Published in final edited form as:

Exp Brain Res. 2014 June ; 232(6): 1941–1951. doi:10.1007/s00221-014-3885-1.

Visual control of trunk translation and orientation during locomotion

E. Anson,

Department of Kinesiology, University of Maryland, College Park, MD, USA

P. Agada,

Department of Kinesiology, University of Maryland, College Park, MD, USA

T. Kiemel,

Department of Kinesiology, University of Maryland, College Park, MD, USA

Y. Ivanenko,

Laboratory of Neuromotor Physiology, Santa Lucia Foundation, 00179 Rome, Italy

F. Lacquaniti, and

Laboratory of Neuromotor Physiology, Santa Lucia Foundation, 00179 Rome, Italy

Department of Systems Medicine, University of Rome Tor Vergata, 00133 Rome, Italy

J. Jeka

Department of Kinesiology, University of Maryland, College Park, MD, USA

Department of Kinesiology, Temple University, 1800 N Broad St, Philadelphia, PA 19122, USA

Abstract

Previous studies have suggested distinct control of gait characteristics in the anterior–posterior (AP) and medial–lateral (ML) directions in response to visual input. Responses were larger to a ML visual stimulus, suggesting that vision plays a larger role in stabilizing gait in the ML direction. Here, we investigated responses of the trunk during locomotion to determine whether a similar direction dependence is observed. We hypothesized that translation of the trunk would show a similar ML dependence on vision, but that angular deviations of the trunk would show equivalent responses in all directions. Subjects stood or walked on a treadmill at 5 km/h while viewing a virtual wall of white triangles that moved in either the AP or ML direction according to a broadband input stimulus. Frequency response functions between the visual scene motion and trunk kinematics revealed that trunk translation gain was larger across all frequencies during walking compared with standing. Trunk orientation responses were not different from standing at very low frequencies; however, at high frequencies, trunk orientation gain was much higher during walking. Larger gains in response to ML visual scene motion were found for all trunk movements. Higher gains in the ML direction while walking suggest that visual feedback may contribute more to the stability of trunk movements in the ML direction. Vision modified trunk movement behavior on both a slow (translation) and fast (orientation) time scale suggesting a priority for

minimizing angular deviations of the trunk. Overall, trunk responses to visual input were consistent with the theme that control of locomotion requires higher-level sensory input to maintain stability in the ML direction.

Keywords

Vision; Walking; Trunk control

Introduction

Vision has long been known to provide important information for humans to walk through and interact with their environment (Gibson 1958; Patla 1998). Previous evidence suggests that the visual system decomposes information into a forward motion signal used for navigation and a postural cue to stabilize upright equilibrium (Woolacott 1986).

Investigations have demonstrated that optic flow contributes to multiple aspects of human walking including modulation of gait parameters such as walking velocity and stride length (Varraine et al. 2002; Prokop et al. 1997; Konczak 1994; Lamontagne et al. 2007); foot placement variability (Patla and Vickers 2003; Reynolds and Day 2005; O'Connor and Kuo 2009; McAndrew et al. 2010); steering and obstacle avoidance (Warren et al. 2001; Marigold 2008; Bruggeman et al. 2007; Patla 1998); and postural stability (Warren et al. 1996; Bardy et al. 1999; Logan et al. 2010; McAndrew et al. 2010).

In the current study, we investigate the use of vision to stabilize trunk motion in different planes of movement. Previous studies have shown that kinematic responses to a visual stimulus are larger in magnitude in the medial–lateral (ML) direction than in the anterior–posterior (AP) direction (Bauby and Kuo 2000; Warren et al. 1996; O'Connor and Kuo 2009; McAndrew et al. 2010). Models of passive walkers without active control have been used to interpret such results (McGeer 1990). Kuo (1999) showed that a three-dimensional passive walker is stable in the AP direction but unstable in the ML direction. Stability means that small perturbations to the limit cycle are dissipated, insuring return to a cyclical gait pattern. Thus, differences in passive stability would predict larger responses to a limit cycle perturbation in the ML than the AP direction.

To translate this result from passive walkers to human walkers, Bauby and Kuo (2000) hypothesized that with somatosensory feedback mediated by the spinal cord, the multi-segment legs of humans behave like the single-segment legs of a passive walker. Somatosensory feedback provides AP stability, but high-level neural feedback provided by vision and the vestibular system is necessary for ML stability. As a consequence of noise due to high-level neural feedback, they predicted that lateral foot placement would show greater variability than fore–aft foot placement. They further predicted that removing vision would increase lateral variability more than fore–aft variability. Their experimental results supported these predictions. Human subjects walking over ground with eyes open displayed 79 % more variability in lateral step width than in the fore–aft step length and closing the eyes produced a greater increase in lateral variability than in fore–aft variability. In a related study, O'Connor and Kuo (2009) showed that subjects walking on a treadmill were 10 times

more sensitive to visual scene movement in the ML than AP direction (O'Connor and Kuo 2009). These modeling and experimental results suggest that vision plays a greater role in stabilizing the gait cycle in the ML direction than in the AP direction.

The studies cited above are based on gait parameters such as step width and length variability. To gain a better understanding of the locomotor control system, it is important to consider control of the trunk as well. Logan et al. (2010) recently emphasized that trunk motion in response to visual scene motion while walking can be decomposed into two simultaneously occurring components: absolute trunk position in space (translation) and trunk orientation with respect to vertical. Despite a strong mechanical coupling between trunk translation and orientation, the response to visual scene motion was different. They showed that gain relative to visual stimulation in the fore–aft direction was smaller for trunk orientation than trunk translation, which was interpreted as vision simultaneously contributing to different sub-tasks (upright stability vs. navigation) of walking. The larger gain for trunk translation reflected visual scene motion “pushing” the trunk (body) in space to a greater extent than causing the trunk to lean. Moreover, ML and AP visual scene motion has directional effects on ML and AP trunk translation variability during walking, with greater effects compared with control conditions (McAndrew et al. 2010). Their results suggest a directionally specific increase in trunk displacement variability in response to visual scene motion (i.e., ML variability increased more with ML visual scene motion). Such results suggest that vision may play a greater role in stabilizing trunk displacement in the ML direction than in the AP direction, similar to findings with foot placement (O'Connor and Kuo 2009). Most of the studies referenced above focused on low frequency visual scene motion corresponding low frequency (longer time scale) responses (McAndrew et al. 2010; O'Connor and Kuo 2009). It is unclear whether directionally specific behavior of trunk motion holds at higher frequencies that would require a much faster response.

However, control of trunk orientation during walking has not been studied extensively. Being the most massive segment of the body, the trunk must be balanced as the legs propel the body forward, and any deviation from vertical must be actively counteracted to resist gravitational forces that drive further deviation. This aspect of trunk control has no passively stable direction, meaning that all deviations from vertical must be actively controlled to maintain upright equilibrium. We hypothesized that such active control depends on high-level neural control provided by proprioceptive, visual, and vestibular feedback. Based on this hypothesis, we predicted that visual scene motion in both the AP and ML directions would have similar effects on trunk *orientation*, whereas trunk *translation* will be more strongly affected by visual scene motion in the ML direction.

Methods

Subjects

Fourteen healthy subjects voluntarily participated in this study, six males and eight females (mean age 22.1 ± 4.8 , range 18–36). All subjects were by self-report free from any neurological disorder, balance disorder, vertigo or recent musculoskeletal injury. This study was approved by the Institutional Review board at the University of Maryland. All subjects provided written informed consent prior to participation in this experiment.

Apparatus

Virtual reality environment

Subjects walked or stood on a treadmill (Cybex Trotter 900T, Cybex International, Inc., USA) approximately 12 inches in front of a 52" wide screen TV (Samsung LN52A550, Samsung, USA) while wearing goggles to limit vertical peripheral vision, as shown in Fig. 1. The resultant field of view was 124° horizontally and 94° vertically. The visual scene consisted of 401 randomly spaced and oriented white triangles measuring 1.2 cm (height) × 1.2 cm (base) on a black background. The virtual display was created using CAVELib software (Mech-dyne, USA), synched to a desktop computer (Dell WORK-STATION PWS650Dell, USA). Visual signals were created offline (MATLAB, the Mathworks, USA) and generated using Labview (National Instruments, USA) on a desktop computer (Optiplex GX620 Dell, USA).

Visual signals

The visual display consisted of translational oscillations of the virtual wall of triangles in the sagittal or frontal planes. A random number generator was used to create white noise signals with a mean of zero that corresponded to the position of the visual display in the static condition, see Fig. 2. Positive (negative) values corresponded to reduction (increase) in triangle size to indicate motion of the scene away from (toward) the subject in the sagittal plane and positive (negative) values corresponded to rightward (leftward) motion of the visual scene in the frontal plane. A different seed was used to initialize the random number generator for each trial for each subject. The white noise signals were filtered using a first-order low-pass Butterworth filter with a cutoff frequency of .02 hz, and an eighth-order low-pass Butterworth filter with a 5 hz cutoff frequency (Logan et al. 2010). This served to smooth the motion of the visual scene and limit motion frequencies to the low frequency range of postural sway. An external trigger synchronized display motion with the data acquisition computer. Across subjects and directions, the average root-mean-square error of the visual signal was .94 cm and 1.52 cm/s. Across subjects and directions, the average apparent translation of the visual scene was ± 2.6 cm with maximum values of ± 4.2 cm. The visual angle of the triangles for the static condition was 2.4°, and the angular change for the AP motion condition was $\pm .525^\circ$, which corresponded to the maximum apparent linear AP displacement of ± 4.2 cm. In the ML motion condition, there was no change in visual angle for the triangles.

Kinematics

Kinematics was recorded from the right side of the body and the trunk with respect to a global coordinate system using a single camera bank, three lenses, Optotrak (Northern Digital, Canada) camera system at a sampling frequency of 120 hz. Anatomical locations that were used for the placement of infrared diodes included fifth metatarsal, heel, lateral malleolus, lateral femoral condyle, greater trochanter, third lumbar spinous process, seventh cervical spinous process, acromion, and mediolateral center of the back of the head (Logan et al. 2010). The addition of midline markers at the lumbar and cervical spine served to reduce the effect of axial rotation of the trunk during walking on the 3D measurements. Lumbar position was defined as the AP or ML displacement of the marker on the lumbar

vertebrae. Neck position was defined as the AP or ML displacement of the marker on the cervical vertebrae. Trunk angle was defined as the AP or ML difference in position of the cervical and lumbar markers (Logan et al. 2010; Anson et al. 2013). The difference between cervical and lumbar translations in the AP or ML direction approximates the trunk angle relative to vertical in the sagittal or frontal plane, respectively, when this angle is small. Foot markers were used for calculation of gait parameters.

Procedure

All subjects verified that they were able to walk comfortably at the required speed of 5 km/h while viewing a static image of the visual scene prior to beginning any perturbation trials. Height of the TV was adjusted for each subject to ensure the focus of expansion corresponded to the subject's approximate eye height. Subjects were instructed to look straight ahead, but not to focus on any single triangle. Subjects were also instructed not to look for the edges of the TV screen for spatial orientation. Subjects were advised if a trial would be a standing or walking trial, but they were blinded to the condition of visual stimulus motion. All subjects were given approximately 30 s to reach a steady-state walking pattern prior to initiation of the trial. After reaching steady state, subjects were asked whether they were ready prior to beginning each 250-s trial. The experimental design included five conditions: (1) standing with an AP visual stimulus, (2) standing with an ML visual stimulus, (3) walking (5 km/h) with an AP visual stimulus, (4) walking (5 km/h) with an ML visual stimulus, (5) walking (5 km/h) with a static visual stimulus, as a control condition. Each condition was presented in random order as a block of trials, and this process was repeated for a total of three blocks. Standing rest breaks of one minute were given between each trial, and a seated rest for 3–5 min was provided between blocks or as needed to prevent fatigue.

Data analysis

A phase-dependent response of the legs, but not the trunk, to moving visual stimuli during walking has been reported which violates the linear assumptions of our analysis methods (Logan et al. 2010). Therefore, our kinematic analysis is confined to responses of the trunk which remained essentially linear throughout the gait cycle.

Spectral analysis

Fourier transforms of the AP or ML visual scene (translation) and kinematics (lumbar and neck translation, and trunk angle) are calculated. One-sided power spectral densities (PSDs) and cross-spectral densities (CSDs) using Welch's method (Bendat and Piersol 2000) with a 20-s Hanning window and one half overlap were then calculated with these transforms. The PSDs and CSDs are averaged across trials for each subject. For each subject, the PSDs and CSDs were binned on a linear logarithmic scale up to 3.7 Hz, resulting in 10 frequency bins. The frequencies included in each of the ten bins are as follows: .05, .1, .15, .2–.3, .35–.45, .5–.7, .75–1.1, 1.15–1.65, 1.7–2.5, and 2.55–3.7 Hz. The frequencies are averaged in each bin for plotting purposes resulting in the following ten frequencies: .05, .1, .15, .25, .4, .6, .925, 1.4, 2.1, and 3.125 Hz.

Gain and phase were computed to characterize the magnitude and timing of the kinematic response to the visual perturbations at each of the ten frequency bins of the frequency response functions (FRF). Gain is computed as the absolute value of the FRF, $H_{xy}(f)$ and phase is the argument of the FRF, $H_{xy}(f)$ converted to degrees.

Complex coherence was computed using the binned PSD and CSD values as

$C_{xy}(f) = P_{xy}(f) / \sqrt{P_{xx}(f) P_{yy}(f)}$, where $P_{xy}(f)$ is the CSD of the stimulus (x) and the kinematic response variable (y). The FRF averaged across subjects was defined as

$\bar{H}_{xy}(f) = \bar{C}_{xy}(f) \sqrt{\bar{P}_{yy}(f) / \bar{P}_{xx}(f)}$ where $\bar{C}_{xy}(f)$ is the mean complex coherence and $\bar{P}_{yy}(f)$ and $\bar{P}_{xx}(f)$ are the geometric means of the PSDs (Kiemel et al. 2008). This method weights subjects according to the coherence relative to the visual stimulus in each bin, similar to methods employed in similar studies (Warren et al. 1996; Kiemel et al. 2008; Logan et al. 2010).

Due to our probe consisting of a wide range of frequencies, statistical tests were performed on each frequency bin of the FRF in the complex plane. These first statistics on the FRF, at each frequency bin, were performed to ensure coherence between the visual stimulus and the kinematic response variables over the full range of frequencies for which we are reporting gain and phase. First, 95 % confidence intervals (CIs) were computed using the percentile-t method with 4,000 bootstrap re-samples and 400 nested re-samples for variance estimation (Zoubir and Boashash 1998). The bootstrapping method allows for an improved estimate of the average behavior (and variance) of a theoretical population based on a smaller set of existing subject data. The average FRF value for each frequency bin is calculated from 4,000 virtual data sets that pulled 14 samples (allowing for re-sampling) from the existing 14 subject data set. This results in an improved population-based estimate of the average behavior. The variance estimation is calculated with 400 virtual data sets for each of the 4,000 virtual data sets that are used to estimate the mean FRF. The variance estimation is used to calculate 95 % CI using the percentile-t method, which indicates whether a response is different from a reference value. We first compare all responses to zero, and then subsequent comparisons across conditions (i.e., standing vs. walking, AP vs. ML) only include “real” responses. The FRF was considered to have a “real” coherent response when the confidence region did not include zero in the complex plane ($\alpha = .05$). Log gain and phase of coherent FRFs are plotted with error bars representing $\pm$ the standard deviation of 10,000 bootstrap re-samples using the percentile-t method (Zoubir and Boashash 1998). To determine whether posture and locomotion responses are different for each stimulus direction, gain ratios and phase differences were computed using 4,000 bootstrap re-samples and 400 nested re-samples, and a 95 % CI was computed using the percentile-t method described above (Zoubir and Boashash 1998). This procedure was repeated to determine whether the ML response was different from the AP response for both posture and locomotion. To determine speed (standing vs. walking) by frequency bin effects, gain ratios and phase differences were first computed for neighboring frequency bins and then computed again across speed (standing vs. walking) using 4,000 bootstrap re-samples and 400 nested re-samples and a 95 % CI was computed using the percentile-t method described

above (Zoubir and Boashash 1998). These 95 % CIs represent the estimated population variability based on the sample variability from our subject pool.

Position variance

Position variance for AP or ML trunk kinematics was computed as the integral of the PSDs using the trapezoid method, after averaging PSDs across trials for each subject. Variance linearly related to the visual scene motion was computed as the product of the kinematic PSD and the magnitude squared coherence ($|C_{xy}(f)|^2$, $C_{xy}(f)$ defined above) between the kinematic and the visual signal. Incoherent variance was the difference between total variance and coherent variance. The independent variables included in the analysis were speed (standing vs. walking), response direction (AP vs. ML), and kinematic segment (neck translation, lumbar translation, and trunk orientation). Three-way (two speeds, two response directions, three kinematic segments) repeated-measures aNOVA with Greenhouse–Geisser adjustment was computed on geometric means for coherent and incoherent position variance ($\alpha = .05$). To determine whether visual scene motion influenced trunk motion in a way not linearly related to the visual stimuli, we compared the total variance for trials without visual scene motion (control) with incoherent variance for conditions when the visual scene translated in the AP or ML directions. Three-way (three stimuli directions, two response directions, three kinematic segments) repeated-measures ANOVA with Greenhouse–Geisser adjustment was computed on geometric means of both total (static stimulus condition) and incoherent position variance ($\alpha = .05$).

Gait kinematics

Using kinematics from the right leg, general gait parameters and their coefficients of variation were calculated. Heel strike was defined as the local minima of the heel marker in the vertical plane, and toe-off was identified from limb axis minima (Borghese et al. 1996; Ivanenko et al. 2004; Logan et al. 2010). The limb axis minimum was defined as the local minimum of the angle formed by the fifth metatarsal–hip axis in the sagittal plane, with the hip being the origin. Gait period for each trial was the average time between successive toe-off events. Stance time for each trial was the average time from heel strike to toe-off. Stride length was computed as the average AP movement of the heel marker between successive heel strikes. Stance percentage was computed as the stance time normalized to the gait cycle. Coefficients of variation were computed using means and standard deviation for these measures within each trial. The coefficient of variation was also calculated for swing time, computed as the duration of time between toe-off and heel strike. The standard deviation of the difference in ML foot position from stride to stride was computed. One-way (three stimuli directions) repeated-measures ANOVA with unstructured covariance the Kenward–Roger method and Tukey–Kramer post hoc adjustment was applied separately to each gait parameter and their coefficient of variation, and alpha was adjusted for 12 comparisons (corrected $\alpha = .004$).

Results

Gain and phase

Gain—Figure 3 illustrates three main results from the frequency response analysis. First, Fig. 3a, c shows how gain of the neck and lumbar markers is consistently higher across all frequencies during locomotion compared with standing posture for both visual stimulus directions, AP, and ML. The gain of these individual markers represents the translation of the trunk in the sagittal and frontal planes in response to the visual stimulus. In both the AP and ML directions, neck and lumbar translation gain was significantly greater ($p < .05$) during walking than standing posture in the majority of frequency bins (AP neck: 1–2, 4–8; AP lumbar: 1–2, 4–8, 10; ML neck: 1–5, 8–10; ML lumbar: 1–5, 7–9). The pattern of results clearly indicates higher overall gain during walking for translation of the upper body.

The second major result involves gain of the trunk angle, which represents how the visual stimulus influences orientation of the trunk with respect to vertical in the sagittal and frontal planes, and which showed a different gain pattern than translation. Trunk angle gain was not different between standing and walking at low frequencies, but was significantly greater during walking compared with standing at higher frequencies ($\alpha = .05$), shown in Fig. 3e. In the AP and ML directions, the middle and higher frequencies (AP trunk: bins 5–8, 10; ML trunk: bins 4–5, 7) show consistently higher trunk angle gain during walking ($p < .05$).

Third, both translation (lumbar and neck) and orientation (trunk angle) gain is higher in response to a visual stimulus in the ML direction than the AP direction during walking, but not during standing posture ($p < .05$). For neck and lumbar translation, ML gain was higher than AP gain across a broad range of frequencies (neck: 1, 2, 4, 5, 7, 8, and 10; lumbar: 1, 2, 4, 5, 8, 10). For trunk orientation, ML gain was higher than AP gain at middle and higher frequencies (4, 5, 7, 8, 10). Differences in AP and ML standing posture gain were only observed for a single frequency bin (5) for both translation and orientation ($p < .05$). Overall, these results indicate a kinematic (translation vs. orientation) by speed (standing vs. walking) by direction (AP vs. ML) interaction.

Phase—Regardless of direction, or kinematic variable, phase started at positive values at the lowest frequencies, indicating a visual lead relative to a kinematic variable (neck, lumbar, trunk angle), and decreased with increasing frequency to negative values, indicating a visual lag. For neck and lumbar translation, phase values were very similar across frequency. At high frequencies, lumbar phase values were more negative for locomotion than standing posture ($p < .05$). For trunk angle, phase values tended to be higher for locomotion than standing posture in the middle frequency range.

Kinematic variance

To investigate the visual influence on overall variability, variance was partitioned into variance coherent with the visual signal and incoherent with the visual signal, shown in Fig. 4. Coherent variance reflects variance in the response that is directly caused by motion of the visual scene. Incoherent variance is the difference between total variance and the coherent variance, i.e., that not caused by the visual scene motion. Control variance refers to

total variance during the static visual scene condition. Although there are numerous effects which are expected, such as overall higher variance for walking than standing, there are two findings that are particularly revealing about trunk control. First, similar to previous findings on foot placement (O'Connor and Kuo 2009), directional effects for trunk angle variance in response to visual stimulation are observed not with standing but only with walking, with the ML direction displaying higher coherent variance than the AP direction ($p < .001$). Second, trunk translation shows consistently higher variance for the ML direction than the AP direction during walking but not standing ($p < 0001$), for all walking conditions. However, trunk angle shows a directional effect, with larger ML variance *only* for the coherent portion of variance ($p < .0001$). Trunk angle variance not caused by visual scene motion was equivalent in the AP and ML directions.

During walking, variance not caused by visual scene motion was significantly higher than variance in the control condition for translation in all directions ($p < .05$), but not for orientation. Translation variance not caused by visual scene motion and translation variance in the control condition both display directional effects which were greater in the ML direction ($p < .0001$). The implications of these results for control of the trunk are discussed below.

Gait parameters

The ensemble averages for each gait parameter are presented in table 1. Across condition, comparisons made with Tukey–Kramer adjustments demonstrate that the coefficient of variation for right leg stance time during the ML visual scene motion was significantly greater than during the AP visual scene motion condition ($p < .004$). The standard deviation of the difference in ML foot placement from stride to stride also demonstrated a significant condition effect with ML visual scene motion resulting in greater variability in ML foot placement compared with either the AP visual scene or the static visual scene conditions ($p < .004$).

Discussion

The purpose of this study was to gain a more complete understanding of trunk control during locomotion. A moving visual scene was used to probe the use of vision in stabilizing trunk translation and orientation. Our results were consistent with our hypothesis that vision plays a greater role in stabilizing trunk translation in the ML direction than in the AP direction. The results did not support our hypothesis that the use of visual information to stabilize trunk orientation during walking would be similar in the AP and ML directions.

Gain responses to visual scene motion

Gain of the trunk relative to visual scene motion was larger during walking than standing, as previous studies have found (Logan et al. 2010). More striking was that trunk gain showed a directional dependence during walking: across all frequencies, ML gains were larger compared with the AP direction for trunk translation and at higher frequencies for trunk orientation (see Fig. 3). Such directional dependence in response to visual scene motion was not observed during standing. This is similar to the finding of greater sensitivity to ML

visual scene motion reported by O'Connor and Kuo (2009). Their sensitivity measure was based on a comparison of cOP variability between a static visual scene and a moving visual scene. Here, we compared gain of the trunk between AP and ML visual scene motion conditions. Others have reported a directional effect during standing in response to platform tilt based on integrated proprioceptive and vestibular feedback demonstrating that postural control during stance is not always symmetrical in the AP and ML directions (Allum et al. 2008).

These results for trunk translation are similar to previous findings cited above showing a directional dependence to kinematic responses during walking. Bauby and Kuo (2000) and O'Connor and Kuo (2009) interpreted such results as evidence of the importance of high-level visual and vestibular feedback to stabilize walking in the side-to-side direction, somatosensory feedback being thought sufficient to stabilize walking in the fore-aft direction. Our translation results are also consistent with McAndrew et al. (2010) who suggested a similar conclusion for control of trunk translation: the ML direction seems inherently less mechanically stable, requiring more neural control that depends on sensory feedback. It may not be surprising that trunk translation shows a similar directional dependence as step variability (O'Connor and Kuo 2009); any translation of the legs will passively carry the trunk along or vice versa (hurt et al. 2010), an effect that is clearly a function of the mechanical linkage between the trunk and legs. Supporting this argument is the higher variability of the ML foot placement from stride to stride in the condition with ML visual scene motion (see table 1). A direction-dependent interaction of trunk displacement and leg displacement during perturbed standing on a moving platform has previously been interpreted as a function of the biomechanical linkage of the legs and trunk (Preuss and Fung 2008). However, there is no such simple relationship between leg/step translation and trunk orientation relative to vertical. Alternatively, the larger responses in the ML direction for translation reflect a response to a perceived change in navigational direction. Subjects were instructed not to fixate a point indicating path direction, nor was there a circular component to the visual display (Buccello-stout et al. 2013), but the ML translation may have been perceived as a change in heading.

Unlike trunk translation gain, which displayed higher ML gains across the frequency spectrum, trunk orientation gain showed a directional dependence only at mid-to-high frequencies, with peak gain responses in the ML direction (see Fig. 3e). Trunk orientation is not more mechanically stable or resistant to mechanical perturbations in either the AP or ML direction (Gardner-Morse and Stokes 2001). Unlike experiments that impose ML treadmill translations which mechanically displace the subject (McAndrew et al. 2010; sinitski et al. 2012), trunk orientation responses driven by sensory feedback from visual scene motion in this experiment cannot be explained as a direct mechanical response to the perturbation. The mid-to-high frequency directional dependence suggests a visual feedback mechanism as a more likely candidate to explain the observed responses (Warren et al. 1996). In response to visual roll perturbation, individuals either leaned their trunk or deviated their path, which was interpreted as visuo-vestibular integration for trunk control (Keshner and Kenyon 2000). Unlike previous work that describe coordinated head and body motion during walking or turning (Imai et al. 2001), the present analysis reports only on the kinematic behavior directly related to the visual scene motion in the FRFs and the coherent variance. It

is possible that the trunk orientation motion included a visuo-vestibular interaction to facilitate head stabilization that could not be identified (Pozzo et al. 1991). The direction-dependent trunk orientation responses to visual perturbations during walking would not be predicted by standing postural responses that depend on mechanical stability (Ivanenko et al. 2000), or the directional interaction of leg segments and trunk (Preuss and Fung 2008). The trunk orientation gains observed in this study further demonstrate differences in upright trunk orientation control between standing and walking. Future studies providing treadmill perturbations and mechanical perturbations to the trunk in addition to sensory perturbations should explore the relationship between mechanical coupling of the trunk and legs as well as the interaction of mechanical and neural control for upright orientation of the trunk during walking.

At low frequencies, trunk orientation displayed either no detectable response or gains similar to those observed during standing. These low frequencies, from .05 to .15 Hz, are only about one-tenth the frequency of the gait cycle (≈ 1 Hz). Considering the larger overall variance observed with walking compared with standing, trunk responses to visual scene motion at these low frequencies may be too small to be detectable.

We observed a time difference between trunk translation and orientation in response to visual stimulation. Peak gains for trunk orientation occurred at frequencies above 1 Hz while maximal gains for translation (both lumbar and neck) occurred between .25 and .6 Hz (see Fig. 3). This suggests that trunk orientation movements respond on a shorter time scale than trunk translation movements (Kiemel et al. 2010). This time scale difference suggests different cost functions associated with translation and orientation, which may reflect the consequences of a disturbance while walking. A deviation from the intended path (translation) temporarily speeds up or slows down forward progression, which may be less deleterious compared with deviations in trunk orientation that threaten upright equilibrium. Corrections for lateral path deviations caused by lateral translation of the body could easily be corrected by appropriate placement of the foot at the next step (O'Connor and Kuo 2009). The more rapid orientation response may serve as a mechanism to prevent the head and trunk from exceeding a safe range of angular displacement from vertical, reducing fall risk. This is consistent with the concept that corrections in whole body angular momentum occur during double support (Robert et al. 2009), rather than waiting for the next step. Future studies could explore the flexibility of this orientation over translation prioritization to determine whether the observed relationship is fixed or adaptive.

Variance

While gain indicates the response to the visual scene motion, decomposing total variance into coherent and incoherent components illustrates trunk behavior that is not directly caused by the visual stimulation. Coherent variance depends on the gain at each frequency and the PSD of the visual scene motion. Since the PSD of the visual scene motion was the same in all conditions, one expects similar effects for gain and coherent variance. This was observed: coherent variance was higher in the ML direction for both trunk translation and orientation during walking (filled squares in Fig. 4b), and there was no directional dependence during standing (filled squares in Fig. 4a). For incoherent variance and variance

in the control condition (open squares and circles in Fig. 4b), directional dependence was observed for trunk translation but not trunk orientation, effects that are consistent with our original hypotheses. This is exemplified by incoherent variance (open squares) representing greater variance than in the control condition (open circles) for translation in Fig. 4b. The addition of visual scene motion may have led to reduced reliability of visual input for position control while walking on the treadmill, resulting in less resistance to visual perturbation (Logan et al. 2010). This helps to explain the larger incoherent variability for translation with visual scene movement compared with the static visual condition, since proprioceptive and vestibular input provide limited information regarding absolute position in space to compensate for less reliable visual input.

In contrast, proprioception and vestibular inputs could provide adequate sensory input to stabilize trunk orientation when visual scene motion becomes less reliable. The increase in variance from standing to walking reflects a decrease in stability with a moving base of support (walking) compared with a stationary base of support (standing) as has been suggested by Logan et al. (2010). However, during walking, there was no increase in incoherent variance compared with the control condition for the trunk angle. Persistent upright stability from redundant sensory input could facilitate an increase in coupling of the trunk angle to motion of the visual scene. Alternatively, the consistency of trunk angle variance regardless of visual scene motion may suggest an emphasis on a stable platform for the head during walking (Pozzo et al. 1991). This may explain the lack of directional effect as well as the lack of difference for the trunk angle variance between the control condition and incoherent variance from conditions with visual scene motion.

Conclusion

A number of studies have suggested that visual control of leg characteristics during locomotion is different in the AP and ML directions. The current results add to this perspective, illustrating that trunk translation *and* orientation show a directional dependence during walking. This may not be surprising for translation of the body, as trunk translation is mechanically tied to translation of the legs. A mechanical explanation, however, is less straightforward for orientation of the body to upright during walking. Our results show stronger responses of trunk orientation to visual scene motion in the side-to-side direction, indicating that visually mediated control of upright orientation demonstrates directional dependence that operates on a faster time scale than trunk translation.

Acknowledgments

This study was supported by the National Science Foundation grant Bcs 0924883, J. Jeka and T. Kiemel, PIs. Eric Anson was supported in part by scholarships from the Foundation for Physical Therapy, Inc. The study sponsors had no role in any aspect of the experiment from design to manuscript writing.

References

- Allum J, Nijhuis L, Carpenter M. Differences in coding provided by proprioceptive and vestibular sensory signals may contribute to lateral instability in vestibular loss subjects. *Exp Brain Res.* 2008; 184:391–410. [PubMed: 17849108]

- Anson E, Rosenberg R, Agada P, Kiemel T, Jeka J. Does visual feedback during walking result in similar improvements in trunk control for young and older healthy adults? *J NeuroEng Rehabil.* 2013; 10:110. [PubMed: 24274143]
- Bardy B, Warren W, Kay B. The role of central and peripheral vision in postural control during walking. *Percept Psychophys.* 1999; 61(7):1356–1368. [PubMed: 10572464]
- Bauby C, Kuo A. Active control of lateral balance in human walking. *J Biomech.* 2000; 33:1433–1440. [PubMed: 10940402]
- Bendat, J.; Piersol, A. Random data: analysis and measurement procedures. Wiley; New York: 2000.
- Borghese N, Bianchi L, Lacquaniti F. Kinematic determinants of human locomotion. *J Physiol.* 1996; 494:863–879. [PubMed: 8865081]
- Bruggeman H, Zosh W, Warren W. Optic flow drives human visuo-locomotor adaptation. *Curr Biol.* 2007; 17:2035–2040. [PubMed: 18023350]
- Buccello-Stout RR, Cromwell RL, Bloomberg JJ, Whorton EB. Sensorimotor adaptation training's effect on head stabilization in response to lateral perturbation in older adults. *J Aging Phys Act.* 2013; 21:272–289. [PubMed: 23006335]
- Gardner-Morse M, stokes I. Trunk stiffness increases with steady-state effort. *J Biomech.* 2001; 34:457–463. [PubMed: 11266668]
- Gibson J. Visually controlled locomotion and visual orientation in animals. *Br J Psychol.* 1958; 49:182–194. [PubMed: 13572790]
- Re-printed in Gibson J. Visually controlled locomotion and visual orientation in animals. *Br J Psychol.* 2009; 100:259–271. [PubMed: 19351451]
- Hurt CP, Rosenblatt N, Crenshaw JR, Grabiner MD. Variation in trunk kinematics influences variation in step width during treadmill walking by older and younger adults. *Gait Posture.* 2010; 31:461–464. [PubMed: 20185314]
- Imai T, Moore ST, Raphan T, Cohen B. Interaction of the body, head, and eyes during walking and turning. *Exp Brain Res.* 2001; 136:1–18. [PubMed: 11204402]
- Ivanenko Y, Solopova I, Levik Y. The direction of postural instability affects postural reactions to ankle muscle vibration in humans. *Neurosci Lett.* 2000; 292:103–106. [PubMed: 10998559]
- Ivanenko Y, Poppele R, Lacquaniti F. Five basic muscle activation patterns account for muscle activity during human locomotion. *J Physiol.* 2004; 556:267–282. [PubMed: 14724214]
- Keshner E, Kenyon R. The influence of an immersive virtual environment on the segmental organization of postural stabilizing responses. *J Vestib Res.* 2000; 10:207–219. [PubMed: 11354434]
- Kiemel T, Elahi A, Jeka J. Identification of the plant for upright stance in humans: multiple movement patterns from a single neural strategy. *J Neurophysiol.* 2008; 100:3394–3406. [PubMed: 18829854]
- Konczak J. Effects of optic flow on the kinematics of human gait: a comparison of young and older adults. *J Motor Behav.* 1994; 26(3):225–236.
- Kuo A. Stabilization of lateral motion in passive dynamic walking. *Int J Robot Res.* 1999; 18(9):917–930.
- Kiemel T, Logan D, Ivanenko Y, Lacquaniti F, Jeka J. A comparison of the effects of visual-scene motion on walking and standing and the role of stability. *Proceedings of the 16th US National Congress of Theoretical and Applied Mechanics.* 2010
- Lamontagne A, Fung J, McFayden B, Faubert J. Modulation of walking speed by changing optic flow in persons with stroke. *J Neuroeng Rehabil.* 2007; 4:22. [PubMed: 17594501]
- Logan D, Kiemel T, Dominici N, Cappellini G, Ivanenko Y, Lacquaniti F, Jeka J. The many roles of vision during walking. *Exp Brain Res.* 2010; 206:337–350. [PubMed: 20852990]
- Marigold D. Role of peripheral visual cues in online visual guidance of walking. *Exercise Sport Sci R.* 2008; 36(3):145–151.
- McAndrew P, Dingwell J, Wilken J. Walking variability during continuous pseudo-random oscillations of the support surface and visual field. *J Biomech.* 2010; 43:1470–1475. [PubMed: 20346453]
- McGeer T. Passive dynamic walking. *Int J Robot Res.* 1990; 9(2):62–82.

- O'Connor S, Kuo A. Direction-dependent control of balance during walking and standing. *J Neurophysiol.* 2009; 102:1411–1419. [PubMed: 19553493]
- Patla A. How is human gait controlled by vision? *Ecol Psychol.* 1998; 10(3–4):287–302.
- Patla A, Vickers J. How far ahead do we look when required to step on specific locations in the travel path during locomotion? *Exp Brain Res.* 2003; 148:133–138. [PubMed: 12478404]
- Pozzo T, Berthoz A, Lefort L, Vitte E. Head stabilization during various locomotor tasks in humans II. Patients with bilateral peripheral vestibular deficits. *Exp Brain Res.* 1991; 85:208–217. [PubMed: 1884759]
- Preuss R, Fung J. Musculature and biomechanics of the trunk in the maintenance of upright posture. *J Electromyogr Kinesiol.* 2008; 18:815–828. [PubMed: 17449280]
- Prokop T, Shubert M, Berger W. Visual influence on human locomotion modulation to changes in optic flow. *Exp Brain Res.* 1997; 114:63–70. [PubMed: 9125452]
- Reynolds RF, Day BL. Visual guidance of the human foot during a step. *J Physiol.* 2005; 569(2):677–684. [PubMed: 16179363]
- Robert T, Bennett B, Russell S, Zirker C, Abel M. Angular momentum synergies during walking. *Exp Brain Res.* 2009; 197(2):185–197.
- Sinitski E, Terry K, Wilken J, Dingwell J. Effects of perturbation magnitude on dynamic stability when walking in destabilizing environments. *J Biomech.* 2012; 45:2084–2091. [PubMed: 22749389]
- Varraine E, Bonnard M, Pailhous J. Interaction between different sensory cues in the control of human gait. *Exp Brain Res.* 2002; 142:374–384. [PubMed: 11819046]
- Warren W, Kay B, Yilmaz E. Visual control of posture during walking: functional specificity. *J Exp Psychol Hum.* 1996; 22(4):818–838.
- Warren W, Kay B, Zosh W, Duchon A, sahuc S. Optic flow is used to control human walking. *Nat Neurosci.* 2001; 4(2):213–216. [PubMed: 11175884]
- Woolacott, M. Gait and postural control in the aging adult.. In: Bles, W.; Brandt, T., editors. *Disorders of posture and gait.* Elsevier; Amsterdam: 1986. p. 325-336.
- Zoubir A, Boashash B. The bootstrap and its application in signal processing. *IEEE signal Proc Mag.* 1998; 15:56–76.

Fig. 1. Illustration of the experimental setup. Subjects stood or walked on the treadmill in front of a virtual display of randomly oriented *white triangles* on a *black background*. Subjects wore goggles which prevented them from seeing the borders of the TV

Fig. 2.

Exemplar time and frequency content of visual scene motion shown for 60 s from a single trial. The position of the visual scene in the static condition corresponded to the zero value during trials with visual scene motion. *Positive (negative)* values indicate that the virtual wall of triangles was “moving away” (toward) from the subject during the AP stimulus conditions. During ML stimulus conditions, *positive (negative)* values indicate movement of the virtual wall of triangles to the *right (left)*

Fig. 3. Gain and phase plots for condition comparison, only frequency bins significantly different from zero have been plotted. Frequency response functions (gain and phase) for *translation*: **a** lumbar gain, **b** lumbar phase, **c** neck gain, **d** neck phase, and *orientation*: **e** trunk gain, **f** trunk phase in response to visual scene motion. *Error bars* represent bootstrapped standard error

Fig. 4.

Coherent and incoherent position (subplots **a** and **b**) variance. *Open squares* represent variance incoherent with dynamic visual scene motion and *filled squares* represent variance coherent with dynamic visual scene motion. *Circles* represent total variance with stationary visual scene. *AP* and *ML* references on the *x*-axis correspond to both kinematic direction and visual stimuli direction. Comparisons between incoherent variance for dynamic visual scene conditions and total variance for the static visual scene condition are shown in subplot **b**. Lumbar refers to translation, while trunk refers to trunk angle. *Error bars* represent standard error of the mean

Table 1

General gait parameters for all locomotion conditions

General gait parameters Parameter	Stimulus motion		
	AP	Static	ML
Gait period	1.03	1.04	1.02
C_V	.02	.01	.02
Gait frequency (s)	.97	.97	.99
Stride length (cm)	147.2	148.08	146.45
C_V	.02	.02	.02
Stance time (s)	.64	.65	.63
C_V	.02	.02	.03 [*]
Stance (%)	62.46	62.51	62.43
C_V	.02	.02	.02
SD of ML difference in foot placement (cm)	2.47	2.47	3.82 ^{*,†}
Swing time C_V	.04	.04	.06

C_V is the coefficient of variation for the corresponding gait parameter

^{*} ML stimulus condition significantly different from Static condition ($p < .004$)

[†] ML stimulus condition significantly different from AP condition ($p < .004$)