Direction dependent control of balance during walking and standing

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Abstract

Human walking has previously been described as “controlled falling.” Some computational models, however, suggest that gait may also have self-stabilizing aspects requiring little central nervous system control. The fore-aft component of walking may even be passively stable from step to step, whereas lateral motion may be unstable and require motor control for balance, as through active foot placement. If this is the case, walking humans might rely less on integrative sensory feedback, such as vision, for anterio-posterior (AP) balance than medio-lateral (ML). We tested whether healthy humans (N = 10) exhibit such direction-dependent control, by applying low-frequency perturbations to the visual field (a projected virtual hallway) and measuring foot placement during treadmill walking. We found step variability to be nearly ten times more sensitive to ML perturbations than AP, as quantified by the increase in root-mean-square step variability per unit change in perturbation amplitude. This is not simply due to poorer physiological sensitivity of vision in the AP direction: Similar perturbations applied to quiet standing produced reversed direction dependence, with an AP sensitivity 2.3 times greater than ML. Tandem (heel-to-toe) standing yielded ML sensitivity 3.0 times greater than AP, suggesting that the base of support influences the stability of standing. Postural balance nevertheless appears to require continuous, integrative motor control for balance in all directions. In contrast, walking balance requires step-by-step, integrative control for balance, but mainly in the lateral direction. In the fore-aft direction, balance may be maintained through an “uncontrolled,” yet passively stabilized, series of falls.
Introduction

The central nervous system (CNS) uses integrative sensory feedback to control balance and compensate for instabilities. The upright human body, for example, is unstable and its balance is continuously stabilized through the integration of visual, vestibular, proprioceptive, and other sensory inputs. Other tasks may use sensory information in a discrete rather than continuous manner. In particular, walking has periodic dynamics, where the discrete step-by-step stability may be quite different from posture. This may therefore dictate differences in active control, as well as how sensory information is integrated and used for step-by-step stabilization. An implication of these differences is that clinical tests of standing balance may not capture some aspects of gait stability. Here we present an experimental study of the role of vision in the control of balance during walking, contrasted with its role in upright standing. We propose that the dynamics of walking may provide a degree of passive, step-by-step stability that is not present in standing.

The inverted pendulum dynamics of the upright body make posture unstable if not for CNS control. The CNS actively balances the head, trunk, and legs on the ground with corrective torques based on sensory feedback (Horak and Macpherson 1996; Johansson and Magnusson 1991). This control relies on both local spinal reflexes (Allum 1983; Carpenter et al. 1999) and higher level integration of visual, vestibular, and other inputs (e.g., Nashner et al. 1982). Reduction of sensory information typically degrades posture control, and the combined loss of both visual and vestibular inputs makes posture considerably less stable despite the remaining presence of proprioceptive inputs (Black et al. 1983). Integrative feedback control is demonstrated even more directly by active body sway, which can be induced simply from experimental perturbations of the sensory inputs. For example, vision can be driven by an artificial visual field (e.g., Keshner and Kenyon 2000; Mahboobin et al. 2005; Peterka 2002), and vestibular inputs can be manipulated by galvanic stimulation (e.g., Fitzpatrick et al. 1994; Inglis et al. 1995). The instability induced by multisensory loss demonstrates the necessity of integrative feedback, and the sensitivity of posture to driven inputs quantifies the contributions of sensory inputs to that integration.
Walking also requires CNS control, but in different ways. As in posture, the upright head and trunk are
continuously balanced through integrative feedback (Keshner et al. 1988), demonstrated for example by
their real-time sensitivity to sinusoidal visual perturbations (Keshner and Kenyon 2000; Warren et al.
1996). But unlike posture, walking also cyclically places the body center of mass beyond the base of
support, interpreted by some as “controlled falling” (Perry 1992). Continuous-time stability therefore
appears not to be strictly required for the body as a whole, as long as the periodic gait is stable. Stability
usually requires CNS control, but it is possible that some degree of step-to-step stability may be afforded
through passive dynamics. Passive dynamic walking machines, for example, can walk stably with no
feedback control whatsoever (McGeer, 1990). The difference between continuous and step-to-step
stability is demonstrated by a passive dynamic walking toy that is unable to stand up, but can walk stably
down a ramp (Coleman and Ruina 1998). In a three-dimensional computational model of dynamic
walking (Kuo, 1999), we found fore-aft motion to exhibit passive dynamic stability, and the lateral
motion a high degree of instability. The lateral instability is easily controlled through active adjustment of
lateral foot placement with each step, driven by sensory feedback. But no feedback is necessary for the
model’s step-to-step stability in the fore-aft direction.

If such stability applies to human walking, only the lateral component of active, step-to-step control
would be expected to require higher-level integrative feedback. This feedback would provide sensing of
body orientation and motion similar to that used for continuous-time control of posture. But there would
be little need for integrative feedback for the fore-aft motion, because lower-level propriospinal feedback
may be sufficient for the legs to support body weight and behave like pendulums. Indirect evidence for
direction-dependent stability is given by previous observations that human subjects walk with greater
lateral than fore-aft step variability (Bauby and Kuo 2000). Moreover, removal of visual feedback results
in a much larger increase in the lateral variability. If step-to-step stability is indeed different from postural
stability, the difference might help explain why clinical tests of posture do not always predict gait ability.
(Shimada et al. 2003; Visser et al. 2008). The contribution of vision to step-by-step walking stability has yet to be quantified, but could be assessed by perturbing the visual field along multiple directions, as has been demonstrated in posture (Streepey et al. 2007).

The purpose of the present study was to evaluate the sensitivity of step-to-step foot placement to perturbations of the visual field. We hypothesized that walking is dynamically unstable in the medio-lateral (ML) direction and therefore actively stabilized through integrative feedback control of foot placement. In contrast, walking might be passively stable in the anterior-posterior (AP) direction, so that little control is needed for anterior-posterior (AP) foot placement. Here we use “passive” to refer to the dynamics of limbs whose behavior may be regulated by propriospinal control, but with little integrative control directly influencing foot placement. We expected that ML foot placement would be highly sensitive to ML perturbations to the visual field, but that AP foot placement would be relatively insensitive to AP perturbations. To control for the possibility that observed sensitivities are simply due to direction-dependencies in visual processing rather than the task dynamics, we also compared walking to an analogous set of continuous balance tasks. During standing, we expected the degree of instability, and hence sensitivity to visual perturbations, to depend on the base of support and therefore the type of stance. For both step-to-step balance during walking and continuous balance during standing, we hypothesized that the visual contribution to active control increases with the degree of passive instability.

**Materials and Methods**

We measured the effect of visual perturbations on COP variability, as an indicator of the degree of integrative control during both walking and standing (Figure 1). For walking, COP variability quantified contributions of discrete, step-to-step foot placement to active control (Bauby and Kuo 2000). For standing, it quantified the continuous application of balancing torque against the ground. Given ideal sensors and no disturbances, both walking and standing would be expected to exhibit no variability. But more realistically, internal and external perturbations and imperfect sensors could contribute to variability.
of discrete (foot placement) COP during walking, and continuous COP during standing. We induced
visual sensory perturbations with a virtual reality environment, and quantified both types of variability
with the root-mean-square (RMS) variability in the ML and AP directions. During walking, these
correspond to RMS variability in step width and step length, respectively. Variabilities were recorded as a
function of visual field perturbations, yielding direction-dependent sensitivity measures. We applied
oscillatory perturbations to the visual field during walking and two types of standing, with the feet placed
side-by-side (“normal”) or heel-to-toe (“tandem”). Sensitivities to perturbations were quantified as the
change in RMS variability per unit change in perturbation amplitude.

From our computational models of walking, we expected greater instability in the lateral direction. This
would be manifested as a high sensitivity of ML variability to ML perturbations, referred to as “ML/ML
sensitivity,” and a lower AP/AP sensitivity (Figure 1, right column). In contrast, we expected standing to
be generally unstable, perhaps with the degree of instability depending on direction. Empirical
observations suggest that normal stance is more unstable in the AP direction (Marigold and Eng 2006;
Paulus et al. 1984), and tandem stance in the ML direction (Hong et al. 2007), perhaps due to differences
in the base of support (Day et al. 1993; Henry et al. 2001; Horak et al. 2005). This leads to expectations of
greater AP/AP sensitivity during normal stance, and greater ML/ML sensitivity during tandem stance.

**Experiment**

Volunteer human subjects performed walking or standing with visual field perturbations applied through
a virtual reality display (see Figure 2). Ten subjects (6 male, 4 female, aged 24.3 ± 4.1 years; body mass
73.1 ± 15.4 kg; leg length 0.92±0.08 m; mean ± s.d.) provided informed consent and participated in this
study. All were healthy adults with no known visual conditions or impairments affecting daily walking
function; including dizziness, vestibular conditions, somatosensory loss, or neurological disorders. Both
walking and standing were performed on a split-belt instrumented treadmill (Collins et al. 2009) used to
record COP during each trial. The visual field consisted of a virtual dark hallway tiled with randomly
placed white rectangles (Warren et al. 1996). This field moved at the walking speed (AP direction) for walking trials, and zero speed for standing trials, and perturbations were superimposed on this nominal motion, with the intent of giving subjects a sensation of self-motion. The virtual reality display used a single video projector producing an image on a wide-view screen. The screen was 3 m high and 3 m wide, curved into a roughly semi-circular shape to provide about 180° horizontal and 145° vertical viewing angles, with subjects placed about 0.75 m away from the front of the screen. The image was rear-projected, with geometry distorted to compensate for screen curvature. We did not apply head tracking compensation, but to increase sense of immersion, subjects wore eyewear designed to block the field of view below the screen, including their feet and the stationary ground surrounding the treadmill.

Subjects were presented with oscillatory perturbations of the visual field in the form of translational sinusoids at 0.25 Hz in the horizontal plane. This low frequency was selected based on reports that perturbation frequencies between 0.20-0.25 Hz significantly affect balance while avoiding visual discomfort (Jeka et al. 2006; Sparto et al. 2006; Warren et al. 1996) and that vision is most sensitive below 1Hz (Yoneda and Tokumasu 1986). Perturbations with lateral component were applied with a small additional rotation to keep the vanishing point at the end of the virtual hallway. This was to ensure that the forward direction was always directed toward the center of the end of the hallway, so that any perceived self-motion induced only a balance correction but not a heading correction. Subjects were instructed to look forward and use the visual information as naturally as possible as they walked toward the end of the hallway.

During the walking conditions, subjects walked at a constant speed of 1.25 m/s on the treadmill while viewing a virtual hallway, where the walls moved past them at the same speed as the treadmill belt. Prior to the study, subjects were given a 5 minute training trial to acclimate themselves to the virtual environment. They were then exposed to continuous perturbations of the visual flow in two sets of walking trials, the first set testing the effect of perturbation amplitude on step variability, and the second
testing the effect of perturbation direction. In the first set, subjects were exposed to sinusoidal
perturbations superimposed on the visual flow at amplitudes of 0 (control condition), 0.05, 0.15, 0.25, and
0.35 m in both the M-L and A-P directions. The second set tested applied perturbations in directions
uniformly distributed at 0, 30, 60, 90, 120, and 150 degrees relative to M-L direction, all at the single
amplitude of 0.25 m. All walking trials were 5 minutes long and presented in random order, with a short
break given after every third trial.

We also performed an additional set of trials to test for interaction of hallway speed and perturbation
direction. These were performed on only five of the subjects, who performed a subset of the preceding
tests under identical conditions except with the virtual hallway kept stationary (“No Flow” condition) as
in standing trials. Thus the perturbations were superimposed on a static view of the hallway. The
conditions included the 0 m (control) and 0.25 m perturbation amplitude conditions, both repeated in the
ML and AP directions. This set of tests was used to determine whether the visual flow of the moving
hallway interferes with self-motion perception during walking.

During the normal standing conditions, subjects stood on the treadmill with feet placed at shoulder width
while viewing a stationary hallway. For the tandem standing conditions, subjects stood on the treadmill
with one (self-selected) foot in front of the other in a heel to toe configuration, with that configuration
maintained for all such trials. For all standing trials, subjects were additionally instructed to maintain an
even weight distribution between the legs. The standing trials consisted only of two amplitudes and two
directions. Sinusoidal perturbations in either the M-L or A-P direction were applied at amplitudes of 0
and 0.05 m in randomized trials that lasted 2 minutes.

We recorded instantaneous COP from continuous ground reaction force and moment signals for all trials.
Ground reaction forces and moments were measured from force plates mounted underneath each
treadmill belt. The forces and moments were sampled at 1200 Hz and low pass filtered with a 25 Hz cut-off frequency using a fourth order, zero-phase-shift Butterworth filter.

**Analysis**

Variability for walking and standing was quantified using COP as follows. In the walking trials, we measured RMS variability in step length and step width recorded from the instantaneous COP, which was estimated at mid-step over at least 350 steps. Mid-step was determined as the time point during a step when the vertical ground reaction force was at a minimum and below body weight. Step length was defined as the AP distance between the centers of pressure at mid-step of two consecutive steps plus the distance of treadmill travel during the step. The distance of travel was calculated as the product of treadmill belt speed and the time between consecutive mid-step events. Step width was defined as the lateral distance between the consecutive centers of pressure. The step length and width measurements for left-right and right-left steps were then individually high-pass filtered at a cutoff of 15 steps before calculating RMS measures for all steps. The filter was used to remove low frequency components of step placement associated with slow changes in walking speed and heading. All length measurements were also normalized by the subject’s leg length before computing statistics and group averages. Center of pressure estimates of foot placement during treadmill walking (Donelan et al. 2004) are less precise than kinematic measures (Bauby and Kuo 2000), especially for step length variability, because the foot remains relatively stationary with respect to the ground during the support phase while the COP progresses forward from the heel to the toe. Imprecision in mid-step event timing then adds to AP COP variability. We therefore concentrated not on absolute variability in step length and width, but in the sensitivity of variability to perturbation amplitude across trials. Average step length and step width were also calculated to determine whether adding visual noise affects systematic control of foot placement. These checks ensure that the overall variability measured from foot placement is a result of the applied visual noise and not a change in control strategy. For the standing trials, the effect of the visual perturbations was assessed directly by measuring RMS COP displacement in both the M-L and A-P
directions over a two minute interval. Before computing RMS measures, the COP data was first high-pass
filtered at a cutoff frequency of 0.1 Hz (Carpenter et al. 2001) to examine COP motion occurring near the
same frequency as the perturbations, and to remove low frequency shifts in posture and weight-bearing
that have less to do with balance stabilization (Zatsiorsky and Duarte 1999).

We defined sensitivity metrics to quantify perturbation amplitude dependent changes in walking and
standing variability. These were defined as the change in COP variability per unit change in perturbation
amplitude (i.e. slope of variability vs amplitude) and labeled as follows: The ML/ML sensitivity for the
walking trials corresponds to the slope of step width variability vs. ML perturbation amplitude. Similarly,
AP/ML sensitivity for the standing trials corresponds to the slope of AP RMS COP displacement vs. ML
perturbation amplitude. These sensitivities quantify how COP variability changes as a function of
perturbation amplitude during both walking and standing, and may be interpreted as follows. If a
perturbation increase induces the same amplitude increase in COP variability, the subject may sense the
visual field movement entirely as self-motion, yielding a sensitivity value of one. The CNS would be
expected to use a great deal of other information for self-motion feedback, and so sensitivities are
generally expected to be much smaller than one.

We summarized changes in step width and step length variability with perturbation direction using
ellipses fitted to the data. Each ellipse was determined through a least squares circular regression of the
RMS variability across subjects, as a function of perturbation direction. Direction dependence was
characterized by the elliptical eccentricity, defined as the ratio of the distance between the foci to the
length of the major axis. (A circle has zero eccentricity, and a line segment has unit eccentricity).

We tested our hypotheses with the following statistical tests. To determine effects on average step length
and width, we performed repeated measures analysis of variance (ANOVA) with perturbation amplitude
and direction as factors. To determine effects on step variabilities, we performed repeated measures
analysis of covariance (ANCOVA), with perturbation amplitude as one factor and direction as the other. This test yielded estimates of perturbation sensitivities, which were used to indicate whether visual information about side-to-side movement is more heavily weighted than that of fore-aft movement for controlling step-to-step balance during walking. For the standing conditions, we again used repeated measures ANCOVA to test whether AP/AP sensitivity was significantly greater than ML/ML sensitivity. Also calculated were ML/AP and AP/ML sensitivities for both walking and standing. Finally, we tested whether the directional eccentricity of the elliptical fits was significant for both step length and width variability, using a paired t-test. All statistical tests were performed with a maximum Type I error rate of 0.05.

Results
Perturbations of the visual scene induced increases in variability during both walking and standing. The sensitivity to perturbation amplitude depended upon both the task (walking vs. standing) and the direction of perturbation (ML vs. AP). For all tasks, subjects showed greatest sensitivity in the direction of predicted instability: ML/ML sensitivity was greatest for walking and tandem standing and AP/AP sensitivity was greatest for normal standing. Details of these results and additional within-task comparisons are reported below, beginning with results for control conditions to facilitate comparisons.

During the walking control condition, subjects walked at 1.25 m/s with an average step length 0.683 m (± 0.033 SD, standard deviation) and step width of 0.159 m (± 0.041 SD). Step length (or AP) variability was 0.019 m (± 0.008 SD) and step width (or ML) variability was 0.025 m (± 0.007 SD), both expressed as root-mean-square (RMS) deviations of discrete, step-to-step COP. Step width variability was 31% greater than step length variability ($P = 0.024$, paired t-test). During the normal standing condition, AP variability was 0.0025 m (± 0.0009 SD) and ML variability was 0.0011 m (± 0.0004 SD), both expressed as RMS deviations of continuous COP. AP variability was 2.3 times greater than ML variability ($P = 8.7e-5$) in this case. During the tandem standing condition, subjects exhibited AP variability of 0.0050 m
(± 0.0034 SD) and ML variability of 0.0043 m (± 0.0014 SD). Compared to normal standing, AP variability was 2.0 times greater ($P = 0.060$) and ML variability was 3.9 times greater ($P = 6.6e-5$) during tandem standing.

Visual perturbations had little effect on mean step parameters. Mean step length varied by at most 1.2% across perturbation directions ($P = 0.0014$, repeated measures ANOVA) and 2.6% across perturbation amplitudes ($P = 0.010$). Mean step width varied by insignificant amounts, 0.8% across direction ($P = 0.63$) and 7.4% across amplitude ($P = 0.51$). There was no evidence of significant amplitude-direction interaction ($P = 0.057$).

Visual perturbations had much greater effect on step variabilities, which varied approximately linearly with perturbation amplitude depending on perturbation direction (Figure 3). For example, the slope of ML variability due to ML perturbations (i.e., the ML/ML sensitivity) was 0.123 (± 0.075 SD), with a significant amplitude dependence ($P = 5.7e-4$), with $R^2 = 0.81$. Not only did ML perturbations affect step width variability, but they also caused an increase in step length variability, with AP/ML sensitivity of 0.017 (± 0.014 SD, $P = 0.0047$) with $R^2 = 0.82$. In contrast, AP perturbations had little effect at all; the sensitivities were much smaller—no greater than 0.013—and not significantly different from zero ($P = 0.34$ for ML/AP sensitivity, $P = 0.12$ for AP/AP sensitivity).

Variability during both types of standing also increased with perturbation amplitude (Figure 4), depending on the direction of perturbation. In normal standing, AP COP variability increased with both perturbation directions: AP/AP sensitivity was 0.040 (± 0.031 SD, $P = 0.0044$) with $R^2 = 0.83$, and the AP/ML sensitivity was a small but significant 0.024 (± 0.013 SD, $P = 0.0005$) with $R^2 = 0.94$. In contrast, ML variability was relatively insensitive; the ML/ML sensitivity ($P = 0.20$) and ML/AP sensitivity ($P = 0.30$) were not significantly different from zero. During tandem standing, the ML/ML sensitivity was
0.032 (± 0.014 SD, $P = 4.2e-5$), with $R^2 = 0.95$. The other sensitivities were not significantly different from zero (AP/ML sensitivity, $P = 0.87$; AP/AP sensitivity $P = 0.26$; ML/AP, $P = 0.20$).

Perturbation sensitivities followed the trends predicted by task dynamics (Figure 5). During walking, the ML/ML sensitivity was about 9.4 times greater than the AP/AP sensitivity ($P = 0.0005$, repeated measures ANCOVA). But variabilities during normal standing exhibited an opposite trend, with an AP/AP sensitivity about 2.3 times greater than ML/ML sensitivity ($P = 0.039$, repeated measures ANCOVA). During tandem standing, the main sensitivity was ML/ML, which was 3.0 times greater than the AP/AP sensitivity ($p = 0.0051$). Even though variability was measured in different ways for walking and standing (continuous COP vs. discrete steps), the sensitivities to visual perturbations were of roughly the same order of magnitude. The most important comparison is therefore between sensitivities for each task, showing walking to be relatively far more sensitive in the ML direction than AP, and standing to have the converse effect, to a somewhat lesser degree.

Step variabilities also varied with perturbation direction intermediate to AP and ML (Figure 6). Perturbations in 30° increments resulted in variabilities that changed relatively smoothly between the two extremes. These increments also demonstrate how ML perturbations affected both step width and length variabilities, through the eccentricity of ellipses fitted to polar plots of variability as a function of perturbation direction. For step width variability, the ellipse demonstrated significantly greater variability in the ML direction ($P = 1.1 e-10$), corresponding to an eccentricity of 0.78. For step length variability, the eccentricity of the ellipse was 0.17 and not significantly different from that of a circle ($P = 0.64$).

The effect of visual perturbations on walking was similar even with the nominally stationary visual field (see Figure 5, No Flow condition). In fact, the visual field condition had no significant effect on the primary sensitivities (normal flow vs. no flow: ML/ML $P = 0.18$; AP/AP $P = 0.50$). More importantly,
ML/ML sensitivity was significantly greater than AP/AP sensitivity (by a factor of 3.58, \( P = 0.0079 \)), even when the average speed of the visual field was zero relative to the subject.

**Discussion**

This study was designed to determine whether human walking has passive dynamic stability in the AP direction, but not in the ML direction. We had hypothesized that ML instability would require integrative control of foot placement in that direction. We applied visual field perturbations in a variety of directions and amplitudes, and measured their effect on foot placement variability. For comparison, we also tested the effect of visual perturbations on normal and tandem standing, hypothesizing that the base of support would determine directions of greatest instability. Our results revealed an amplitude and direction dependence of visual perturbations on step length and width variability during walking. During standing, COP variability was also sensitive to visual perturbations. The direction dependencies were consistent with our hypotheses: low sensitivity of step length to AP perturbations, high sensitivity of step width to ML perturbations, high sensitivity of the AP component of normal standing, and high sensitivity in the ML direction during tandem standing. These findings have a number of implications for the control of walking and standing, and the role of integrative feedback in motor control in general.

Our results suggest that integrative visual feedback is used more for controlling lateral than fore-aft balance during walking. Direction-dependent sensitivity was predicted from the unstable lateral balance of dynamic walking models, which require active feedback only in the lateral direction (Kuo 1999). The observed high sensitivity of ML foot placement to ML visual perturbations suggests that vision is used to drive lateral foot placement. In contrast, there was no significant sensitivity of foot placement to AP perturbations, indicating little use of vision in that direction for balance. In dynamic walking models and machines, passive stability is afforded by the pendulum-like motion of the legs and the step-to-step transition, in which the heelstrike collisions dissipate more or less energy when perturbations respectively add or subtract energy (Kuo 2002; Wisse et al. 2005). This results in a motion that is stable over discrete
steps (also referred to as “limit cycle” stability), despite having inverted pendulum instability in continuous time. Interestingly, we found ML perturbations to also affect step length variability, as indicated by significant AP/ML sensitivity. This may be due to dynamical coupling between step width and step length, as observed in our computational models (Bauby and Kuo 2000). Passive dynamics may afford walking a degree of limit cycle stability in the AP direction without need for integrative control. But stability in the ML direction appears to depend on the integration of sensory feedback regarding ML motion of the body, for adjusting lateral foot placement.

We also observed direction dependence in the continuous-time control of standing. The higher sensitivity to AP than ML visual perturbations suggests that AP balance may be actively and integratively controlled to a greater extent than ML balance. This direction dependence may be due to the configuration of the lower extremity, which in the sagittal plane resembles a multi-segment inverted pendulum. But in the frontal plane (ML direction) the two legs, pelvis, and ground form a four-bar linkage, which might be passively less unstable than an inverted pendulum. This may explain why subjects were quite insensitive to ML visual perturbations during normal standing. Others have also observed that increased stance width allows subjects to respond with smaller active postural responses, when perturbed either physically (Henry et al. 2001) or visually (Day et al. 1993; Hong et al. 2007) in the ML direction. The configuration is quite different in tandem standing, where the base of support is much reduced in the ML direction. Subjects weighted vision differently in that condition, consistent with how stability is expected to vary with configuration.

A potential concern regarding these results is that direction-dependent visual sensitivity might be an artifact of physiological limitations in visual processing. The low AP/AP sensitivity during walking might then be explained by poor ability to detect motion in that direction. This however appears unlikely, because subjects exhibited high AP/AP sensitivity during standing. Another concern is that the AP flow of the visual field during walking might reduce visual sensitivity to perturbations in the AP direction.
compared to standing. But this appears not to be the case, because walking sensitivity was similar even when perturbations were added to a stationary hallway (see Figure 5, No Flow condition), even though the visual field was identical to that of standing. Other evidence suggests that the CNS can indeed sense perturbations to a moving visual field, because AP visual motion is still sensed and used for continuous-time stabilization of the head and trunk during walking (Keshner and Kenyon 2000), and bulk flow has little effect on this control (Warren 1996). Another possible issue is that visual perturbations in AP and ML directions might simply be fundamentally different. Whether or not this is the case, self-motion perception will generally depend on visual field motion in multiple directions. Our data revealed continuously-varying responses as a function of perturbation direction (Figure 6), suggesting that the CNS can integrate multi-directional information even if AP and ML directions are sensed differently. It appears that the CNS does detect and respond to AP visual information during walking, but uses it selectively for continuous-time postural stabilization and very little for step-to-step, limit-cycle stabilization.

Our findings are subject to several limitations. The visual perturbations only produced an imperfect illusion of self-motion, due to the limited resolution and fidelity of the computer projected display, such as lack of stereoscopic head tracking in the virtual reality system. These limitations may have reduced the ability to detect significant sensitivities. Perturbations were also restricted to relatively low frequencies, where vestibular organs have low sensitivity, to avoid large conflicts between visual and vestibular input. Higher perturbation frequencies (and perhaps amplitudes) may induce greater conflict, which might produce different effects, as has been observed with sensory perturbations to posture (Peterka 2002). We did not test low or high enough amplitudes to detect such effects. In our tests, the sensation of self-motion could be considered relatively strong, because all subjects were generally sensitive to perturbations, and none were excluded from the analysis, as is necessary in some other studies (Warren et al. 1996). Our estimates of COP during treadmill walking were also of limited precision in the AP direction, due to imperfect estimation of AP COP from a moving treadmill belt (Donelan et al. 2004). This may have
introduced a constant offset in estimates of AP step variability, but this would have little effect on
sensitivity measures, which were based on the slope of that variability. Finally, our measures of
perturbation sensitivity were based on aggregate step variability rather than a correlation between
individual perturbations and succeeding steps. We consider aggregate sensitivity to perturbations to
provide better evidence of active control than previous studies using removal of vision (Bauby and Kuo
2000). It would however be more direct to detect active foot placement control on a step-by-step basis.

A general theme of this study is that sensory feedback should be weighted based on stability
requirements. Inherently unstable motor tasks require active feedback control for stability. Tasks or task
directions with the greatest instability require more feedback, while others may require little feedback.
Moreover, such feedback requirements should not be specific to vision. For example, proprioceptive
perturbations have been applied using vibration of lower limb muscles, resulting in large effects on
standing posture in the AP direction but small effects on walking (Courtine et al. 2007), consistent with
the hypothesized direction of passive stability. Another example is aging, which has been associated with
greater increases in ML than AP step variability (Dean et al. 2007; Owings and Grabiner 2004a; b). This
may be due to age-related deficits affecting not just vision but also a variety of other modalities. Another
approach to the same theme is to perturb stability rather than sensory input. Accordingly, we have
previously applied external lateral stabilizers to artificially improve lateral stability of human subjects,
with the result of reduced ML step variability (Donelan et al. 2004).

Another theme is that discrete, step-to-step stability may be quite different from continuous-time stability.
Our three-dimensional model of walking is unstable in the ML direction but stable in the AP direction
(Kuo 1999). That same model, placed in the normal standing posture, is stable in the ML direction but
unstable in the AP direction. It is, in fact, typical for dynamic walking robots to be designed solely for
step-by-step, limit cycle stability, with little or no regard for standing stability (Coleman and Ruina 1998;
Collins et al. 2005). Standing posture is characterized by continuous feedback control, much of it
homonymous. For example, perturbations to the ankle trigger to feedback torques at the ankle (Park et al. 2004). There are also significant heteronymous contributions, but even these may be attributed directly to keeping the body upright. In contrast, step-by-step control of walking appears much more indirect and heteronymous. The hip torque that adjusts lateral foot placement is apparently triggered not by hip proprioceptors but by integrative information from the preceding step. The effect of that adjustment is to change body orientation, not directly but through the dynamics of the subsequent step-to-step transition.

Our findings may also have implications for the neural control of walking. Multiple levels of hierarchical feedback contribute to control, and are coupled through shared muscle groups, body dynamics, and interaction with environment. Neuronal circuits within the spinal cord produce a variety of short-latency reflexes and behaviors driven by proprioceptive and other local sensory feedback. These circuits are sufficient to produce walking in spinalized cats (Grillner and Wallen 1985), by supporting body weight and producing the basic stepping pattern. It is unclear whether humans have a similar degree of spinal control, but our results are consistent with other indirect observations that suggest this possibility (Duysens and Van de Crommert 1998; MacKay-Lyons 2002). Dynamic walking models indicate that pendulum dynamics can account for much (if not all) of the stepping pattern, and interaction with step-to-step transitions can passively produce AP adjustment of foot placement with no need for active control. Humans may use spinal reflexes to produce low-level behaviors similar to the passive dynamics of models, making little use of integrative (e.g., visual and vestibular) feedback simply because it is not necessary. Higher level feedback may, however, be necessary for lateral stability. Even though spinalized cats can walk, they also tend to have poor lateral stability (e.g., Belanger et al. 1996; Brustein and Rossignol 1998), evidently lacking active, step-to-step foot placement control. These components rely more heavily on visual, vestibular, and other feedback, integrated at the level of the brain stem and cerebellum. Hierarchical organization would allow spinal control to regulate most of the fore-aft walking motion, and higher levels of the CNS to integrate multisensory feedback for balance.
We have thus far assumed that vision is used integratively for walking balance, as it is for posture. An alternative possibility is that CNS performs directional weighting of vision separate from other inputs. Extrastriate areas, particularly the V5-MT region, are responsive to patterns of movement across many directions and are organized into columns that are sensitive to specific directions of motion (Kandel and Wurtz 2000 Ch. 27). The anatomical arrangement of the MT and MST regions of the visual cortex, in direction-specific columns, provides a convenient means to weight particular directions of sensed motion. It is conceivable that task- and direction-dependent weighting is performed through selection and gating of these columns, perhaps contributing to cortical control of foot placement. Our preferred hypothesis, however, is that lateral foot placement control is a more automatic (and less cortical) response, sharing similar sensory integration circuitry to posture. Visual information might then contribute continuously to sensory integration in the brain stem and cerebellum (which also receive input from V5-MT). This could yield a single, model-based estimate of body state used to drive continuous-time posture control during standing and walking (e.g., Kuo 2005; Maurer et al. 2006), and also sampled step-to-step for driving discrete foot placement. This estimate might then be selectively weighted more for ML than AP control, without necessarily adjusting visual weighting at the cortical level. Although the present experiment uses vision for perturbations, a more general hypothesis is that multiple other sensors also contribute to state estimation and balance control, similarly weighted as a function of task dynamics. Just as we have assumed that the passive dynamics of our computational model can be realized by local reflexes in the human, these are mere working hypotheses that remain to be tested experimentally.

A potential application of this work is a new means to quantify balance during walking. Quantitative clinical assessments of posture such as computerized dynamic posturography (NeuroCom International, Clackamas, OR) typically apply sagittal plane perturbations, either by translating the body directly or by perturbing visual or somatosensory inputs during quiet standing. Although some tests appear related to fall risk, many do not assess non-sagittal motions, which are also considered clinically relevant to balance during walking (e.g., Marchetti and Whitney 2006; Schrager et al. 2008), and also predict fall risk well
(Maki et al. 1994; Piirtola and Era 2006). Lateral COP variability during tandem stance and lateral step
variability during walking may be useful indicators of balance, and lateral perturbations to vision appear
to reveal how visual information is integrated for this control. The influence of other inputs might be
emphasized by artificially removing normal visual cues, akin to the “visual sway-referencing” used in
dynamic posturography (Nashner et al. 1982). Virtual reality environments have previously proven useful
for assessment of posture control (Keshner and Kenyon 2000; Streepey et al. 2007). They could
potentially also be used to selectively render ML or other visual cues inaccurate, and perhaps reveal poor
integration of vestibular and other sensory information. Such perturbations or sway-referencing could
then be applied to both walking and tandem stance, to provide data complementary to normal dynamic
posturography.

Walking and tandem balance both appear to have inherent instabilities in the lateral direction. We have
shown that visual perturbations induce substantial lateral variability in discrete foot placement during
walking, and continuous COP variability during standing. These two measures serve as indicators of
active balance control, and their sensitivity to perturbations quantifies the degree to which an input such
as vision contributes to that control. In contrast to lateral balance, the fore-aft component of walking has
little dependence on vision. The dynamics of the legs may afford passive, step-by-step stability to this
component, so that the central nervous system has little need to control it with integrative feedback. The
importance of dynamics is further highlighted by the visual dependence of standing, which can be
reversed by changing the configuration of the legs and thereby the base of support. The CNS can
selectively and flexibly weight sensory information for feedback control, both for continuous-time control
of balance and step-by-step control of walking. It may also harness the self-stabilizing aspects of dynamic
walking, where a series of uncontrolled falls can nonetheless be stable on a step-by-step basis.
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Disclosures

The authors have no conflicts of interest to disclose.
References


Figure 1. Predictions of sensitivity to visual perturbations, for walking, normal standing, and tandem standing. Previous computational models (Kuo 1999) predict that walking may have passive dynamic stability in the AP direction but instability in the medio-lateral (ML) direction that is controlled with active foot placement. An indicator of active control is step variability, measured through the center of pressure (COP) under each foot. Models predict high sensitivity of ML (step width) variability to ML visual perturbations (“ML/ML sensitivity”). Ellipses denote covariance of step variability, computed from root-mean-square step deviations. The stability of standing is expected to depend on the base of support, with greater instability in the AP direction for normal standing, and the ML direction for tandem (heel-to-toe) standing. Variability of continuous COP, as opposed to step-to-step COP in walking, quantifies posture control. High AP/AP sensitivity to visual perturbations is expected during normal standing, and high ML/ML sensitivity during tandem standing.

Figure 2. Experimental set-up. Subjects walked or stood on an instrumented treadmill displaying a virtual hallway moving at the same speed as the treadmill belt. Visual perturbations were superimposed on the hallway motion, and their effect was measured using center-of-pressure variability. Virtual reality display uses a single projector and curved rear projection screen to provide wide viewing angle and immersive feeling of moving within a tiled hallway. Split belt treadmill recorded the instantaneous center of pressure (dashed line).

Figure 3. Variability of walking as a function of AP and ML visual perturbations. Step variability data (filled circles), defined as root-mean-square (RMS) deviations of step width and length, are plotted against perturbation amplitude. Data were fit well by a linear relationship (solid lines for linear regression fits); we defined perturbation sensitivity as the change in step variability per unit change in perturbation amplitude (i.e. slope of linear fit). Step width generally exhibited greater variability than step length. Only ML perturbations produced significant changes in step variability. Error bars denote standard deviation. Asterisks (*) denote significant sensitivity ($P < 0.05$).
Figure 4. Variability of normal and tandem standing as a function of AP and ML visual perturbations. Center of pressure (COP) variability data (filled circles), defined as root-mean-square (RMS) deviations in the AP and ML directions, are plotted against perturbation amplitude. Linear regression fits (solid lines) to data yield slopes quantifying sensitivity to perturbations. During normal standing (left), AP variability was generally greater than ML variability, and more sensitive to visual perturbations in both directions. During tandem standing, there was greater variability than normal standing, but only the ML/ML sensitivity was significant. Error bars denote standard deviation. Asterisks (*) denote significant sensitivity ($P < 0.05$).

Figure 5. Summary of mean perturbation sensitivities for walking, normal standing, and tandem standing. Two sensitivities are compared: ML/ML (i.e., sensitivity of ML variability to ML perturbations) and AP/AP (see Figures 3 and 4). During walking and tandem standing, ML/ML sensitivity was significantly greater than AP/AP sensitivity (asterisks denote $P < 0.05$). The sensitivities were reversed for normal standing. The differential sensitivity remained in effect during walking with a nominally stationary visual field (“No Flow”), indicating that the contrast with normal standing is not due to differences in visual field motion. Walking sensitivities are consistent with model predictions of passive dynamic stability from step to step, and standing results are consistent with static stability expected from the base of support.

Figure 6. Step width and length variability as a function of visual perturbation direction. Data points show mean and standard deviation of RMS variability for perturbations with amplitude 0.25m, along with ellipses fitted to these data (solid lines). Variabilities in the control conditions with no perturbations are shown for comparison (dashed circles). Step width variability was greatest for perturbations in the ML direction, whereas step length variability did not change significantly with perturbation direction.
Supplementary Table Legend

Supplementary Table 1. Summary statistics for control conditions and mean sensitivities for walking and standing conditions. Asterisk (*) denotes statistical significance ($P < 0.05$).
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Walking

ML Perturbations

AP Perturbations

Sensitivity = $\frac{\Delta y}{\Delta x}$
Sensitivity

Walking
Walking (No Flow)
Normal Standing
Tandem Standing
Step Width Variability

Step Length Variability

- Data (RMS)
- Ellipsoidal Fit
- Control