but whether the exhibited responses are functionally specific. Data from those who do not sway would be uninformative about this question. We thus set a criterion...
sinusoidal displacements of the head were superimposed upon this basic flow pattern. In the translation condition, an oscillatory motion simulating translation of the eye in the horizontal plane was added. The peak-to-peak amplitude of simulated eye displacement was $A = 0.2$ e (32 cm), equal to 1/7 of the hallway width. In the rotation condition, an oscillatory motion simulating pitch and roll of the body about an axis through the ankles was added. The peak-to-peak amplitude of rotation was 10°, corresponding to an eye displacement of 28 cm. For both conditions, we tested two frequencies of oscillation, $f = 0.25$ and 0.40 Hz, and six directions of simulated head motion, $\alpha = -60^\circ, -30^\circ, 0^\circ, 30^\circ, 60^\circ$, and $90^\circ$, where $0^\circ$ corresponds to the long axis of the hallway (perpendicular to the screen) and $90^\circ$ corresponds to the short axis of the hallway (parallel to the screen), yielding 12 basic trial types. The displays were geometrically correct for a fixed station point 1 m from the screen. Self-produced head movements during walking introduced slightly anomalous motion perspective consistent with the flat screen rather than a hallway in depth. This would tend to have a conservative effect on sway responses.

Body position in three dimensions was recorded with a two-camera ELITE infrared motion analysis system (Bioengineering Technology and Systems, Milan), at a sampling rate of 100 Hz. The cameras were placed on the right side of the participant, such that measurements were accurate to 1 mm in the sagittal plane (AP direction) and 2 mm in depth (lateral direction), by our own pendulum tests. A 1.5 cm passive reflecting marker was mounted on the right side of the participant’s neck, at a location that minimized motion due to neck flexion and extension. Motion of the neck marker was used to determine the direction and amplitude of body sway. Because of initial software limitations, data samples in Experiment 1 were 10 s in duration; those in Experiments 2 and 3 were 40 s in duration. A sample was initiated by a signal from the Iris workstation at the onset of a display cycle, so that the relative phase between the display and postural sway could be measured.

**Procedure**

Participants were instructed to “Walk down the center of the hallway and try to stay oriented to it. Let the display push you around—just go with the flow. Don’t fight it or consciously try to anticipate it.” They were also instructed to fixate the far end of the hallway and to keep the mask positioned so that it blocked the edges of the display. To familiarize participants with the apparatus, they were given 5 min of practice walking on the treadmill with the room lights on, followed by 5–10 min of practice walking with the control display while wearing the mask, and 5–10 min of practice walking with oscillation displays (randomly selected from the first condition, 1 min each). On each test trial, the display was presented for approximately 20 s to allow the participant to achieve a steady state, and then two consecutive 10-s data samples were collected. Test trials were blocked by translation and rotation conditions with a brief rest period in between, and the order of conditions was counterbalanced over participants. In each condition, the 12 basic trial types were presented twice in a randomized order, yielding four data samples for each. A control trial preceded every 6 test trials, for a total of 48 experimental trials and 8 control trials in one 2-hr session. The session ended with a set of debriefing questions.

**Data Analysis**

The discrete Fourier transform (DFT) was computed on several of the neck marker time series for each participant. Very little energy was present above 2.0 Hz, so the data were filtered with a zero-phase fourth-order Butterworth low-pass filter with a cutoff frequency of 8.0 Hz (Winter, 1979).

Our main interest in these experiments was to determine the degree to which body sway was driven by the oscillatory display. A sample trial appears in Figure 4a, showing lateral sway on a control trial due to the stride cycle and on a translation trial with a 90° driver (solid curves). The DFT for the translation trial appears in Figure 4b, showing a major peak at the driver frequency of 0.25 Hz, a minor peak at the stride frequency around 0.8 Hz, and little activity above 1.0 Hz. For each trial, we cross-correlated the motion of the neck marker with the display by fitting marker position in the horizontal plane with a cosine function at the frequency of the driver (dotted curve in Figure 4a), such that

\[
x = A' \cos(2 \pi f t + \phi),
\]

where $f$ is the driver frequency (Hz), $A'$ is sway amplitude (cm), and $\phi$ is the phase of sway relative to the display (in degrees). Amplitude and phase were free parameters determined empirically with a two-parameter linear multiple regression (Cryer, 1986, pp. 33–34). Because the maximum sway could occur in any direction in the horizontal plane, not necessarily the direction of the driver, we computed this cross-correlation at 2° intervals from $-88^\circ$ to $+90^\circ$ (a total of 88 directions) and found the direction with the maximum amplitude ($\alpha'$). For example, the translation curve and cosine fit in Figure 4a are for the maximum amplitude direction of $\alpha' = 80^\circ$. The resulting multiple $R$ value provided an estimate of the degree of coupling between driver and response and was normalized by a z transformation before computing means and standard statistical tests. For control trials, fits were done at both driver frequencies to estimate baseline sway.

Thus, dependent variables for each trial were (a) the direction $\alpha'$, having the maximum amplitude of sway; (b) the peak-to-peak amplitude $A_{\text{max}}$ of sway in that direction; (c) the cross-correlation between the driver and sway in that direction (multiple $R$ of the two-parameter regression); and (d) the phase angle $\phi$ between the driver and sway. Because sway direction and phase are circular variables ranging between 0° and 360°, means were computed using circular statistics (Batschelet, 1981; Mardia, 1972; see Appendix). Axial circular statistics (modulo 180°) were used for computing direction means, and full circular statistics (modulo 360°) were used for the phase means. To assess how well the response direction matched the driver direction across trials, we used circular correlations. Finally, to determine whether sway direction and phase were randomly distributed over trials or significantly clustered about a mean, we used Rayleigh tests of nonhomogeneity, and used 95% confidence intervals, to decide whether the mean was significantly different from a fiducial value (such as a phase angle of 0°).

3 A fixation point was not used, to avoid a stationary landmark and induced motion of the fixation point relative to the oscillating hallway.

4 We used a correlation approach rather than discrete Fourier transformations because of the short 10-s sample duration and its relative simplicity for analyzing many sway directions. In 20 test trials, the correlation method gave identical results to the discrete Fourier transformation analysis at the specified frequency.

5 Because an oscillation is symmetrical about the center point, this spanned the full 360° circumference.
Figure 4. Analysis of a sample trial. (A) Time series of lateral position for a control trial, a translation trial (solid curves), and the cosine fit for the latter (dotted curve). (Driver direction is 90° at 0.25 Hz. Control curve plots position in the 90° direction. Translation curve plots position in the maximum amplitude direction of 80°, fitted curve has \( A' = 22 \text{ cm}, \phi = -179°, \text{ and } R = 0.95 \).) (B) Power spectrum for the translation trial, showing peaks at driver frequency (0.25 Hz) and stride frequency (~0.8 Hz).
Results
All participants reported that their responses were "spontaneous" and that they did not "consciously try to anticipate the display." Mean cross-correlations for each participant appear in Table 1. Five participants (1, 3, 4, 5, and 7) showed a significant difference between experimental and control trials for the cross-correlation between driver and sway (t tests on normalized R values for each participant, p < .05 or better), indicating that the visual driver had a significant effect on their postural sway. Their mean cross-correlations were .645 (SD = .388, N = 480) on experimental trials and .289 (SD = .148, N = 80) on control trials, t(4) = 5.195, p < .01. We consider only their results further. Consistent with the folklore, the remaining 4 participants did not exhibit significant sway, although it is interesting to note that 3 of them reported feeling that they did indeed respond to the displays.

The mean maximum amplitude and the corresponding direction of sway in each condition are represented in Figure 5; collapsed means for each driver direction appear in Table 2. There are several things to note about the plots, which are highly similar for translation and rotation at both driver frequencies. First, the magnitude of sway is relatively large, with peak-to-peak amplitudes of 12 cm in the lateral direction; previous reports suggest that standing sway appears to saturate at 3–4 cm. Second, responses are anisotropic, such that lateral amplitudes are more than twice as large as AP amplitudes. Third, although lateral and AP responses are directionally specific, diagonal responses are generally flattened into the lateral plane. We will discuss the last two points in more detail.

Table 1
Mean Correlations for Stationary Hallway by Participant (Experiment 1)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M</td>
<td>SD</td>
<td>n</td>
</tr>
<tr>
<td>1</td>
<td>.751*</td>
<td>.419</td>
<td>.266</td>
</tr>
<tr>
<td>2</td>
<td>.358</td>
<td>.236</td>
<td>.284</td>
</tr>
<tr>
<td>3</td>
<td>.632*</td>
<td>.355</td>
<td>.291</td>
</tr>
<tr>
<td>4</td>
<td>.627*</td>
<td>.333</td>
<td>.264</td>
</tr>
<tr>
<td>5</td>
<td>.446*</td>
<td>.312</td>
<td>.312</td>
</tr>
<tr>
<td>6</td>
<td>.345</td>
<td>.170</td>
<td>.278</td>
</tr>
<tr>
<td>7</td>
<td>.712*</td>
<td>.383</td>
<td>.313</td>
</tr>
<tr>
<td>8</td>
<td>.264</td>
<td>.141</td>
<td>.214</td>
</tr>
<tr>
<td>9</td>
<td>.395</td>
<td>.254</td>
<td>.324</td>
</tr>
<tr>
<td>1–9</td>
<td>.526</td>
<td>.375</td>
<td>863</td>
</tr>
<tr>
<td>1, 3, 4, 5, 7</td>
<td>.645*</td>
<td>.388</td>
<td>480</td>
</tr>
</tbody>
</table>

Note. N = 96 trials for each experimental participant mean (except P9, N = 95), and N = 16 for each control participant mean. For driver–sway R, asterisks indicate that the experimental cross-correlation was statistically different from the control correlation. For circular r, asterisks indicate that the correlation between driver and sway directions was significant. * p < .05 or better.

Anisotropy
Lateral responses were much larger than AP responses, with peak-to-peak amplitudes of 12 cm (mean gain = .38) as opposed to 5 cm (mean gain = .16). There was still a significant visual influence in the AP direction, however, for AP sway amplitude was statistically greater than the maximum amplitude on control trials, t(158) = 6.101, p < .001. A three-way repeated measures (RM) analysis of variance (ANOVA) on maximum sway amplitude (Transformation × Frequency × Direction) yielded only a main effect of direction, F(5, 20) = 10.306, p < .001, accounting for 41% of the total sum of squares (SS). This bears out the similarity of responses for translation and rotation at both frequencies, and confirms that responses were anisotropic. Why might they be so? It is worth noting that 4 of the 5 participants who swayed significantly reported that lateral displays were "more compelling" than AP displays, and 1 participant volunteered that the AP oscillation was "pretty subtle." Indeed, to the experimenters the AP oscillation was subjectively harder to see than the lateral oscillation.

The cross-correlation between driver and sway exhibited a similar pattern, consistent with the anisotropy (Table 2). A similar ANOVA on z-transformed R values yielded a main effect of direction, F(5, 20) = 11.74, p < .001, 37% of the total SS, confirming that the strongest coupling occurred with the lateral driver and the weakest with the AP driver. A main effect of frequency indicated that .25-Hz displays produced tighter coupling than .4-Hz displays, F(1, 4) = 10.49, p < .05, 13% of the total SS. There was no main effect of transformation type, suggesting that translation and rotation produced about the same strength of coupling, and there were no interactions.

To analyze this anisotropy in more detail, we attempted to predict maximum sway amplitude as a function of driver direction by performing a circular–linear correlation between them on trial data over the range -90° to +90°. This revealed a significant periodic trend in the data, F(2, 477) = 56.411, p < .001, accounting for 19.1% of the total SS. The trend formula was

$$A' = 8.78 + 3.29 \cos(2\alpha + 188.4^\circ),$$

where $A'$ is the predicted maximum sway amplitude (in cm) and $\alpha$ is the driver direction (in degrees). The maximum of this function (8.78 + 3.29 = 12.07 cm) occurs at $\alpha = 85.8^\circ$ (mod 180°) and the minimum (8.78 - 3.29 = 5.49 cm) at $\alpha = -4.2^\circ$ (mod 180°). Thus, sway amplitude significantly depends on driver direction and is at a maximum close to the lateral direction and at a minimum close to the AP direction.

Directional Specificity
Of the 5 participants who swayed significantly, all had significant circular correlations between driver direction and sway direction (Table 1), with an overall correlation across trials of r = .454, p < .001 (N = 480). This indicates
that the direction of postural sway was significantly correlated with the visually specified direction of the driver. For each driver direction, responses across trials were found to be significantly clustered around the mean direction of sway, Rayleigh tests on trial data ranging from \( r = .335 \) to \( r = .787 \), \( p < .001 \) (\( N = 80 \)) for each driver direction, indicating that they were not random but directional. For the AP and lateral displays, the sway direction corresponded closely to the driver, with mean directions of 2° (95% confidence interval of ±16°) for the 0° driver and 88° (±8°) for the 90° driver; the driver was inside the confidence interval for sway in both cases. However, with the diagonal
Table 2

Mean Sway Measures for Stationary Hallway (Experiment 1)

<table>
<thead>
<tr>
<th>Driver direction</th>
<th>Sway direction (degrees)</th>
<th>Sway amplitude (cm)</th>
<th>Gain</th>
<th>Driver–Sway Phase (degrees)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M SD</td>
<td>M SD</td>
<td>M SD</td>
<td>M SD</td>
</tr>
<tr>
<td>Anterior–posterior</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>2.2* 26.7</td>
<td>5.14* 3.16</td>
<td>.16</td>
<td>-.10</td>
</tr>
<tr>
<td>30</td>
<td>59.8* 33.0</td>
<td>7.05* 3.97</td>
<td>.22</td>
<td>.12</td>
</tr>
<tr>
<td>-30</td>
<td>-63.0* 31.4</td>
<td>7.88* 4.39</td>
<td>.25</td>
<td>.14</td>
</tr>
<tr>
<td>60</td>
<td>77.6* 22.9</td>
<td>9.86* 4.83</td>
<td>.31</td>
<td>.15</td>
</tr>
<tr>
<td>-60</td>
<td>-83.6* 21.9</td>
<td>10.70* 5.50</td>
<td>.33</td>
<td>.17</td>
</tr>
<tr>
<td>Lateral</td>
<td>90</td>
<td>87.8* 18.7</td>
<td>.38</td>
<td>.20</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td>12.09* 6.38</td>
<td>.38</td>
<td>.20</td>
</tr>
<tr>
<td>Control</td>
<td>-0.3 35.2</td>
<td>8.78* 5.33</td>
<td>.27</td>
<td>.17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.78 1.43</td>
<td>.289</td>
<td>.148</td>
</tr>
</tbody>
</table>

Note. For sway direction, asterisks indicate that the Rayleigh test of nonhomogeneity for sway direction was significant. For sway amplitude, asterisks indicate that the experimental amplitude was statistically different from the control amplitude. For phase, asterisks indicate that the mean phase angle between driver and sway was statistically different from 0°. For Rayleigh phase $r$, asterisks indicate that the Rayleigh test of nonhomogeneity for phase was statistically significant.

* $p < .05$ or better.

drivers, responses were generally flattened into the lateral plane, with means and confidence intervals of ±61.4° (±25°) for the ±30° drivers and ±80.6° (±12°) for the ±60° drivers; the driver was outside the 95% confidence interval for mean sway direction in all cases. In addition, ±30° rotation yielded sway that was not significantly directional at either .25 and .40 Hz as determined by Rayleigh tests, indicating that there was no preferred direction of response. For all other conditions, the data were significantly directional.

Finally, we should note that a trials analysis on sway amplitude revealed no sign of the adaptation effects previously reported for standing posture (Bronstein, 1986; Delorme & Frigon, 1990). This could be due to our instructions or to differences between standing and walking.

**Driver–Sway Phase**

The mean phase angle between driver and sway in each condition is represented in Table 2. Rayleigh tests of phase correlation (testing the consistency of observed phase across trials) indicated that the data were significantly clustered around a mean in each condition and thus exhibited a preferred phase angle across trials, $r = .44, p < .001$ ($N = 480$). The phase angle was significantly less than zero in all conditions, indicating a large phase delay with a mean of -41.63° ($SD = 60.43°, N = 480$) over all trials. This indicates that observers were following the display oscillation and were not anticipating it. The standard deviation of phase was on the order of 60° in each condition, or 17% of a complete cycle, showing that the phase relation between driver and sway was reasonably consistent over trials. Although the mean phase delay tended to be greater in the AP direction ($-70.2°$) than in the lateral direction ($-45.6°$), a Watson–Williams test for circular variables did not show this difference to be significant, $F(1, 158) = 3.305, ns$. However, the Rayleigh tests were significantly lower in the AP direction ($r = .25$) than in the lateral direction ($r = .66$), $t(158) = 4.19, p < .01$, indicating greater variability in AP phase, consistent with the anisotropy.

**Factors Affecting Visual Responses**

To explore why some participants did not respond significantly to the displays, we ran further tests with 2 of them (Participants 6 and 9), which we briefly describe for methodological interest. First, due to the regular sinusoidal nature of the displays, it is possible that observers discounted the oscillations because they were easily anticipated and rejected. Thus, we collected eight trials using unpredictable displays in which the oscillation was determined by the sum of five sinusoidal components (.075, .175, .275, .475, and .575 Hz) and did not repeat over the course of a trial. Second, if conscious attention can interfere with postural control, we reasoned that responses might be enhanced if attention was diverted to a secondary task. We thus presented sinusoidal displays in a dual-task paradigm, collecting eight trials in which participants read aloud a sequence of single letters presented at the far end of the hallway every 1.5 s, and eight trials in which they counted backward by threes from a randomly selected number. However, none of these manipulations yielded a significant correlation between sway and driver nor an increase in sway amplitude for these 2 participants. It is possible that there are individual differences in the relative reliance on visual and somatosensory information under conflict conditions, which could account for the failure of some observers to respond to purely visual oscillations.

**Discussion**

Experiment 1 provides clear evidence for the directional specificity of AP and lateral responses with both transformation types at both frequencies consistent with adaptive visual control of posture during walking. On the other hand,
Hypotheses: Anisotropy

What might account for the anisotropy in AP and lateral responses? It is possible that the treadmill placed unnatural constraints on the magnitude of adjustments. However, contrary to the observed effect, the narrow belt limited the range of variation in foot placement more in the lateral direction (about ±10 cm) than in the AP direction (about ±20 cm). We can think of three other potential explanations.

Biomechanical stability. It is likely that walking is more biomechanically stable in the AP direction than in the lateral direction. During the double-support phase (20% of the stride cycle), the base of support is three to four times longer than it is wide, and during the single-support phase (80% of the stride cycle), the stance foot is about three times longer than it is wide. This could make posture more vulnerable to visual or mechanical perturbations in the lateral direction than in the AP direction. Such an account predicts that the anisotropy should remain body centered if the observer’s orientation is changed with respect to the hallway (i.e., it should be tied to the axes of the body rather than the axes of the hallway). We test this prediction in Experiment 3.

Somatosensory information. As a consequence of the biomechanics, the somatosensory system may be more sensitive in the AP direction than in the lateral direction. For example, there could be greater resolution for the locus of the center of pressure defined over the feet because the base of support is longer than it is wide, both during single and double support. As a result, lateral balance may be more dependent on visual information than AP balance. This also predicts that the anisotropy should remain body centered.

Visual information. The source of the anisotropy might also be visual. First, flatness cues for the screen itself, such as accommodation, convergence, and disparity, could have reduced the amplitude of sway in AP direction, causing the anisotropy. However, Paulus et al. (1989) have demonstrated that, at a distance of 1 m, such cues have an equal stabilizing influence in both the AP and lateral directions, and thus they could not account for the anisotropy.

Second, there could be a relative velocity effect, such that it is harder to detect an optical oscillation when it is superimposed on a constant base velocity, in accordance with Weber’s Law (Nakayama, 1981). During walking, the AP oscillation is added to a constant forward velocity, whereas the lateral oscillation is added to a zero lateral velocity. In our displays, consequently, an oscillatory expansion–contraction superimposed on a constant expansion may be harder to detect than an oscillatory left–right translation superimposed on a constant expansion. This can be tested by removing the forward velocity component from the display, as we do in Experiment 2.

Third, the anisotropy could be explained by the hypothesis that, in Experiment 1, AP and lateral sway were regulated by different optical information: AP sway by expansion, and lateral sway by motion parallax. In the AP condition (i.e., 0° driver), parallax in the display was minimal and compensatory sway was presumably driven by expansion, whereas in the lateral condition (90° Driver), the oscillatory component of expansion was close to zero and sway was presumably driven by motion parallax. Thus, a difference in magnitude, visual sensitivity, or response gain for these two variables could account for the anisotropy (Paulus et al., 1989). In particular, the magnitude of expansion decreases with distance, so its mean value was relatively low in the AP condition, with oscillation along the major axis of the hallway; in contrast, the magnitude of motion parallax increases with the depth range, so it was maximal in the lateral condition, with oscillation along the minor axis of the hallway. Thus, different magnitudes of expansion and parallax could account for the anisotropy in AP and lateral responses. Of course, the relation between optical variables and AP and lateral axes of the body depends on body orientation to the 3D scene (i.e., to the long axis of the hallway). This hypothesis can thus be tested by manipulating the scene geometry to alter the relative magnitudes of expansion and parallax, as we do in Experiment 2, or by changing the observer’s orientation to the hallway, as in Experiment 3. A visual hypothesis predicts that the anisotropy should remain geographically centered, that is, tied to the axes of the hallway rather than the body.

Several aspects of the data are consistent with the latter hypothesis. First, the coupling between driver and sway was significantly weaker in the AP than in the lateral condition, as would be expected if expansion is less salient than parallax. Second, there was a larger phase lag and a significantly lower phase correlation in the AP than in the lateral condition, as might be expected if expansion became salient later in a sinusoidal cycle.

Lateral Flattening

The expansion–parallax hypothesis could also explain the lateral flattening observed with the diagonal drivers. In a 3D environment with stochastic depth variation, optical expansion and motion parallax are congruent and would both yield directionally specific responses (Figure 1). However, in a planar environment such as the hallway, which eliminates parallax along one dimension, expansion and parallax can be incongruent and yield biased responses (Figure 6). Specifically, in our diagonal conditions, expansion specified sway in the driver direction (Figure 6a), but motion parallax
We attempted to predict the observed direction of sway \( \alpha' \) in the diagonal conditions as the result of independent responses to expansion and motion parallax, as illustrated in Figure 6c. First, optical expansion specifies a sway amplitude \( A_{\text{exp}} \) that is equal to the amplitude of the driver. To estimate the gain of the response to this expansion \( G_{\text{exp}} \), we used data from the AP (0°) condition, which measured the response to a pure expansion of approximately the same magnitude. Second, motion parallax specifies a sway amplitude \( A_{\text{mp}} \) equal to the component of the driver that is parallel to the hallway’s minor axis. We used data from the lateral (90°) condition as a direct measure of the gain of this response \( G_{\text{mp}} \). Finally, we computed the expected direction of sway as the result of the scaled response to expansion \( G_{\text{exp}} A_{\text{exp}} \) and the scaled response to motion parallax \( G_{\text{mp}} A_{\text{mp}} \), such that

\[
\alpha' = \tan^{-1}\left( \frac{G_{\text{exp}} + G_{\text{mp}} A_{\text{mp}}}{G_{\text{exp}} A_{\text{exp}} \cos \alpha} \right) = \tan^{-1}\left( \frac{G_{\text{exp}} + G_{\text{exp}} A_{\text{exp}} \tan \alpha}{G_{\text{exp}} A_{\text{exp}}} \right),
\]

(6)

where \( \alpha \) is the driver direction. This yields predictions that are nearly equal to the observed directions of diagonal sway: for the ±30° drivers, the expected and observed values are ±62.8° and ±61.4° (with a ±25° confidence interval), and for the ±60° drivers, they are ±80.3° and ±80.6° (±12° confidence interval).

A second possibility is that the direction of sway is determined by the direction of the maximum of divergence in the flow field, which bisects the angle between \( T \) and the normal to the surface (Koenderink, 1986; Koenderink & van Doorn, 1976). However, evidence against this account for standing posture was provided by van Asten et al. (1988a).

Thus, the hypothesis that sway is regulated by both optical expansion and motion parallax offers a unified explanation of the anisotropy and lateral flattening, and suggests a new informational variable for postural control. In the following experiments, we attempt to test the competing hypotheses by manipulating forward velocity and scene geometry (Experiment 2) and the orientation of the body to the hallway (Experiment 3).

Experiment 2: Traveling Hall and Traveling Wall

In the second experiment, we examined the visual hypotheses further. First, we tested for a relative velocity effect by eliminating the constant velocity component of the display simulating forward progression, leaving only the sinusoidal component of display motion. This resulted in displays of an oscillating hallway that travels forward with the walking observer. If the anisotropy in Experiment 1 was due to a relative velocity effect along the AP axis, it should be reduced with the traveling hall. On the other hand, if it was due to the 3D structure of the hallway, both the anisotropy and lateral flattening should recur.

Second, we tested the influence of scene geometry by comparing the traveling hall with a traveling wall (an oscillating frontal surface), which eliminates motion parallax in the display. Thus, if the anisotropy in Experiment 1 was
due to motion parallax, the wall should reduce the lateral amplitude. In contrast, there should be no difference in AP amplitude, for we equated the mean magnitude of expansion in the hall and wall displays (about 0.24°/s at peak velocity in the .40 e condition, from Equation 2). Thus, if sway is regulated by expansion and parallax, we would expect the traveling wall to reduce both the anisotropy and flattening, compared with the traveling hall. On the other hand, if these effects are primarily due to biomechanical stability or somatosensory information, there should be little influence of scene geometry. It is important to note that some lateral sway may be expected even in the absence of motion parallax, due to tracking the horizontal excursion of elements on the screen.

Finally, to determine whether sway amplitude is under visual control, we also varied the simulated displacement from .10 to .40 eye heights (16, 32, and 64 cm, peak to peak). If AP sway is regulated by expansion, we should be able to show an effect of the magnitude of expansion on AP amplitude. On the other hand, if the biomechanics or somatosensory information place a hard limit on sway, as appears to be the case for stance at 3–4 cm, response amplitudes might saturate at some value. To simplify the procedure, we only used translation displays at one frequency (.25 Hz) and three driver directions (0°, 30°, and 90°).

Method

Participants

The 4 most responsive participants from Experiment 1 (1, 3, 4, and 7) were used in Experiments 2 and 3. Two were paid and 2 volunteered.

Apparatus and Procedure

The apparatus of Experiments 2 and 3 was identical to that of Experiment 1, with the following exceptions: the displays were generated on a Silicon Graphics Iris 4D/310 VGX at a frame rate of 60 Hz, and one 40-s sample was recorded per trial. Participants again walked on the treadmill wearing a field restricting mask while viewing large-screen displays. The hall condition used the same random-patch hallway as in Experiment 1, but without the constant velocity component simulating forward progression. The wall condition simulated a frontal random-patch surface at a distance of 1.5 e (2.4 m) from the eyepoint. In control displays, the hall or wall did not move on the screen, whereas in translation displays an oscillatory .25-Hz driver was added, corresponding to a sinusoidal displacement of the eye in the horizontal plane.

Three driver directions (0°, 30°, and 90°) and three simulated amplitudes of oscillation were used. For AP and lateral displays, peak-to-peak amplitudes were .10, .20, and .40 e (16, 32, and 64 cm, respectively). In an effort to see whether equating the AP component of the diagonal driver might equate the AP response, the amplitudes for 30° displays were slightly greater: .115, .231, and .462 e (18.5, 36.9, and 73.9 cm, respectively). The wall condition was run 1 month before the hall condition, with one session apiece. Instructions were the same as those in Experiment 1. Because participants were already familiar with the apparatus, practice consisted of 2–5 min of walking with the mask and the control display. Four blocks were run in each condition, a block consisting of a control trial followed by the 9 randomized translation trials, yielding a total of 4 control trials and 36 translation trials in a 90-min session. Data analysis was the same as before.

Results

Each participant exhibited a significant postural response to the oscillation in each condition. In the hall condition, the mean cross-correlation between driver and sway was \( R = 0.808 (SD = 0.385, N = 144) \) on translation trials, compared with \( R = 0.141 (SD = 0.084, N = 16) \) on control trials, \( t(158) = 9.58, p < .001 \). In the wall condition, the mean cross-correlation was \( R = 0.694 (SD = 0.391, N = 143) \) on translation trials, and \( R = 0.114 (SD = 0.031, N = 16) \) on control trials, \( t(157) = 7.168, p < .001 \). We thus proceeded with the analysis.

Mean sway in the hall and wall conditions is represented in Figure 7, and the values appear in Tables 3 and 4. Four things are evident from the plots. First, the anisotropy recurs with the traveling hall, but disappears with the traveling wall, due to a decrease in lateral sway. Second, the lateral flattening also recurs with the hall, but disappears with the wall, suggesting that the anisotropy and flattening may have the same origin. Third, sway increases with driver amplitude in all directions, indicating that both AP and lateral sway are visually influenced. Finally, both AP and lateral amplitudes are higher with the traveling hall in Experiment 2 than with the stationary hall in Experiment 1. However, the fact that the anisotropy recurs indicates that it cannot be explained by a relative velocity effect. We discuss these points in detail.

Anisotropy

The results for the anisotropy are detailed in Figure 8 (left and middle bars). Overall, mean sway amplitudes with the AP and lateral drivers were 13.6 cm and 20.8 cm in the hall condition—a difference of 7 cm, precisely the same as in Experiment 1. This difference was nearly eliminated in the wall condition, with amplitudes of 11.7 cm and 12.8 cm, respectively. (Analogously, mean gains were .44 and .65 for the hall, but .37 and .41 for the wall.) A three-way RM ANOVA (Condition \( \times \) Direction \( \times \) Amplitude) on sway amplitude revealed an overall difference between the hall and wall, \( F(1, 3) = 16.704, p < .05, 19\% \) of the total SS, and a main effect of driver amplitude, \( F(2, 6) = 30.265, p < .001 \). 41\% of the total SS, but no overall effect of driver direction, \( F(2, 6) = 2.705, ns \). However, the key result was a significant Condition \( \times \) Direction interaction, \( F(2, 6) = 10.747, p < .01 \), 5.5\% of the total SS, demonstrating that the anisotropy was significantly greater with the hall than with the wall. Post hoc Tukey tests indicated that only the hall’s lateral amplitude was significantly different from the other three conditions (\( p < .05 \) or better). Thus, the wall eliminated the anisotropy by reducing lateral sway rather than increasing AP sway, consistent with the presented magnitudes of motion parallax and expansion. There was also a small Condition \( \times \) Amplitude interaction, \( F(2, 6) = 13.488, \)
Figure 7. Polar plots of mean sway amplitude (Amp) as a function of mean sway direction for Experiment 2. (A) Traveling hall. (B) Traveling wall. (Translation, 0.25 Hz. Note that the amplitude scale denotes half of the total peak-to-peak amplitude represented by each curve.)

p < .01, 0.6% of the total SS, indicating that the effect of driver amplitude was greater with the hall than with the wall.

Cross-correlations between driver and sway followed the same pattern, with overall means for the AP and lateral drivers of $R = .733$ and $R = .853$ in the hall condition, $r(94) = 4.167, p < .001$ (on trial data), as opposed to $R = .669$ and $R = .730$ in the wall condition, $r(93) = 1.32, ns$ (see Tables 3 and 4 for breakdown by condition). Thus, the strength of the visual coupling between driver and sway confirms the elimination of the anisotropy with the wall.

**Directional Specificity**

For each driver direction and amplitude, sway direction over trials was significantly clustered around a mean, with Rayleigh tests ranging from $r = .757$ to $r = .994, p < .001$. Thus, responses were not random but directional. In the hall condition, mean sway directions were $2.2^\circ \, (\pm 11^\circ)$ for the $0^\circ$ driver, $54.7^\circ \, (\pm 18^\circ)$ for the $30^\circ$ driver, and $87.0^\circ \, (\pm 4^\circ)$ for the $90^\circ$ driver. The AP and lateral drivers were thus inside the 95% confidence intervals for sway, but the $30^\circ$ driver was outside them at every driver amplitude. Thus, AP and lateral responses were again directionally specific, whereas diagonal responses were flattened into the lateral plane. On the other hand, in the wall condition, sway was directionally specific for all drivers, with mean directions of $-2.6^\circ \, (\pm 9^\circ)$ for the $0^\circ$ driver, $35.5^\circ \, (\pm 20^\circ)$ for the $30^\circ$ driver, and $82.7^\circ \, (\pm 8^\circ)$ for the $90^\circ$ driver. In only one case did the driver direction lie outside the 95% confidence interval (the $90^\circ$ driver at the middle amplitude was $3^\circ$ outside of the interval). Most important, diagonal responses were directionally specific for the first time. Thus, lateral flattening recurred with the traveling hall, but not with the traveling wall.

We can predict the degree of flattening in the hall condition from Equation 6. The expected and observed directions of sway were $53.5^\circ$ and $58.6^\circ \, (\pm 22^\circ)$ for the small driver, $57.4^\circ$ and $54.0^\circ \, (\pm 14^\circ)$ for the middle driver, and $55.5^\circ$ and $51.7^\circ \, (\pm 18^\circ)$ for the large driver. This is consistent with the hypothesis that flattening can be accounted for by postural responses to both expansion and parallax.

**Driver Amplitude**

Sway responses did not appear to saturate, but increased with driver amplitude in all directions, as indicated by the main effect of amplitude and the absence of an Amplitude $\times$ Direction interaction. Both the first-degree and second-degree polynomial contrasts were significant ($p < .05$), indicating both linear and quadratic trends in the relation between driver and sway amplitudes. In the hall condition, peak-to-peak sway increased from 10.8 cm to 18.5 cm (smallest to largest driver) in the AP direction, and from 14.5 cm to 27.9 cm in the lateral direction, pushing the implied limit of the treadmill belt, although the gains drop in half. Tukey tests showed that the difference between the smallest and largest driver was significant in the AP, lateral, and $30^\circ$ directions. Responses were isotropic in the wall condition, increasing from 8.5 cm to 16.4 cm in the AP direction and from 9.3 cm to 16.4 cm in the lateral direction. Thus, in contrast to stance, there appears to be no hard biomechanical or somatosensory limit on sway over this range, and both AP and lateral amplitudes are influenced by visual information.

**Relative Velocity**

With regard to the effect of relative velocity, Figure 9 compares sway amplitudes with the traveling hall and the
Table 3

Mean Sway Measures for Traveling Hallway (Experiment 2)

<table>
<thead>
<tr>
<th>Driver direction</th>
<th>Driver amplitude</th>
<th>Sway direction (degrees)</th>
<th>Sway amplitude (cm)</th>
<th>Gain</th>
<th>Driver-sway R</th>
<th>Phase (degrees)</th>
<th>Rayleigh phase r</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>0</td>
<td>.1</td>
<td>4.9*</td>
<td>13.9</td>
<td>10.83*</td>
<td>.655</td>
<td>.641</td>
<td>.706</td>
</tr>
<tr>
<td></td>
<td>.2</td>
<td>1.2*</td>
<td>11.1</td>
<td>11.41*</td>
<td>.814</td>
<td>.258</td>
<td>.694</td>
</tr>
<tr>
<td></td>
<td>.4</td>
<td>0.9*</td>
<td>3.1</td>
<td>18.55*</td>
<td>9.72</td>
<td>.295</td>
<td>.788</td>
</tr>
<tr>
<td>30</td>
<td>.116</td>
<td>58.6*</td>
<td>18.5</td>
<td>13.41*</td>
<td>5.91</td>
<td>.847</td>
<td>.809</td>
</tr>
<tr>
<td></td>
<td>.231</td>
<td>54.0*</td>
<td>13.0</td>
<td>16.05*</td>
<td>6.65</td>
<td>.502</td>
<td>.809</td>
</tr>
<tr>
<td></td>
<td>.462</td>
<td>51.7*</td>
<td>17.1</td>
<td>21.47*</td>
<td>9.55</td>
<td>.345</td>
<td>.842</td>
</tr>
<tr>
<td>90</td>
<td>.1</td>
<td>85.1*</td>
<td>6.3</td>
<td>14.45*</td>
<td>6.81</td>
<td>.903</td>
<td>.772</td>
</tr>
<tr>
<td></td>
<td>.2</td>
<td>86.6*</td>
<td>5.1</td>
<td>19.90*</td>
<td>7.20</td>
<td>.622</td>
<td>.857</td>
</tr>
<tr>
<td></td>
<td>.4</td>
<td>89.3*</td>
<td>4.1</td>
<td>27.86*</td>
<td>9.39</td>
<td>.445</td>
<td>.904</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td>17.11*</td>
<td>9.24</td>
<td>.44 .23</td>
<td>.808*</td>
<td>.385</td>
<td>-1.6</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td>-26.6</td>
<td>37.2</td>
<td>1.12</td>
<td>0.52</td>
<td>.141</td>
<td>.084</td>
</tr>
</tbody>
</table>

Note. For sway direction, asterisks indicate that the Rayleigh test of nonhomogeneity for sway direction was significant. For sway amplitude, asterisks indicate that the experimental amplitude was statistically different from the control amplitude. For phase, asterisks indicate that the mean phase angle between driver and sway was statistically different from 0°. For Rayleigh phase r, asterisks indicate that the Rayleigh test of nonhomogeneity for phase was statistically significant. * p < .05 or better.

Table 4

Mean Sway Measures for Traveling Wall (Experiment 2)

<table>
<thead>
<tr>
<th>Driver direction</th>
<th>Driver amplitude</th>
<th>Sway direction (degrees)</th>
<th>Sway amplitude (cm)</th>
<th>Gain</th>
<th>Driver-sway R</th>
<th>Phase (degrees)</th>
<th>Rayleigh phase r</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
<td>M</td>
<td>SD</td>
</tr>
<tr>
<td>0</td>
<td>.1</td>
<td>-5.4*</td>
<td>11.8</td>
<td>8.54*</td>
<td>3.75</td>
<td>.53</td>
<td>.23</td>
</tr>
<tr>
<td></td>
<td>.2</td>
<td>-0.9*</td>
<td>10.4</td>
<td>10.31*</td>
<td>4.85</td>
<td>.32</td>
<td>.15</td>
</tr>
<tr>
<td></td>
<td>.4</td>
<td>-1.5*</td>
<td>6.5</td>
<td>16.39*</td>
<td>8.79</td>
<td>.26</td>
<td>.14</td>
</tr>
<tr>
<td>30</td>
<td>.116</td>
<td>34.1*</td>
<td>18.0</td>
<td>7.99*</td>
<td>3.09</td>
<td>.43</td>
<td>.17</td>
</tr>
<tr>
<td></td>
<td>.231</td>
<td>36.7*</td>
<td>16.7</td>
<td>11.22*</td>
<td>4.58</td>
<td>.30</td>
<td>.12</td>
</tr>
<tr>
<td></td>
<td>.462</td>
<td>38.6*</td>
<td>20.0</td>
<td>15.38*</td>
<td>5.65</td>
<td>.31</td>
<td>.08</td>
</tr>
<tr>
<td>90</td>
<td>.1</td>
<td>-83.3*</td>
<td>12.0</td>
<td>9.27*</td>
<td>5.83</td>
<td>.58</td>
<td>.36</td>
</tr>
<tr>
<td></td>
<td>.2</td>
<td>-82.7*</td>
<td>6.6</td>
<td>12.72*</td>
<td>6.93</td>
<td>.40</td>
<td>.22</td>
</tr>
<tr>
<td></td>
<td>.4</td>
<td>-82.0*</td>
<td>11.2</td>
<td>16.39*</td>
<td>6.92</td>
<td>.26</td>
<td>.11</td>
</tr>
<tr>
<td>Overall</td>
<td></td>
<td>11.99*</td>
<td>6.47</td>
<td>.30</td>
<td>.16</td>
<td>.694</td>
<td>.391</td>
</tr>
<tr>
<td>Control</td>
<td></td>
<td>-7.4</td>
<td>39.1</td>
<td>1.28</td>
<td>0.38</td>
<td>.114</td>
<td>.031</td>
</tr>
</tbody>
</table>

Note. For sway direction, asterisks indicate that the Rayleigh test of nonhomogeneity for sway direction was significant. For sway amplitude, asterisks indicate that the experimental amplitude was statistically different from the control amplitude. For phase, asterisks indicate that the mean phase angle between driver and sway was statistically different from 0°. For Rayleigh phase r, asterisks indicate that the Rayleigh test of nonhomogeneity for phase was statistically significant. * p < .05 or better.

stationary hall from Experiment 1 for the corresponding conditions only (.25-Hz translation, 32-cm driver, same 4 participants). With the stationary hallway, the AP and lateral amplitudes were 5.3 and 13.6 cm (gain = .17 and .42); with the traveling hallway, they increased by equal amounts to 11.4 and 20.0 cm (gain = .36 and .62), retaining the same absolute difference of 8 cm. A two-way RM ANOVA on these amplitudes revealed a main effect of driver direction, F(1, 3) = 14.928, p < .05, 44% of the total SS, but neither the effect of velocity, F(1, 3) = 3.883, ns, 24% of the total SS, nor the interaction, F(1, 3) = .012, ns, .01% of the total SS, were significant. Although this analysis showed no statistical difference between stationary and traveling hallways, sway amplitude doubled in all directions, yet the
Driver-Sway Phase

Mean phase angles between driver and sway are given in Tables 3 and 4. In each condition, the phase angle over trials was found to be significantly clustered around a mean, with Rayleigh tests ranging from $r = .741$ to $r = .978$, $p < .001$. In the hall condition, sway was generally in phase with the driver. The only condition in which the mean differed statistically from zero was with the small amplitude AP driver, which had a mean phase angle of $-20.24^\circ$, $p < .05$. Over the remaining translation trials, the mean phase angle was only $-0.78^\circ$ ($SD = 35.5^\circ$, $N = 128$), with a standard deviation equal to just 10% of a cycle. However, there was no overall difference in phase between the AP and lateral conditions, Watson–Williams $F(1, 94) = 2.188$, $ns$, nor was there a difference in the Rayleigh tests. In addition, there was no statistical difference in mean phase between the traveling hall in the present experiment ($0.09^\circ$) and the stationary hall in the corresponding conditions of Experiment 1 ($-16.2^\circ$), Watson–Williams $F(1, 94) = 3.079$, $ns$.

Phase delay increased in the wall condition. Five conditions exhibited significant phase lags ($p < .05$ or better), although the other four were not different from zero. The mean phase angle was $-11.3^\circ$ ($SD = 26.0^\circ$, $N = 144$), with a standard deviation equal to just 7% of a complete cycle, which was significantly greater than the hall condition, Watson–Williams $F(1, 283) = 6.102$, $p < .05$. Phase delay decreased with driver amplitude, possibly because optical velocities became detectable earlier in a sinusoidal cycle. There was no difference in phase between the AP and lateral conditions, Watson–Williams $F(1, 93) = 0.948$, $ns$, nor was there a difference in the Rayleigh tests between conditions.

Discussion

Experiment 2 demonstrates that 3D structure has a predictable influence on the amplitude and direction of sway. First, the anisotropy was replicated with the traveling hall but eliminated by the traveling wall. With the AP ($0^\circ$) driver, the average rate of expansion was equated for the hall and wall, and the resulting amplitudes of AP sway were equivalent. van Asten et al. (1988a) previously reported a similar result for standing posture with hall and wall displays. With the lateral ($90^\circ$) driver, on the other hand, the hall contained a high degree of motion parallax whereas the wall contained no parallax, and the resulting lateral amplitudes were significantly greater for the hall. Cross-correlations between driver and sway exhibit the same pattern. This is consistent with an explanation of the anisotropy in terms of differential responses to expansion and parallax.

However, a potential confound must be considered. In the wall condition, participants presumably regulated lateral sway by tracking the horizontal excursion of elements on the screen, for no depth information was available by which to scale the optic flow. It is possible that the larger lateral amplitudes in the hall condition could simply be responses...
parallel results for the flattening and anisotropy suggest that predicted the direction of sway with the hall from the theory that responses are driven by both optical expansion and these two phenomena have the same visual source. Their Warren, & Kay, in press).

Warren, & Kay, in press).

The results for lateral flattening were identical to those for anisotropy: flattening was replicated with the hall, but the wall can be explained as a response to pure expansion in the driver direction, in the absence of motion parallax. Similarly, directional specificity with the wall was consistent with the flattening and anisotropy suggest that these two phenomena have the same visual source. Their elimination with the wall demonstrates that flatness cues are not the cause of the bias.

In addition, the effect of driver amplitude confirms that both AP and lateral sway are under visual control. In contrast to standing posture, sway does not appear to saturate around 3-4 cm, but can increase up to 18.5 cm AP and 27.9 cm laterally. This demonstrates that the anisotropy is not simply due to a hard biomechanical or somatosensory limit on AP sway.

Finally, any relative velocity effect is similar in the AP and lateral directions, and thus relative velocity cannot account for the anisotropy. Although the absolute amplitudes of sway nearly doubled with the traveling hall over the stationary hall in Experiment 1, the anisotropy and lateral flattening remained the same. This finding has two implications. First, adding a constant velocity AP component affects the oscillatory AP and lateral components equally, presumably because the two-dimensional screen velocities are additive in both cases. Second, an identical pattern of results with the stationary and traveling hall implies that the visual system can decompose information for postural sway from that for forward progression and selectively respond to the former to regulate posture.

In summary, the results of the present experiment suggest that anisotropy and lateral flattening are primarily visual effects due to the geometry of the scene. However, a definitive test requires that we dissociate visual information from somatosensory information and biomechanical constraints. This was the purpose of Experiment 3.

**Experiment 3: Body Orientation**

In the final experiment, we tested the biomechanical and somatosensory hypotheses by rotating the treadmill 90° with respect to the hallway, as illustrated in Figure 10. Participants walked parallel to the screen while looking over their left shoulder at the traveling hallway display used in Experiment 2. The lateral axis of the body is now aligned with the long axis of the hall, and the AP axis of the body is aligned with the minor axis of the hall. If the anisotropy is due to biomechanical constraints or somatosensory information, it would be body centered, so lateral responses should remain larger than AP responses. On the other hand, if it is a visual effect due to 3D scene structure, it would be geographically centered, so the anisotropy should be reversed (i.e., AP responses should now be larger than lateral responses).

Corresponding predictions can be made about lateral flattening. Under the biomechanical and somatosensory hypotheses, the plane of flattening is anchored to the body, such that sway should remain flattened into the lateral plane. But under the visual hypothesis, the flattening would be anchored to the hallway, and sway should now be flattened into the AP plane, as illustrated in Figure 10.

Changing body orientation also tested another aspect of functional specificity: adaptation to rearrangement of the relationship between stimulation and effectors. When looking straight ahead, we previously observed that optical
expansion elicited AP sway and motion parallax elicited lateral sway. Rotating the body 90° with respect to the viewing direction reverses this relationship, such that expansion (0° driver) should now elicit lateral sway, and parallax (90° driver) should elicit AP sway. In other words, compensatory sway is specified relative to the direction of self-motion, regardless of viewing direction or body orientation.

Method

The apparatus was the same as before, but the treadmill was placed parallel to the screen (pointing to the right), with the center of the belt 1.0 m from the middle of the screen. Traveling hallway displays were the same as those used in Experiment 2, with three driver directions (0°, 30°, and 90°, now corresponding to lateral, diagonal, and AP body axes) and three driver amplitudes (.10, .20, and .40 cm for all directions). The 4 participants, procedure, and data analysis were the same as before. In addition, participants were told to look at the far open end of the hallway by turning their heads 90° to the left while walking straight down the treadmill belt, turning the trunk as little as possible.

Results and Discussion

Each participant showed a significant postural response to the oscillating displays in each condition. The mean cross-correlation between driver and sway for translation trials was $R = 0.639$ ($SD = 0.395, N = 142$), whereas for control trials it was $R = 0.160$ ($SD = 0.07, N = 16$), $t(156) = 5.67, p < .001$. We thus proceeded with the analysis.

Mean sway amplitudes and directions are presented in Figure 11, and values appear in Table 5. Several things can be noted in the plot. First, the anisotropy is reversed, such that the AP amplitude is now greater than the lateral amplitude. Second, the previous flattening is also reversed, such that diagonal sway is now flattened into the AP plane instead of the lateral plane. Both anisotropy and flattening thus appear to be geographically centered, not body centered. Third, optical expansion (0° driver) now evokes lateral sway, and motion parallax (90° driver) evokes AP sway, the opposite of previous results. We discuss these points in detail.

Anisotropy

Overall, mean sway amplitudes were 15.2 cm in the AP direction (90° driver) and 7.6 cm in the lateral direction (0° driver), a difference of 7.6 cm as found in the previous two experiments, but now in the opposite direction (right bars in Figure 8). A two-way RM ANOVA (Driver Direction × Driver Amplitude) was performed on maximum sway amplitude. A main effect of driver direction, $F(2, 6) = 7.968, p < .05$, 41% of the total SS, confirmed the anisotropy. There was also a main effect of driver amplitude, $F(2, 6) = 15.796, p < .001$, 30% of the total SS, with significant linear and quadratic trends, and no interaction, $F(4, 12) = 2.271, ns$, again demonstrating a visual influence on the magnitude of sway in all directions.

Cross-correlations between driver and sway were consistent with this pattern (Table 5), with overall means of $R = .701$ in the AP direction and $R = .518$ in the lateral direction, $t(93) = 3.810, p < .001$, on trial data. Thus, the strength of the visual coupling between driver and sway also shows a reversed anisotropy.
To compare rotated and unrotated treadmill conditions, we analyzed the present results and those for the hall from Experiment 2 in a three-way RM ANOVA (Treadmill Orientation × Direction × Amplitude) on sway amplitude in body coordinates. There was a main effect of treadmill orientation, $F(1, 3) = 689.893, p < .001$, 21% of the total $SS$, reflecting an overall decline in amplitude with the rotated treadmill, and a main effect of driver amplitude, $F(2, 6) = 25.838, p < .001$, 31% of the total $SS$, with both linear and quadratic components, but no overall effect of driver direction, $F(2, 6) = .039, ns$. The key result is a significant interaction between treadmill orientation and driver direction, $F(2, 6) = 19.115, p < .01$, 25% of the total $SS$, supporting the reversal of the anisotropy. There was also a small interaction between orientation and amplitude, $F(2, 6) = 19.221, p < .01, 1.7\%$ of the total $SS$, such that driver amplitude had a greater effect in the unrotated condition—more so with the 90° driver than the 0° driver, as indicated by a small three-way interaction, $F(4, 12) = 15.824, p < .001, 2.3\%$ of the total $SS$. In summary, the anisotropy was anchored to the hallway, not the body, consistent with the visual hypothesis.

**Directional Specificity**

For each driver direction and amplitude, the direction of sway across trials was significantly clustered around a mean, with Rayleigh tests ranging from $r = .744$ to $r = .933, p < .05$. The mean did not statistically differ from zero in any condition except with the large 0° driver (lateral), which anticipated the display by a mean phase angle of 17.0°, $p < .05$. Over all other experimental trials, the mean phase angle was -6.1° ($SD = 32.6°, N = 126$), with a standard deviation less than 10% of a cycle, but including 0° in its 95% confidence interval. Thus, as in Experiment 2, participants generally swayed in phase with the traveling hall rather than lagging behind it. There was no difference between the AP and lateral conditions in mean phase, Watson–Williams $F(1, 93) = 0.323, ns$, nor in the Rayleigh tests.
Conclusion

In summary, rotating the treadmill 90° reversed the anisotropy and flattening effects. Thus, contrary to the biomechanical and somatosensory hypotheses, these asymmetries are not body centered but are anchored to the hallway. This is consistent with a visual explanation based on the 3D structure of the scene. The only unexplained result is the overall drop in sway amplitude of about 5 cm with the rotated treadmill, which could be due to the awkward viewing conditions or simply be a session effect.

In addition, Experiment 3 demonstrates that postural control adapts to rearrangement between stimulation and effectors. When looking straight ahead, expansion elicits AP sway and parallax elicits lateral sway, but when looking left, the reverse is true. Visual control laws are thus not anatomically specific relations between a particular retinal pattern and a motor response. Rather, the optic flow specifies the direction of sway, and thus the direction of the required compensatory response. This is precisely what one would expect from an adaptive visual control system.

General Discussion

The results generally support the functional specificity of postural control during locomotion and provide some insight into the visual control laws. First, AP and lateral responses were directionally specific, as expected. Diagonal responses were directionally specific with the wall display, but were unexpectedly flattened into the minor axis of the hallway. There was also an anisotropy in the hallway, which depended on the 3D structure of the scene and was anchored to the axes of the hallway rather than the body, supporting a visual explanation. Second, the pattern of results was the same with both the stationary and traveling hallways. This indicates that the postural control system selectively responds to the oscillatory component of motion specifying sway, separate from the constant velocity component specifying forward progression. Third, postural control readily adapts to rearrangement between stimulation and effectors. Thus, sway responses are functionally specific regardless of viewing direction or body orientation.

We believe this pattern of results can be uniformly explained by the hypothesis that postural sway is regulated by both optical expansion and motion parallax. The biomechanical and somatosensory hypotheses were ruled out by Experiment 3, and other visual explanations were undermined by Experiment 2. In a stochastic 3D environment, expansion and parallax cospecify self-motion, and posture could be stabilized on the basis of their oscillatory components. However, in a truncated visual environment such as a hallway, reliance on parallax can bias the response. Thus, in Experiments 1 and 2, AP balance appears to be regulated by radial expansion and lateral balance by motion parallax of the hallway. The anisotropy may derive from differences in their magnitude, under our open-loop conditions. For example, with the middle driver in Experiment 2, the total angular expansion of the nearest element on the hallway floor was only about 0.3° in one half-cycle (2 s), whereas the total relative motion between the nearest and farthest element on the floor was about 12.3°. Indeed, participants reported that the oscillation of the 0° driver was harder to see than that of the equivalent 90° driver. If expansion were detected less reliably and later in the sinusoidal cycle than parallax, we would expect AP (0°) responses to exhibit smaller sway amplitudes, lower cross-correlations with the driver, larger phase delays, and lower phase correlations than lateral (90°) responses, as generally observed for hallway displays.

This hypothesis can also account for diagonal flattening observed in the hallway. We accurately predicted the direction of diagonal sway as the result of independent responses to expansion and parallax, scaled by the observed gain in these responses. On the other hand, responses with the wall were directionally specific, presumably because, in the absence of parallax, they were determined solely by the focus of expansion. The theory predicts that sway should also be directionally specific and isotropic with a stochastic 3D scene, in which expansion and parallax are congruent. We have since confirmed this prediction for a random 3D cloud of polygons (Bardy et al., in press). This result provides additional evidence that flatness cues are not the source of bias. It also rules out the possibility that the anisotropy is due to a perceived compression of the hallway along the depth axis, for a similar compression would occur with the 3D cloud, yet responses are isotropic.

The hypothesis may also account for a related effect that was reported by Gielen and van Asten (1990) for standing posture. They presented displays of a hallway oscillating along its major axis (like our 0° driver) and varied the eccentricity of gaze with a fixation marker mounted on the screen. The direction of sway was biased toward the opposite side of the driver by an angle equal to the eccentricity of the marker. This can be explained as a consequence of motion parallax between the marker and the hallway, which would bias sway away from the driver direction, for the magnitude of parallax increased with the marker's eccentricity.

Finally, the anisotropy and flattening suggest that posture is not regulated on the basis of a 3D representation of the environment, but rather by specific variables of optic flow. If the postural control system were taking advantage of the available perspective, texture, and motion information for the 3D scene, it would presumably correct for the structure of the hallway, yielding isotropic and directionally specific sway. The lack of reliance on 3D information implies that postural control is not based on an internal 3D model, but rather on task-specific information such as expansion and parallax.

References

Bardy, B., Warren, W. H., & Kay, B. A. (in press). Motion paral-
lax is used to control postural sway during walking. *Experimental Brain Research.*


**Appendix**

**Circular Statistics**

The reason for using circular statistics is the circular nature of variables such as phase, measured from 0° to 360°. Consider that if one were to average the values of 10° and 350°, the desired result is 0°, but the arithmetic mean would be 180°. The use of circular statistics prevents this problem by using vector addition to calculate the mean and standard deviation, following Batschelet (1981). First, take the sine and cosine of each individual measure. Then compute the mean cosine value \(x\) and the mean sine value \(y\). As long as \(x\) and \(y\) are not zero, the mean phase \(\phi\) is

\[
\phi = \tan^{-1}(y/x), \text{ if } x > 0
\]  
\[
\phi = 180 + \tan^{-1}(y/x), \text{ if } x < 0
\]  

(see Batschelet, 1981, for some exceptions). The length of the mean vector \(r\) provides an estimate of the spread of the data because it reflects the directional concentration of the individual measures:

\[
r = \sqrt{x^2 + y^2} \approx 0.5.
\]  

The standard deviation is given (in radians) by

\[
s = [2(1 - r)]^{0.5}.
\]  

Received August 3, 1993

Revision received June 14, 1994

Accepted May 17, 1995