Advanced Age Brings a Greater Reliance on Visual Feedback to Maintain Balance During Walking

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Keywords: optical flow; stability; gait; elderly; sensorimotor;

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Word Count:

Abstract

We implemented a virtual reality system to asses age-related differences in the use of visual feedback to actively control balance during walking between healthy young (n=12, mean age: 24 years) and healthy old (n=11, age: 71 years) adults. Subjects walked on a treadmill for 3 min each while watching a speed-matched, virtual hallway with and without continuous mediolateral (ML) visual perturbations. We used a motion capture system to track center of mass motion (via a sacrum marker) and step placement kinematics (via right and left heel markers). Spectral analysis, detrended fluctuation analysis, and local divergence exponents quantified the effects of age on center of mass (CoM) motion and step placement dynamics. Old and young adults walked normally with comparable CoM spectral characteristics, lateral step placement temporal persistence, and local dynamic stability. However, perturbed visual flow induced significantly larger changes in the spectral characteristics of CoM motion in old vs. young adults. Moreover, we found that visual perturbations disrupted the step-to-step control of lateral step placement and compromised local dynamic stability in old significantly more than young adults. Based on these observations, we propose that advanced age may induce a greater reliance on visual feedback to actively control balance during waking, an effect that may compensate for degradations in somatosensory signaling. Our findings may be particularly relevant to the early diagnosis of sensory-induced balance impairments and also point to the potential use of virtual reality to evaluate the efficacy of sensory rehabilitation and balance training programs in old adults at risk of falls.

1. Introduction

Lateral step placement is an important control variable in the maintenance of balance during walking (Bauby & Kuo, 2000; Donelan, Shipman, Kram, & Kuo, 2004). In contrast to step placement in the direction of movement, which is passively stable, lateral step placement is highly dependent upon the integration of reliable visual, vestibular, and somatosensory feedback (Bauby & Kuo, 2000; Collins & Kuo, 2013; Donelan, et al., 2004; O'Connor & Kuo, 2009; O'Connor, Xu, & Kuo, 2012). It is well recognized that the quality of sensory information declines considerably with advanced age (Patel, Magnusson, Kristinsdottir, & Fransson, 2009). These changes are functionally exacerbated by longer reflex latencies and slower maximum rates of muscle force development in old adults (Dorfman & Bosley, 1979; Thelen, Schultz, Alexander, & Ashton-Miller, 1996). Ultimately, age-related sensorimotor decline may compromise old adults' effective use of lateral step placement to maintain balance during walking, thereby increasing their risk of falling. Indeed, one third of old adults (i.e., 65+ years) fall annually and most of these falls occur during locomotion (Berg, Alessio, Mills, & Tong, 1997; Niino, Tsuzuku, Ando, & Shimokata, 2000).

Evidence from the postural control literature may provide indirect insight into how old adults differ from young adults in their use of sensory feedback to maintain balance during walking. For example, using a unique combination of visual and somatosensory perturbations, Eikema et al. (2013) found that advanced age brought a reliance on visual feedback coupled with a reduced sensitivity to tendon vibration. A common interpretation of these findings is that a preferential decline in somatosensory feedback with age brings an increased reliance on visual feedback for postural control (Eikema, Hatzitaki, Konstantakos, & Papaxanthis, 2013; Jeka, Allison, & Kiemel, 2010; Sundermier, Woollacott, Jensen, & Moore, 1996; Yeh, Cluff, &

Balasubramaniam, 2014). In addition, Yeh et al. (2014) found that visual reliance in old adults was direction-dependent, with greater sensitivity to visual perturbations in the mediolateral control of posture. The well documented age-related increase in visual reliance suggests that there may also be a unique role of visual feedback in old adults' control of lateral step placement and balance during walking.

Removing or disrupting visual feedback impairs the control of lateral step placement during walking in young adults (Bauby & Kuo, 2000; McAndrew, Dingwell, & Wilken, 2010; O'Connor & Kuo, 2009; O'Connor, et al., 2012). For example, compared to normal walking, Bauby and Kuo (1999) found that step width variability disproportionately increased when young adults walked with their eyes closed. More recently, O'connor and Kuo (2009) and O'connor et al. (2012) have used virtual reality to reveal that the control of lateral step placement in young adults is compromised more by mediolateral than anterior-posterior visual perturbations. If old adults rely more on visual feedback than young adults to maintain balance during walking, we would anticipate more pronounced effects of visual perturbations on their control of lateral step placement.

Dynamic analysis of center of mass (CoM) motion and step placement can provide insights into the sensorimotor control of balance during walking. For example, spectral analysis can quantify one's dynamic response to visual perturbations (Loughlin & Redfern, 2001), and the temporal dynamics of CoM motion can delineate old adults at risk of falls (Latt, Menz, Fung, & Lord, 2009). In addition, lateral step placement has emerged as a balance control variable during walking, suggesting a high probability for step-to-step dependence. Detrended fluctuation analysis (DFA) quantifies step-to-step correlations and is commonly used to study walking in healthy adults and those with neurological impairment (Dingwell & Cusumano, 2010; Hausdorff,

et al., 1997). Finally, local dynamic stability quantified via maximum divergence exponents is strongly associated with falls risk in old adults and characterizes one's resilience to naturally occurring perturbations arising from both internal (e.g., age-related neuromuscular noise) and external (e.g., altered visual flow) factors (Kang & Dingwell, 2008; Toebes, Hoozemans, Furrer, Dekker, & van Dieen, 2012). Together, these analyses represent robust metrics to investigate the disparate role of visual feedback in old and young adults' maintenance of balance during walking.

The purpose of this study was to investigate whether old adults rely more on visual feedback than young adults to actively control balance during walking. We implemented a virtual reality system to perturb visual flow during treadmill walking and quantified the effects on center of mass (CoM) motion and step placement dynamics. We hypothesized that perturbed visual flow would: 1) induce a change in the spectral characteristics of CoM motion, 2) disrupt the step-to-step control of lateral step placement, and 3) compromise local dynamic stability in old but not young adults.

2. Methods

2.1 Subjects

12 healthy young (mean ± standard deviation, age: 23.6 ± 3.8 years, mass: 70.7 ± 11.3 kg, leg length: 0.82 ± 0.05 m) and 11 healthy old adults (age: 71.2 ± 4.2 years, mass: 66.9 ± 9.6 kg, leg length: 0.75 ± 0.04 m) participated. Subjects provided written informed consent as per the University of Wisconsin Health Sciences Internal Review Board. All subjects completed a health questionnaire based on recommendations of the American College of Sports Medicine (ACSM, 2014). We excluded subjects based on the following: BMI≥30, sedentary lifestyle, first degree

family history of coronary artery disease, cigarette smoking, high blood pressure, high cholesterol, diabetes or prediabetes, orthopedic or neurological condition, taking medication that causes dizziness, or any unanticipated falls in the prior six months.

2.2 Experiment

We first assessed subjects' preferred overground walking speed from the average of two times taken to traverse the middle 4 m of a 10 m walkway when asked to walk at a normal, comfortable speed (Old: 1.28 ± 0.10 m/s, Young: 1.36 ± 0.12 m/s, p=0.11). Subjects then completed all treadmill walking conditions at their preferred overground speed. Subjects walked on a dual-belt, force-sensing treadmill (Bertec, Inc., Columbus, OH) while viewing a speed-matched virtual hallway (**Figure 1**). The virtual hallway, designed to previously published specifications (O'Connor & Kuo, 2009; O'Connor, et al., 2012), was rear-projected onto a semicircular screen approximately 2.75 m high and 2.25 m wide which surrounded the treadmill. To account for the screen's curvature, a custom Matlab (Mathworks, Inc., Natick, MA) routine distorted the geometry of the image, composed of a dark hallway with randomly placed white rectangles and doors at regular intervals (*see supplementary material*). We asked the subjects to look forward, but provided no further instructions to allow subjects to naturally adapt to the visual information. Old adults walked while wearing a support harness connected overhead. Note that three old adults were unable to complete the treadmill walking trials at their preferred overground speed without holding onto the handrails. To accommodate these subjects, we decreased their treadmill speed by 10% before collecting data.

In random order, subjects walked while watching the virtual hallway with and without continuous mediolateral (ML) visual perturbations. Perturbations consisted of a sum of two sinusoids (0.135 and 0.442 Hz) with 0.175 m amplitudes, applied as rotations in the frontal plane

about the subject's nominal position. An algorithm applied a secondary rotation to constrain the hallway's end. These perturbations retained the smaller amplitude sinusoids from a perturbation previously found to significantly affect young adults' lateral foot placement (O'Connor, et al., 2012). After subjects became comfortable walking without using the handrails (~1 min), we recorded kinematic and ground reaction force (GRF) data for 3 min per trial. A motion capture system operating at 100 Hz recorded the three-dimensional positions of retroreflective markers placed on subjects' sacrum (a surrogate for their CoM) and right and left posterior calcanei.

2.3 Data Analysis

We low-pass filtered marker trajectories using a fourth-order Butterworth filter and a 12 Hz cuff-off frequency. By design, visual perturbations elicited considerable mediolateral (ML) deviations in step placement such that subjects often placed consecutive steps on the same treadmill. Consequently, we were unable to rely on GRF measurements to identify gait cycle events (i.e., heel-strikes). Instead, we identified the instant of right and left heel-strikes based on the anterior-posterior heel positions relative to the sacrum marker (Zeni, Richards, & Higginson, 2008). Zeni et al. (2008) found that this technique identified heel-strikes during walking to within 0.0167 s compared to those identified more conventionally using the vertical GRF. We analyzed at least 300 consecutive steps for each 3 min trial.

We quantified old and young adults' dynamic response to visual perturbations via three analyses. First, we used spectral analysis to quantify the intensity of visual perturbation frequencies in ML sacrum kinematics. Matlab routines computed the fast Fourier transform (FFT) and power spectral density of the ML sacrum marker trajectories during normal and visually perturbed walking. We calculated for each condition the average FFT and energy-

normalized power spectral density at each of the two visual perturbation frequencies (Loughlin & Redfern, 2001).

Second, we assessed the statistical persistence of lateral step placement. To do this, we constructed time series of step widths from the ML distance between calcaneous markers across successful steps, averaged during midstance prior to heel-rise (i.e., 12-25% of each stride) (Perry & Burnfield, 2010). These time series contained alternating left and right step widths, as illustrated in **Figure 1**. We then quantified the temporal persistence of step width in these time series using detrended fluctuation analysis (DFA). Prior studies have most often used linear DFA to remove 1st order trends arising from nonstationarities in step kinematics during walking (Dingwell & Cusumano, 2010; Hausdorff, et al., 1997). However, due to the prevalence of nonlinear processes in neuromuscular control (Guastello, 2006; Ting, et al., 2009), nonlinear DFA has the potential to reveal clinically relevant information not captured by linear DFA (Deffeyes, et al., 2009). Therefore, we used 1st and 2nd order DFA to compute the mean square roots of detrended residuals of step width over a range of steps between 4 and N/4, where N was the total number of steps (Dingwell & Cusumano, 2010). We interpreted the scaling exponents (α_{1D} and α_{2D}) of the relation between the root mean square (RMS) residual of step width and the number of steps as follows: $\alpha = 0.5$ indicates uncorrelated white noise; $\alpha < 0.5$ indicates that deviations in one direction are likely to be followed by deviations in the opposite direction (i.e., anti-persistent); and $\alpha > 0.5$ indicates that deviations in one direction are likely to be followed by deviations in the same direction (i.e., persistent).

Finally, we calculated maximum divergence (Lyapunov) exponents from time series of right and left heel positions relative to the sacrum position. There is no consensus in the literature as to which variables to include in local dynamic stability analyses of walking. Therefore, we

adopted time series most consistent with the purpose of this study - those corresponding to foot trajectories and CoM motion. Consistent with prior studies in young adults (McAndrew, Wilken, & Dingwell, 2011), visual perturbations introduced considerable nonstationarities in the ML marker positions. Therefore, we opted to exclude the ML kinematics from our local dynamic stability analysis (see Discussion for alternative approaches and outcomes). We implemented for all subjects and conditions one quarter of their average stride time as the embedding delay (Virgin, 2000) and determined the corresponding embedding dimension (d_E=5) using a 10% criterion in a false nearest neighbors analysis (Kennel, Brown, & Abarbanel, 1992). We then calculated the average maximum exponential rates of divergence of pairs of initially neighboring trajectories using procedures outlined in detail previously (Kang & Dingwell, 2008; Rosenstein, Collins, & De Luca, 1993; Toebes, et al., 2012). We time normalized the divergence curves to account for differences in subjects' stride period, and computed short-term (λ_s, 0 to 1 stride) and long-term (λ_L, 4 to 10 strides) divergence exponents for each subject, where larger positive values imply larger local *in*stability (Kang & Dingwell, 2008).

2.4 Statistical Analysis

An analysis of variance (ANOVA) for repeated measures tested for significant main effects of and interactions between age and condition on CoM spectral peak values, DFA scaling exponents, and short- and long-term divergence exponents using a $p < 0.05$ criterion. We further evaluated significant main effects of age and condition using independent-samples t-tests and post-hoc pairwise comparisons, respectively.

3. Results

Visual perturbations uniquely affected the relation between ML sacrum motion and lateral step placement during walking in old adults. Lateral step placement delimited ML sacrum motion during both normal and visually perturbed walking in young adults, and during normal walking in old adults (**Figure 2**). In contrast, visual perturbations disrupted this systematic behavior in old adults, frequently leading to lateral step placements that fell beneath or even contralateral to the instantaneous ML sacrum position.

3.1. Center of mass spectral characteristics

Relative to normal walking, ML sacrum kinematics in both age groups exhibited significantly greater signal intensity at the two visual perturbation frequencies ($p < 0.01$) (**Figure 3**). However, this effect was significantly larger for old adults (age $\times$ condition, $p < 0.01$). For example, although their spectral characteristics did not differ during normal walking, old adults averaged an order of magnitude larger change in peak power spectral density than young adults in response to visual perturbations ($p < 0.01$) (**Figure 3**).

3.2. Step-to-step control of lateral step placement

During normal walking, time series of step widths for both old and young adults exhibited prolonged phases over which consecutive steps became progressively wider or narrower (**Figure 4A**). Indeed, lateral step placement was equally temporally persistent (i.e.,

$\alpha \gg 0.5$) in old and young adults walking normally ($p > 0.32$) (**Figure 4B**). However, visual

perturbations eliminated the temporal persistence of step width in old but not young adults (old vs. young, α_{1D}: 0.51 ± 0.09 vs. 0.61 ± 0.06, p<0.01; α_{2D}: 0.50 ± 0.09 vs. 0.68 ± 0.05, p<0.01). The decorrelation in old adults' lateral step placement during visually perturbed walking was qualitatively evidenced by indiscriminate step-to-step fluctuations in step width (**Figure 4A**).

3.3. Local dynamic stability

Old and young adults exhibited similar short-term (0 to 1 strides) and long-term (4 to 10 strides) local divergence exponents during normal walking (p=0.73 and p=0.17 for λ_S and λ_L, respectively) (**Figure 5**). However, compared to normal walking, short-term divergence exponents increased significantly more for old than young adults in response to visual perturbations (old: 1.38 ± 0.20 vs. 1.14 ± 0.05; young: 1.20 ± 0.10 vs. 1.12 ± 0.12; age × condition, p=0.01). Visual perturbations elicited a 226% larger increase in short-term divergence exponents for old vs. young adults, indicating significantly greater local *in*stability. Visual perturbations did not significantly alter long-term divergence exponents in old or young adults (p=0.08 and p=0.12, respectively) (**Figure 5**).

4. Discussion

Our findings provide compelling evidence that old adults rely more on visual feedback than young adults to actively control balance during walking. As hypothesized, perturbed visual flow induced significantly larger changes in the spectral characteristics of CoM motion in old vs. young adults. Moreover, and also as hypothesized, we found that visual perturbations disrupted the step-to-step control of lateral step placement and compromised local dynamic stability in old significantly more than young adults. As we discuss in more detail below, these findings may be particularly relevant to the early diagnosis of sensory-induced balance impairments and also

point to the potential use of virtual reality to evaluate the efficacy of sensory rehabilitation and balance training programs for old adults at risk of falls.

Studies of the postural control of standing have revealed that advanced age is accompanied by a reliance on visual feedback (Jeka, et al., 2010; Sundermier, et al., 1996; Yeh, et al., 2014) coupled with a reduced sensitivity to somatosensory perturbations (Eikema, et al., 2013; Thelen, Brockmiller, Ashton-Miller, Schultz, & Alexander, 1998). These changes are attributed to age-related sensory reweighting, predicated on a decline in the quality of somatosensory signaling in old adults. Our findings extend these observations and imply that age-related sensorimotor adaptations manifest in old adults' utilization of sensory feedback to maintain balance during walking. We arrived at this conclusion by interpreting the results of three dynamic analyses each shown previously to provide unique insights into age-related balance impairment (Dingwell & Cusumano, 2010; Hausdorff, et al., 1997; Latt, et al., 2009; Loughlin & Redfern, 2001). In this study, spectral analysis, detrended fluctuation analysis, and local divergence exponents revealed an enhanced role of visual feedback in old adults' active control of lateral step placement and balance during walking.

Old and young adults walked normally with comparable spectral characteristics of ML sacrum motion that were largely prescribed by their stride frequencies (~1 Hz). Remarkably, through a complex series of sensorimotor pathways, visual perturbation frequencies permeated the spectral characteristics of old and young adults' ML sacrum motion. However, the markedly greater prevalence of visual perturbation frequencies in the ML sacrum motion of old adults alludes to a fundamental change in their sensorimotor control of walking. Similar to age-related changes reported for postural control (Eikema, et al., 2013; Jeka, et al., 2010; Sundermier, et al.,

1996; Yeh, et al., 2014), an increase in visual feedback "gain" or a decrease in visual inhibition with age may underlie old adults' enhanced sensitivity to visual perturbations during walking.

In contrast to the continuous control of posture, ML motion of the body's CoM during walking is believed to be primarily controlled on a step-to-step basis by adjusting lateral step placement (Bauby & Kuo, 2000; Collins & Kuo, 2013; O'Connor & Kuo, 2009; O'Connor, et al., 2012). Thus, visually-induced changes in the control of lateral step placement may underlie the enhanced prevalence of visual perturbation frequencies in the ML CoM motion of old adults. Walking normally, lateral step placement in old and young adults exhibited temporal persistence, such that a wide right step was likely to be following be a wide left step (and vice versa). Intuitively, this step-to-step dependence effectively delimits fluctuations in ML CoM motion (**Figure 2**), and is therefore an important characteristic of normal walking (Collins & Kuo, 2013; Hof, van Bockel, Schoppen, & Postema, 2007). However, as hypothesized, we found that visual perturbations eliminated the step-to-step temporal persistence of lateral foot placement in old but not young adults. Prior studies have shown that patients with various central nervous system disorders exhibit a similar decorrelation in step parameters that parallels their degree of functional impairment. Thus, our findings strongly suggest that the central nervous system of old adults prioritizes visual feedback for the active control of lateral foot placement during walking.

We interpret the visually-induced changes in ML CoM motion and lateral step placement as highly relevant to old adults' active control of balance during walking. In line with this premise, and as hypothesized, visual perturbations compromised the local dynamic stability of old significantly more than young adults. Specifically, we found that the feet and CoM trajectories of old adults exhibited remarkably less short-term (0 to 1 stride) stability than young adults in response to visual perturbations. The sensitivity of this short-term time scale to visual

perturbations is consistent with prior studies in young adults (McAndrew, et al., 2011). Old adults' short-term local dynamic *in*stability is often interpreted in the context of their inability to recover from an unexpected trip or fall during walking (Kang & Dingwell, 2008; Toebes, et al., 2012). Indeed, short-term local dynamic *in*stability in particular is strongly associated with falls history in old adults (Toebes, et al., 2012). Old adults may thus be less resilient to perturbations and more prone to falling during walking when visual information is poor, absent, or incorrect.

We acknowledge that there are alternative approaches in local dynamic stability analyses to manage the nonstationarities in marker positions that arise during perturbed walking. For example, McAndrew et al. (2010) studied visual perturbations in young adults and used marker velocity time series to calculate local dynamic stability. We explored this alternative, recognizing that appropriately incorporating ML marker kinematics in our state space reconstruction may better unify these outcomes with the DFA analysis of lateral step placement. However, incorporating ML marker kinematics, either as position or velocity time series, yielded divergence curves with substantially nonlinear short-term regions and thus, no properly defined maximum divergence exponent (Dingwell, 2006). Nevertheless, our primary findings were largely insensitive to the specific state space reconstruction; alternative approaches that included ML marker kinematics similarly revealed that visual perturbations elicited significantly larger reductions in short-term local dynamic stability for old vs. young adults (110% and 123% for position and velocity time series, respectively, $p<0.01$).

There are several important limitations of this study. First, we used heel marker trajectories that do not account for changes in foot rotation that could influence subjects' base of support during walking. Also, we interpret old adults' enhanced sensitivity to visual perturbations during walking as implying an increased reliance on visual feedback compared to

young adults. However, we did not investigate age-related changes in the relative sensitivity of subjects to visual, vestibular, and somatosensory perturbations. A possible alternative is that advanced age brings a greater sensitivity to sensory perturbations in general. However, Jeka et al. (2010) found visual reliance during the postural control of standing even after controlling for visual, vestibular, and somatosensory acuity. Finally, we did not assess the relative quality of subjects' sensory feedback systems, and thus cannot establish a causal link between somatosensory decline and the increased sensitivity to visual perturbations observed here for old vs. young adults.

5. Conclusions

Taken together, our findings suggest that advanced age fundamentally alters the integration and relative contributions of visual feedback to actively control balance during walking. Compared to young adults, we propose that the reduced quality of somatosensory feedback and longer reflex latencies commonly reported with advancing age (Dorfman & Bosley, 1979; Patel, et al., 2009) may shift the sensorimotor locus of walking to one of visual reliance in old adults. Consequently, visual perturbations exposed age-related changes relevant to the active control of balance that were not readily apparent during normal, unperturbed walking. Based on this observation, we envision novel clinical tests in which visual perturbations applied during walking make possible the early diagnosis of sensory-induced balance impairments in old adults. Our findings also forecast the promising potential of virtual reality to evaluate the efficacy of sensory rehabilitation and balance training programs for old adults at risk of falls.

Schoenberg for their help with data collection and processing. We also thank Richard Wiebe,

Ph.D. for his helpful insights regarding the analysis of maximum divergence exponents.

Conflicts of Interest

The authors have no conflicts of interest to disclose.

References

ACSM. (2014). *American College of Sports Medicine. Resource Manual For Guidelines For Exercise Testing and Prescription* (7th ed.). Baltimore, MD.

Bauby, C. E., & Kuo, A. D. (2000). Active control of lateral balance in human walking. *J Biomech, 33*, 1433-1440.

Berg, W. P., Alessio, H. M., Mills, E. M., & Tong, C. (1997). Circumstances and consequences of falls in independent community-dwelling older adults. *Age Ageing, 26*, 261-268.

Collins, S. H., & Kuo, A. D. (2013). Two independent contributions to step variability during over-ground human walking. *PLoS One, 8*, e73597.

Deffeyes, J. E., Kochi, N., Harbourne, R. T., Kyvelidou, A., Stuberg, W. A., & Stergiou, N. (2009). Nonlinear detrended fluctuation analysis of sitting center-of-pressure data as an early measure of motor development pathology in infants. *Nonlinear Dynamics Psychol Life Sci, 13*, 351-368.

Dingwell, J. B. (2006). Lyapunov exponents. In M. Akay (Ed.), *The wiley encyclopedia of biomedical engineering* (pp. 14). New York, NY: John Wily & Sons, Inc.

Dingwell, J. B., & Cusumano, J. P. (2010). Re-interpreting detrended fluctuation analyses of stride-to-stride variability in human walking. *Gait Posture, 32*, 348-353.

Donelan, J. M., Shipman, D. W., Kram, R., & Kuo, A. D. (2004). Mechanical and metabolic requirements for active lateral stabilization in human walking. *J Biomech, 37*, 827-835.

Dorfman, L. J., & Bosley, T. M. (1979). Age-related changes in peripheral and central nerve conduction in man. *Neurology, 29*, 38-44.

Eikema, D. J., Hatzitaki, V., Konstantakos, V., & Papaxanthis, C. (2013). Elderly adults delay proprioceptive reweighting during the anticipation of collision avoidance when standing. *Neuroscience, 234*, 22-30.

Guastello, S. J. (2006). Motor control research requires nonlinear dynamics. *Am Psychol, 61*, 77-78.

Hausdorff, J. M., Mitchell, S. L., Firtion, R., Peng, C. K., Cudkowicz, M. E., Wei, J. Y., & Goldberger, A. L. (1997). Altered fractal dynamics of gait: reduced stride-interval correlations with aging and Huntington's disease. *J Appl Physiol (1985), 82*, 262-269.

Hof, A. L., van Bockel, R. M., Schoppen, T., & Postema, K. (2007). Control of lateral balance in walking. Experimental findings in normal subjects and above-knee amputees. *Gait Posture, 25*, 250-258.

Jeka, J. J., Allison, L. K., & Kiemel, T. (2010). The dynamics of visual reweighting in healthy and fall-prone older adults. *J Mot Behav, 42*, 197-208.

Kang, H. G., & Dingwell, J. B. (2008). Effects of walking speed, strength and range of motion on gait stability in healthy older adults. *J Biomech, 41*, 2899-2905.

Kennel, M. B., Brown, R., & Abarbanel, H. D. (1992). Determining embedding dimension for phase-space reconstruction using a geometrical construction. *Phys Rev A, 45*, 3403-3411.

Latt, M. D., Menz, H. B., Fung, V. S., & Lord, S. R. (2009). Acceleration patterns of the head and pelvis during gait in older people with Parkinson's disease: a comparison of fallers and nonfallers. *J Gerontol A Biol Sci Med Sci, 64*, 700-706.

Loughlin, P. J., & Redfern, M. S. (2001). Spectral characteristics of visually induced postural sway in healthy elderly and healthy young subjects. *IEEE Trans Neural Syst Rehabil Eng, 9*, 24-30.

McAndrew, P. M., Dingwell, J. B., & Wilken, J. M. (2010). Walking variability during continuous pseudo-random oscillations of the support surface and visual field. *J Biomech, 43*, 1470-1475.

McAndrew, P. M., Wilken, J. M., & Dingwell, J. B. (2011). Dynamic stability of human walking in visually and mechanically destabilizing environments. *J Biomech, 44*, 644-649.

Niino, N., Tsuzuku, S., Ando, F., & Shimokata, H. (2000). Frequencies and circumstances of falls in the National Institute for Longevity Sciences, Longitudinal Study of Aging (NILS-LSA). *J Epidemiol, 10*, S90-94.

O'Connor, S. M., & Kuo, A. D. (2009). Direction-dependent control of balance during walking and standing. *J Neurophysiol, 102*, 1411-1419.

O'Connor, S. M., Xu, H. Z., & Kuo, A. D. (2012). Energetic cost of walking with increased step variability. *Gait Posture, 36*, 102-107.

Patel, M., Magnusson, M., Kristinsdottir, E., & Fransson, P. A. (2009). The contribution of mechanoreceptive sensation on stability and adaptation in the young and elderly. *Eur J Appl Physiol, 105*, 167-173.

Perry, J., & Burnfield, J. M. (2010). *Gait analysis: normal and pathological function* (2nd ed.). Thorofare, NJ: SLACK Incorporated.

Rosenstein, M. T., Collins, J. J., & De Luca, C. J. (1993). A practical method for calculating largest Lyapunov exponents from small data sets. *Physica D: Nonlinear Phenomena, 65*, 117-134.

Sundermier, L., Woollacott, M. H., Jensen, J. L., & Moore, S. (1996). Postural sensitivity to visual flow in aging adults with and without balance problems. *J Gerontol A Biol Sci Med Sci, 51*, M45-52.

Thelen, D. G., Brockmiller, C., Ashton-Miller, J. A., Schultz, A. B., & Alexander, N. B. (1998). Thresholds for sensing foot dorsi- and plantarflexion during upright stance: effects of age and velocity. *J Gerontol A Biol Sci Med Sci, 53*, M33-38.

Thelen, D. G., Schultz, A. B., Alexander, N. B., & Ashton-Miller, J. A. (1996). Effects of age on rapid ankle torque development. *J Gerontol A Biol Sci Med Sci, 51*, M226-232.

Ting, L. H., van Antwerp, K. W., Scrivens, J. E., McKay, J. L., Welch, T. D., Bingham, J. T., & DeWeerth, S. P. (2009). Neuromechanical tuning of nonlinear postural control dynamics. *Chaos, 19*, 026111.

Toebes, M. J., Hoozemans, M. J., Furrer, R., Dekker, J., & van Dieen, J. H. (2012). Local dynamic stability and variability of gait are associated with fall history in elderly subjects. *Gait Posture, 36*, 527-531.

Virgin, L. N. (2000). *Introduction to experimental nonlinear dynamics: a case study in mechanical vibration*. Cambridge, UK: Cambridge University Press.

Yeh, T. T., Cluff, T., & Balasubramaniam, R. (2014). Visual reliance for balance control in older

    adults persists when visual information is disrupted by artificial feedback delays. *PLoS*

    One, 9, e91554.

Zeni, J. A., Jr., Richards, J. G., & Higginson, J. S. (2008). Two simple methods for determining

    gait events during treadmill and overground walking using kinematic data. *Gait Posture,*

    27, 710-714.

Figure Captions

Figure 1. We implemented a virtual reality system to perturb visual flow during treadmill walking and quantified the effects on center of mass (CoM) motion and step placement dynamics. We used heel marker data to construct time series of alternating left and right step widths.

Figure 2. Relation between ML sacrum motion and lateral step placement during normal (black line) and visually perturbed (blue line) waking for representative old and young subjects.

Figure 3. Group average spectral characteristics of the ML sacrum marker in old and young adults. Single asterisks (*) indicate significant difference between normal and visually perturbed walking, and double asterisks (**) indicate significant difference between old and young adults (p<0.05).

Figure 4. Detrended fluctuation analysis results. (A) Step width time series over 90 consecutive steps extracted from the 300 analyzed during normal (black line) and visually perturbed (blue line) walking for representative old and young subjects. (B) Mean (standard error) 1st and 2nd order scaling exponents of the relation between the root mean square (RMS) residual of step width and number of steps. We interpreted these scaling exponents as follows: $\alpha = 0.5$ indicates uncorrelated white noise; $\alpha < 0.5$ indicates that deviations in one direction are likely to be followed by deviations in the opposite direction (i.e., anti-persistent); and $\alpha > 0.5$ indicates that deviations in one direction are likely to be followed by deviations in the same direction (i.e., persistent). Single asterisks (*) indicate significant difference between normal and visually perturbed walking, and double asterisks (**) indicate significant difference between old and young adults ($p < 0.05$).

Figure 5. Local dynamic stability results. (A) Mean (standard error) divergence curves (Dingwell, 2006) for old and young adults during normal (black line) and visually perturbed (blue line) walking. (B) Mean (standard error) maximum short-term and long-term divergence exponents, where larger positive values are indicative of greater local dynamic *in*stability. Single asterisks (*) indicate significant difference between normal and visually perturbed walking, and double asterisks (**) indicate significant difference between old and young adults ($p < 0.05$).

Table 1. Goodness of fit (R^2) for estimates of DFA and maximum local divergence exponents

	DFA, α (1st order)		DFA, α (2nd order)		λ_S		λ_L	
	Old	Young	Old	Young	Old	Young	Old	Young
Normal	0.96 (0.02)	0.96 (0.03)	0.95 (0.02)	0.94 (0.04)	0.99 (~)	0.99 (~)	0.98 (0.01)	0.98 (0.02)
Visually Perturbed	0.95 (0.03)	0.97 (0.01)	0.92 (0.03)	0.94 (0.02)	0.99 (~)	0.99 (~)	0.96 (0.05)	0.96 (0.03)

Values are mean (standard deviation). DFA: detrended fluctuation analysis. λ_S and λ_L refer to the maximum short- and long-term local divergence exponents. Tildes (~) indicate standard deviation < 0.005.

ML

SW(i+2)

SW(i+1)

SW(i)

Sacrum
Trajectory

Young Subject   **Old Subject**

- L. Heel at Footstrike
- R. Heel at Footstrike
— Sacrum

Visually Perturbed

Normal

5 s

L ←→ R   L ←→ R

0.5 m   0.5 m

(A)

Young Subject

Normal

Visually Perturbed

Step Width

Old Subject

Normal

Visually Perturbed

Step Width

0 10 20 30 40 50 60 70 80 90

step #

(B)

■ Normal
■ Visually Perturbed

α (1st Order)

1.00

0.75

0.50

0.25

0

**

Young   Old

α (2nd Order)

1.00

0.75

0.50

0.25

0

**

Young   Old

(A)

Young

Old

(B)