

Identifying the control of physically and perceptually evoked sway responses with coincident visual scene velocities and tilt of the base of support

Yun Wang · Robert V. Kenyon · Emily A. Keshner

Received: 11 July 2009 / Accepted: 2 November 2009 / Published online: 19 November 2009
© Springer-Verlag 2009

Abstract In this study, we have explored whether the impact of visual information on postural reactions is due to the same perceptual mechanisms that produce vection. Pitch motion of the visual field was presented at varying velocities to eight healthy subjects (29.9 ± 2.8 years) standing quietly on a stationary base of support or receiving a 3° toes-up tilt of the base of support. An infrared motion system recorded markers placed on body segments to record angular displacement of head and ankle and calculate whole body center of mass. Onset of the visual field motion and base of support movement were synchronized in all trials. We found that in the first 2 s following onset of visual field motion, both direction and amplitude of the linear displacement of whole body center of mass and angular displacement of the head, hip, and ankle were modulated by the velocity of visual scene motion. When the visual scene rotated in upward pitch, subjects overshot their initial vertical position with amplitudes that increased as velocity of the visual field increased. This behavior was even more

evident when the base of support was tilted. These responses were much shorter than those observed in studies of vection. The dependence of the postural response amplitudes on the velocity of the visual field suggests, however, that there might be well-shared control pathways for visual influences on postural reactions and postural sway elicited by an illusion of self-motion.

Keywords Posture · Virtual reality · Vection · Sensory re-weighting · MST

Introduction

Attempts to determine whether the impact of visual information on postural reactions is due to the same perceptual mechanisms that also produce the sway resulting from the illusion of self-motion produced by an optic flow field and known as vection (Clément et al. 1985; Previc and Mullen 1991; Previc and Donnelly 1993) have produced conflicting results. Studies that examined body sway on a stable surface while in the Romberg position (Tanahashi et al. 2007; Kuno et al. 1999) concluded that postural sway and sway elicited by vection relied upon a shared central mechanism. When standing on an unstable support surface such as foam (Guerraz and Bronstein 2008) or a sinusoidally moving platform (Keshner et al. 2004) so that the direction of the two sway responses could be differentiated, it was observed that postural instability occurred earlier and in the opposite direction from the later vection response. The different time course and mismatch between the direction of postural responses and the direction of vection supported an earlier conclusion that the perceptual and postural sway responses were not generated from a single visual control mechanism (Previc and Donnelly 1993).

Y. Wang (✉)

Department of Infant Education, Iwakuni Junior College,
Ohtsu-Cho 2-24-18, Iwakuni 740-0032, Japan
e-mail: yun-wang@iwakuni.ac.jp

R. V. Kenyon

Department of Computer Science,
University of Illinois-Chicago, Chicago, IL, USA

E. A. Keshner

Department of Physical Therapy, College of Health Professions,
Temple University, Philadelphia, PA, USA

E. A. Keshner

Department of Electrical and Computer Engineering,
Temple University, Philadelphia, PA, USA

But more recent studies of automatic postural reactions on perturbed base of support (Dokka et al. 2009; Keshner et al. 2007; Keshner and Dhaher 2008) have demonstrated a direct relationship between the velocity and direction of the visual flow field and the orientation and amplitude of motion at individual segments of the body such as the head, hip, and knee. An extensive literature, ranging from behavioral studies (Dichgans et al. 1975; Slobounov et al. 2006; Tanahashi et al. 2007; Thurrell and Bronstein 2002) to neuroimaging studies (Brandt et al. 2002; Kleinschmidt et al. 2002; Wiest et al. 2001) has demonstrated that both vestibular and visual inputs interact at the brain stem and cortical levels during vection and contribute to the illusion of self-motion. The short latency effects of visual information during motor execution (Day and Guerraz 2007; Miles 1998) could be involved in these early visually evoked postural behaviors as they have been shown to suppress vestibular signals through sub-cortical visual pathways.

Evidence also exists, however, to support the hypothesis of a single mechanism operating to control the postural and perceptual behaviors. In studies employing galvanic vestibular stimulation (GVS), a GVS-induced directional effect was obvious during locomotion both when visual information was and was not available (Bent et al. 2000, 2004; Jahn et al. 2000; Fitzpatrick et al. 1999). This behavior was attributed to both an altered perception of vertical and postural instability resulting from the GVS-induced body tilt. With unexpected environments, such as a tilting room, a mismatch between the world and the physical motion produces a sensory conflict that interferes with the ability to distinguish between visual field motion and motion of the body (Dichgans et al. 1972; Lackner and DiZio 1988). This results in spatial disorientation even during self-initiated motion (Previc and Donnelly 1993; Previc 1992) and suggests single processor acting in response to these combined inputs.

If there were a single controller for the postural reactions and the visually generated perception of vection, then we would expect these responses to be parametrically linked even during dynamic stabilization tasks (Previc and Donnelly 1993). For example, a significant effect of visual field velocity was observed on the peak angular velocities of the head in healthy young adults within 500 ms of a platform tilt (Keshner et al. 2007; Keshner and Dhaher 2008). However, in these studies, the whole body posture response was not evaluated and the observed changes may have been due to visual tracking behaviors of the head. Thus, in this study, we have hypothesized that if the postural responses induced by visual information were elicited by the short latency optokinetic reflexes, then we would expect modification of the automatic postural reactions that occur in response to a physical destabilization. To explore this possibility, we examined the postural restabilizing response that occurs after the early proprioceptively generated lower limb

responses of 90–120 ms subside (Keshner et al. 1987), but before vection sway response emerges (Keshner and Kenyon 2000). Specifically, we have provided pitch motion of the visual field at varying velocities while imposing an upward tilt of the base of support. Our results demonstrate that wide field of view motion affects the vertical orientation of the body in space differentially when standing on an earth-referenced base of support or following the automatic reaction to a tilted base of support which might explain the disagreements in the literature about shared visual control mechanisms underlying physically and perceptually generated sway responses.

Methods

Subjects

Eight subjects (5 male, 3 female) naïve to virtual environments participated in this study (mean \pm SD for age 29.9 ± 2.8 years, height 1.70 ± 0.07 m, weight 67.3 ± 13.4 kg). All were free of any known musculoskeletal or neurological disorders which may have impacted their performance. All subjects were informed of the procedures and provided written consent in accordance with the Institutional Review Board of Feinberg School of Medicine, Northwestern University.

Apparatus

Subjects viewed a virtual environment projected via a stereo-capable projector (Electrohome Marquis 8500) mounted behind a 1.2 m \times 1.6 m back-projection screen. A full-color stereo workstation field (1,024 \times 768 stereo) was projected at 120 Hz onto the screen. A dual Pentium IV PC with an nVidia 3000 graphics card created the imagery projected onto the screen. Field sequential stereo images generated by the PC were separated into right and left eye images using liquid crystal stereo shutter glasses worn by the subject (Crystal Eyes, StereoGraphics Inc.). The centers of projection used to produce images for each eye were generated with 7 cm spacing between them [approximately equal to the average interpupillary distance (IPD)]. The stereo update rate of the scene (how quickly a new image was generated by the graphics computer) was 60 stereo frames/s.

The scene consisted of a room containing round columns with patterned rugs and painted ceiling. The columns were 6.1 m apart and rose 6.1 m off the floor to the ceiling. The rug patterns were texture mapped on the floor and consisted of ten different patterns. The interior of the room measured 30.5 m wide \times 6.1 m high \times 30.5 m deep. Subjects were positioned on a platform so that it appeared that they were placed in the center of the virtual room between two rows

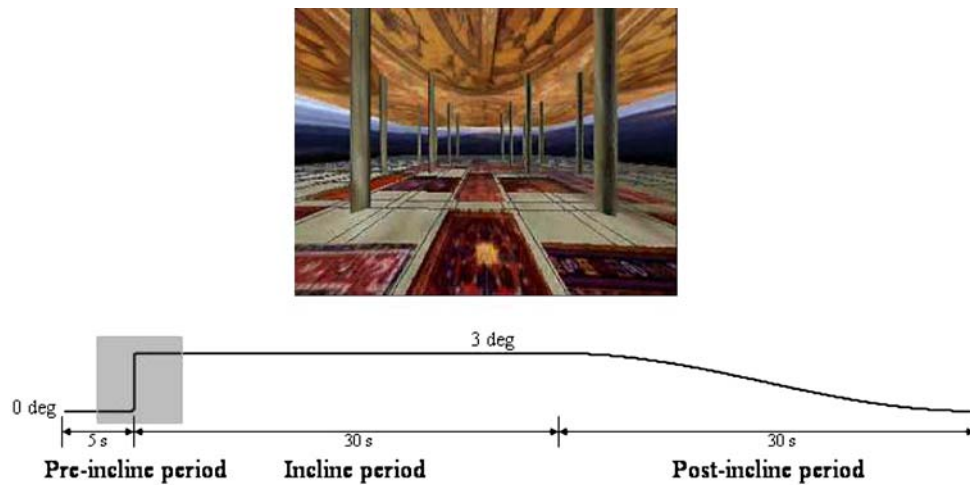


Fig. 1 *Upper panel* The visual scene of the virtual environment was viewed by the subjects. The virtual scene was externally driven at one of four constant velocities in the pitch-up direction: 0°/s (visible but stationary relative to head motion, VR_0), 30°/s (VR_30), 45°/s (VR_45), and 60°/s (VR_60). *Lower panel* The schema of the experimental setup. All trials were 65 s in duration. Trials in which the platform was inclined consisted of a pre-incline period of 5 s when the

support surface was held horizontal, an incline period of 30 s when the surface was maintained in the toe-up position following the 30°/s ramp, and a post-incline period of 30 s when the surface slowly returned to the horizontal at a constant velocity of 0.1°/s. In this paper, we will present data (highlighted) only during the incline period and for the same period of time with the stationary platform

of columns. Since the platform was 26.6 cm above the laboratory floor, the image of the virtual room was adjusted so that its height matched the platform height (i.e., the virtual floor and the top of the sled were coincident). Beyond the virtual room was a landscape consisting of mountains, meadows, sky and clouds. The floor was the distance from the subject's eyes to the virtual floor, and the nearest column was 4.6 m away. The resolution of the image was 7.4 min of arc per pixel when the subject was 40 cm from the screen. The view from the subjects' position was that objects in the room were both in front of and behind the screen. The axis of virtual scene rotation was approximately located at the interaural axis for each subject.

Subjects stood upon a platform (Neurocom Inc., Clackamas, OR, USA) that either remained stationary or rotated in the sagittal plane (3° of dorsiflexion) with a constant velocity ramp of 30°/s. A six-camera Motion Analysis (Motion Analysis, Inc.) system was used to capture joint motion at 120 Hz. Infrared markers were attached bilaterally on the second metatarsophalangeal joint, lateral malleolus, lateral epicondyle of the tibia, greater trochanter of the femur, acromion process, lateral epicondyle of the humerus, styloid process of the ulna, second metacarpophalangeal joint, zygomatic arch, and the external auditory meatus of the ear. Markers were also placed on C-7, L4/L5 joint of the spine and on the occipital region of the head.

Procedures

Subjects stood comfortably on the platform with the feet side-by-side, at hip width and with their upper arms at their

sides and bent at the elbows. Foot position was marked on the platform and reproduced across trials. Subjects were asked to maintain an erect posture while standing in the dark or in front of a virtual scene with natural visual motion.

The virtual scene was externally driven at one of four constant velocities in the pitch-up direction: 0°/s (visible but stationary relative to head motion, VR_0), 30°/s (VR_30), 45°/s (VR_45), and 60°/s (VR_60). All trials were 65 s in duration. Trials in which the platform was inclined consisted of a pre-incline period of 5 s when the support surface was held horizontal, an incline period of 30 s when the surface was maintained in the toe-up position following the 30°/s ramp, and a post-incline period of 30 s when the surface slowly returned to the horizontal at a constant velocity of 0.1°/s. In this paper, we will present data only from the incline period and the same period of time with the stationary platform (Fig. 1).

Onset of virtual scene and platform movement were synchronized in all trials. Following each trial, there was a rest period with eyes closed for approximately 1 or 2 min. A total of 30 trials were presented in a pseudo-random (balanced) order that included 3 trials of each of the five visual conditions and the two platform conditions.

Data processing

Previous studies showed that there were no directionally specific postural responses orthogonal to the displacement of a visual scene (Gielen and van Asten 1990; van Asten et al 1988; Wolsley et al 1996). All of our experimental

conditions were in the anterior–posterior direction; therefore, we will only present data from responses in the anterior–posterior direction.

Whole body COM was calculated by a weighted average of the COM of each body segment (Guerraz et al. 2001a, b). A line drawn between the markers on the external auditory meatus of the ear and the occiput was used to calculate head angular position relative to gravitational vertical. A line drawn between the markers on the L4/L5 joint of the spine and C-7 was used to calculate trunk angular position relative to space. Head angular displacement relative to the trunk was the difference between this line and a line drawn between the markers on the external auditory meatus of the ear and the occiput. Angular motion of the upper leg (thigh) was defined as a line drawn between the greater trochanter of the femur and the lateral epicondyle of the tibia. The difference between this line and the line of the trunk defined the hip angular displacement. Ankle joint position was the angle between the line from the second metatarsophalangeal joint to lateral malleolus and the line from lateral malleolus to lateral epicondyle of the tibia in the sagittal plane. All data were low-pass filtered using a fourth-order Butterworth digital filter at 4 Hz.

Previous studies from this laboratory (Keshner et al. 2007; Keshner and Dhaher 2008) reported that the effect of visual field motion on the postural responses was observed 500–1,000 ms following onset of a platform tilt. Thus, in this study, we examined the mean position of whole body COM and angular displacement of the head and ankle segments over a 2.5-s period (Guerraz et al. 2001a, b) before stimulus onset and from 1.2 to 3.7 s after the onset of stimulus motion for each experimental condition. The difference between these two

periods was calculated as the amplitude of the COM, head, and ankle in response to a sustained 3° tilt of the base of support (the platform). The first 1.2 s following stimulus onset was excluded from the computation to allow the initial automatic postural reaction to subside (Nashner and Berthoz 1978; Guerraz et al. 2001a, b). When the visual scene motion was combined with a toe-up platform, the latency of whole body COM, angular displacement of the head and ankle segments was determined as the time at which the whole body COM, angular displacement of the head and ankle segments reached its peak in response to the experimental condition prior to the corrective adjustment.

Comparisons across the visual scene conditions (dark, VR_0, VR_30, VR_45, and VR_60) were made with a one-way, repeated measures ANOVA. When there was a significant effect, Bonferroni post hoc comparisons at $p < 0.05$ were made to determine differences. Effects of platform movement (stable and toe-up) were analyzed separately on the same variables.

Results

Whole body COM displacement

There was a significant main effect of visual condition ($F(4, 28) = 11.8, p < 0.001$) on COM displacement. When the platform was stable and the visual scene was moving, subjects exhibited motion of the COM in the backward direction (Fig. 2, top panel) which increased in amplitude in the pitch-up direction as the velocity of the visual scene increased (Table 1). Post hoc tests revealed significant

Fig. 2 Typical COM displacements in the anterior–posterior (AP) direction averaged across three trials from a representative subject in both the stable and toe-up conditions. The onset of stimulus motion is shown as a solid line. The dashed line indicates 1.2 s after stimulus onset which served as the beginning of the measure of post-stimulus postural adjustment. Forward motion is in the upward direction on the plot

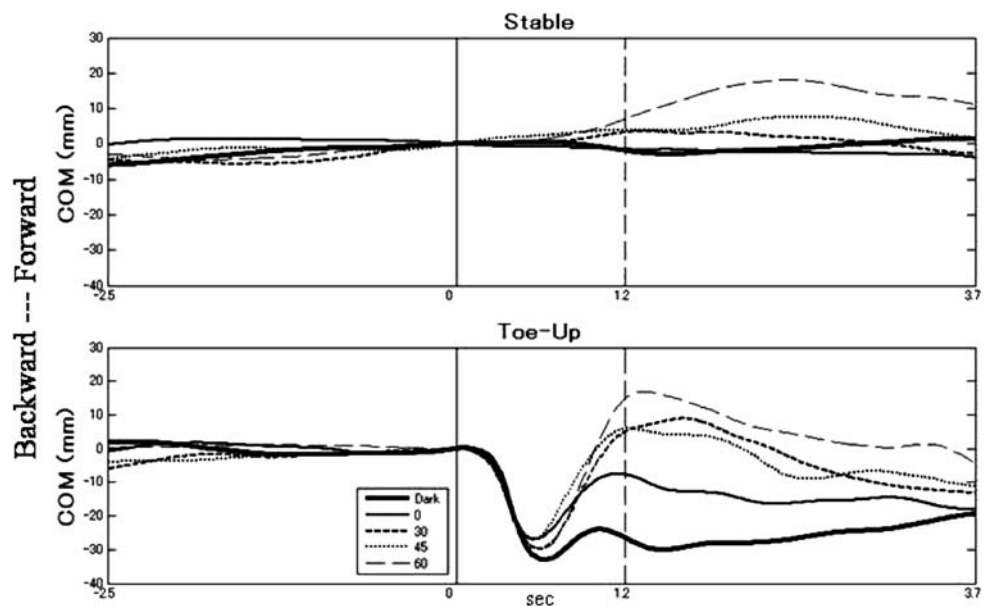


Table 1 Mean ± SE of the amplitude of displacement in response to the platform tilt

Visual condition platform	0°/s (VR_0)		30°/s (VR_30)		45°/s (VR_45)		60°/s (VR_60)			
	Stable	Toe-up	Stable	Toe-up	Stable	Toe-up	Stable	Toe-up		
COM displacement (mm)*	1.67 ± 1.67	-18.50 ± 4.65	0.16 ± 2.32	-16.32 ± 5.67	4.89 ± 1.17	0.12 ± 4.58	9.25 ± 1.48	-1.45 ± 3.18	10.71 ± 1.25	3.25 ± 4.42
Head displacement in space (°)	0.28 ± 0.19	-0.26 ± 0.31	0.17 ± 0.22	0.23 ± 0.55	0.75 ± 0.22	0.98 ± 0.79	1.02 ± 0.31	0.78 ± 0.71	1.27 ± 0.34	1.57 ± 0.75
Hip angular displacement (°)*	-0.11 ± 0.08	0.10 ± 0.34	-0.16 ± 0.12	0.001 ± 0.45	0.05 ± 0.10	0.66 ± 0.34	0.15 ± 0.17	0.75 ± 0.29	0.23 ± 0.08	1.1 ± 0.36
Ankle angular displacement (°)	-0.05 ± 0.04	-0.72 ± 0.37	-0.02 ± 0.07	-2.53 ± 0.39	-0.08 ± 0.08	-3.41 ± 0.35	-0.22 ± 0.10	-2.74 ± 0.32	-0.21 ± 0.11	-3.69 ± 0.39

*Significant ($p < 0.05$) differences observed with incrementing visual scene velocities (see text for specific comparisons)

differences in COM displacement between the visual velocity of 60°/s (VR_60) and dark ($p < 0.01$), 0°/s (VR_0) ($p < 0.001$), and 30°/s (VR_30) ($p < 0.05$). Significant differences were also seen between the 45°/s visual velocity (VR_45) and dark ($p < 0.01$) and between 45°/s (VR_45) and 0°/s (VR_0) ($p < 0.001$).

When the visual scene motion was combined with a toe-up platform (Fig. 2, bottom panel), the initial forward body sway in response to an upward tilt of the platform was followed by a corrective backward return at a mean latency of 710 ± 70 ms following the tilt onset. There was no significant main effect of visual velocity on the latency of the COM motion (Table 2). There was, however, a significant main effect of visual velocity ($F(4, 28) = 14.2, p < 0.001$) on the magnitude of backwards COM motion (Table 1). In the dark, the COM moved further from the initial position and was not fully corrected to return to the initial vertical position (Fig. 2). With 0°/s of visual motion, there was more backward corrective motion than in the dark, but subjects still did not return to initial vertical. In contrast, when the visual scene was moving, subjects overcompensated and even moved their COM beyond the initial vertical position. Post hoc analyses revealed that the magnitude of COM motion in the dark and at 0°/s was significantly different from all other visual velocities ($p < 0.001$).

Head angular displacement relative to gravitational vertical

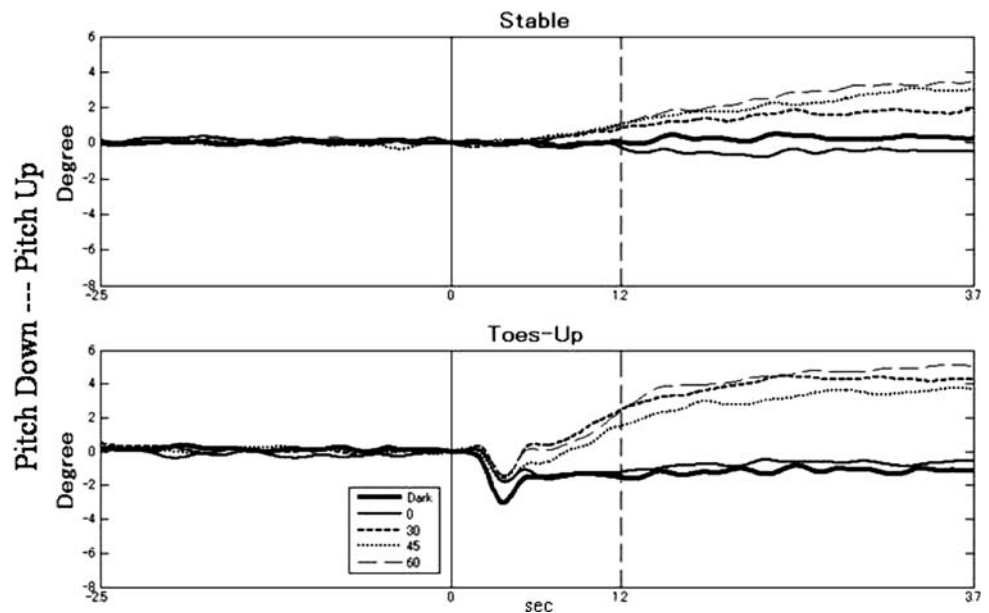
When the platform was stable, visual motion induced an upward pitch response of the head in the same direction as the scene (Fig. 3, top panel). With increasing velocity of the visual scene, the magnitude of head angular displacement in the upward direction also increased (Table 1). This increasing head angular displacement exhibited a significant change from approximately 0° with 0°/s of visual motion to approximately 1.5° with 60°/s of visual motion ($F(4, 28) = 5.8, p < 0.01$). Post hoc tests confirmed that head angular displacements with a visual scene velocity of 60°/s were significantly greater than those with a dark ($p < 0.05$) or 0°/s visual scene ($p < 0.05$).

When the visual scene motion was combined with a toe-up platform, a transient pitch-down head response occurred. This was followed by an upward pitch motion of the head at a latency of 570 ± 80 ms after stimulus onset and no significant effect of visual velocity (Table 2). In the dark and 0°/s tasks, the head did not fully return to its initial vertical position. When the visual scene was moving, however, the upward pitch motion of the head overshot the initial vertical head position (Fig. 3, bottom panel). A significant main effect of visual velocity on head angular displacement in space was observed ($F(4, 28) = 2.8, p < 0.05$) but no significant difference across individual scene velocities appeared (Table 1).

Table 2 Mean \pm SE of the response latency following onset of platform tilt (s)

Visual Condition	Dark	0°/s (VR_0)	30°/s (VR_30)	45°/s (VR_45)	60°/s (VR_60)	Mean \pm SD
COM movement	0.77 \pm 0.09	0.79 \pm 0.08	0.68 \pm 0.03	0.69 \pm 0.07	0.62 \pm 0.03	0.71 \pm 0.07
Head movement in space	0.54 \pm 0.06	0.55 \pm 0.11	0.56 \pm 0.07	0.59 \pm 0.06	0.61 \pm 0.10	0.57 \pm 0.08
Ankle angular movement	0.57 \pm 0.07	0.59 \pm 0.07	0.55 \pm 0.05	0.58 \pm 0.06	0.67 \pm 0.07	0.59 \pm 0.06

Fig. 3 Typical pitch angular displacements of the head relative to space averaged across three trials from a representative subject in both the stable and toe-up conditions. The moment of the onset of stimulus motion is shown as a *solid line*. The *dashed line* indicates 1.2 s after stimulus onset that served for the beginning of the measure of post-stimulus postural adjustment. Pitch upward motion is in the upward direction on the plot



Head angular displacement relative to the trunk

Although there were no significant effects of visual scene velocity on angular displacement of the head relative to the trunk, there were emerging effects. When the base of support was stable, the head moved in the pitch-up direction relative to the trunk after about 1.2 s of viewing pitch-up visual scene motion at the two highest velocities (top panel, Fig. 4). In the toes-up condition (bottom panel, Fig. 4), there were pronounced oscillations of the head with respect to the trunk in the first 1,000 ms of the base of support disturbance. The head initially pitched down with the trunk following the plantar flexion tilt of the base of support. This was followed by an upward pitch and another downward pitch before reaching a plateau. The magnitude of this oscillation appeared to vary with velocity of the visual scene as previously reported (Keshner et al. 2007). Once the oscillations subsided, the head was held pitched down with respect to the trunk as would be expected if the head was compensating for backward motion of the trunk as seen in the COM (lower panel, Fig. 2).

Hip angular displacement

Changes in visual scene velocity elicited distinct increments in the changes of the thigh position relative to the trunk (i.e., the hip angle) as visual scene velocity increased (Fig. 5).

There was a significant effect of visual velocity with both the stable ($F(4, 28) = 2.27, p < 0.05$) and toe-up platform ($F(4, 28) = 4.07, p < 0.01$). Paired comparisons revealed significant differences between DARK and VR_60 ($p < 0.002$) with both platform conditions. Combining a toe-up platform with visual scene motion produced significantly larger ($F(4, 35) = 12.52, p < 0.05$) angular displacements of the hip than when toe-up motion of the platform occurred in the dark or with 0°/s visual scene velocity (Table 1).

Ankle angular displacement

The presence of visual motion with a stable platform produced increased dorsiflexion motion at the ankle (Fig. 6, top panel). A significant main effect of visual velocity ($F(4, 28) = 2.8, p < 0.05$) on ankle angular displacement (Table 1) emerged, but with no significant differences appearing between scene velocities. When the platform moved in toe-up, an obvious dorsiflexion of the ankle occurred with the motion of platform and reached its peak angular displacement approximately 590 \pm 60 ms after stimulus onset (bottom, Fig. 6). There was no main effect ($F(4, 28) = 0.855, p > 0.05$) of visual condition on this latency (Table 2). A significant main effect of visual velocity ($F(4, 28) = 5.6, p < 0.01$) on ankle angular displacement (bottom, Fig. 6) emerged, and post hoc tests revealed that

Fig. 4 Typical pitch head angular displacements relative to the trunk averaged across three trials of a representative subject in both the stable and toe-up conditions. Onset of stimulus motion is shown as a *solid line*. The *dashed line* indicates 1.2 s after stimulus onset that served for the beginning of the measure of post-stimulus postural adjustment. Pitch upward motion is in the upward direction on the plot

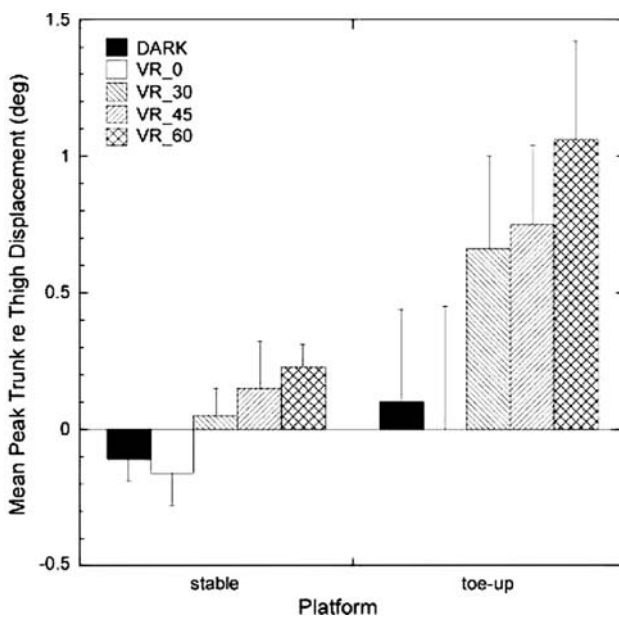
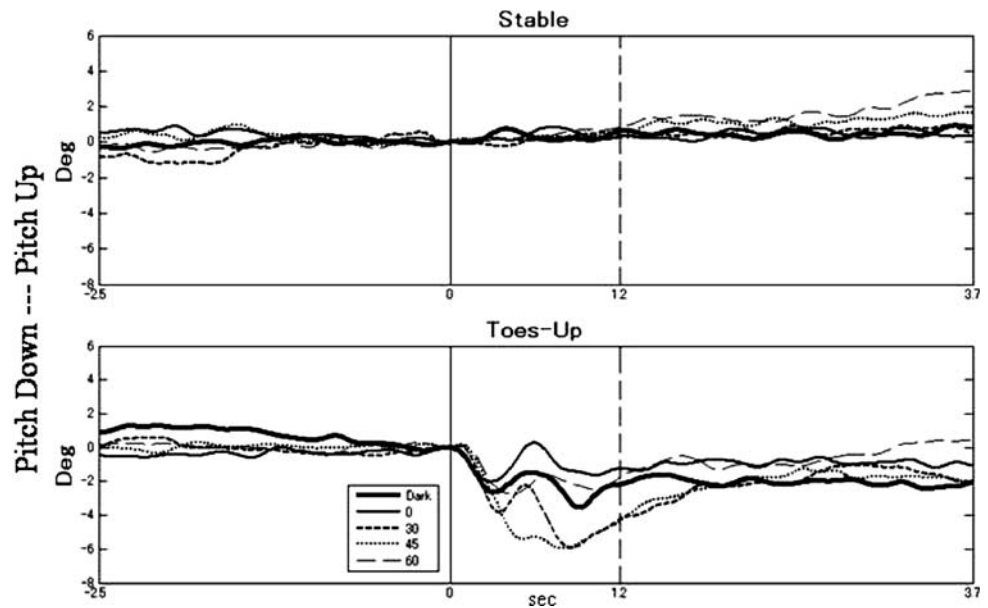


Fig. 5 Mean peak angular displacement and standard error of the thigh relative to the trunk (hip angle) across all subjects at each visual velocity in both the stable and toe-up conditions

ankle angular displacement with a 60°/s visual velocity was significantly greater than with the dark ($p < 0.05$) and 0°/s visual scenes ($p < 0.01$). There was also a significant difference in ankle angular displacement ($p < 0.05$) with the 45 and 60°/s visual scene velocities.

Discussion

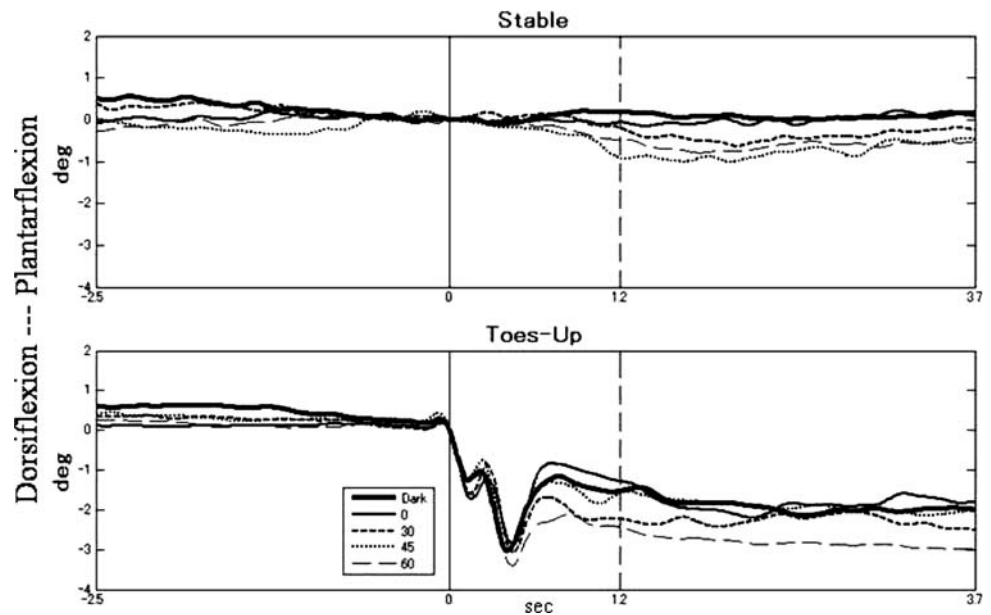
The goal for postural orientation, whether it is in response to a physical disturbance or a perceptual illusion of motion,

is to maintain the center of gravity over the base of support which is usually achieved by alignment with respect to the perceived direction of gravity. The ability to return to a vertical orientation appears to depend very much on the information conveyed by the ongoing sensory array (Dichgans et al. 1972; Keshner and Kenyon 2000). In this study, initial observed responses throughout the body were in the compensatory direction to the mechanical disturbance of the base of support. It was only after the body reacted to that mechanical disturbance and was returning to the upright position that we observed responses indicating that the visual field began to exert a strong influence on the amplitude of the response.

Restabilizing responses exhibited differences in both direction and amplitude when the visual field was dark or stationary and when the visual field was moving in upward pitch. When the visual field was dark or stationary and the base of support was also stationary, subjects were able to maintain their initial vertical orientation. With a tilted platform, however, the initial vertical orientation was not recovered. In the dark or with a earth-fixed visual field, subjects retained a body angle close to the angle produced by the tilt of the platform as if they were relying on the base of support inputs to supply the signal indicating vertical (Kluzik et al. 2005, 2007). A tilted platform with a moving visual field, however, produced a compensatory response that showed a definitive overshoot of the initial vertical as subjects traveled in the same direction of pitch as the visual scene.

When only the visual scene was moving and the base of support was stationary, the subjects experienced a conflict between the visual perception of motion and the vestibular and proprioceptive systems signaling an absence of physical motion. The increase in the amplitude of center of mass

Fig. 6 Typical ankle angular displacements averaged across three trials from a representative subject in both the stable and toe-up conditions. Onset of stimulus motion is shown as a *solid line*. The *dashed line* indicates 1.2 s after stimulus onset that served for the beginning of the measure of post-stimulus postural adjustment. Plantar flexion motion is in the upward direction on the plot



motion in the backward direction as the velocity of the visual scene increased likely reflects an effort by the postural control system to stabilize body position with respect to the perceived environmental conditions. These corresponding changes in velocity of the body with velocity of the visual scene suggest some dynamical interaction between the canals and otoliths when signaling the actual gravitational vector and the visual system's motion signal (Dijkstra et al. 1994; Green et al. 2005). Thus, when the base of support was stationary, the postural sway of the body was strongly linked to the motion of the visual scene. This would suggest that the subject was considering the environmental motion when forming a reaction that would maintain posture, but at latencies much shorter than the 8–10 s latencies expected fromvection (Dichgans et al 1975; Guerraz and Bronstein 2008; Keshner and Kenyon 2000; Keshner et al. 2004; Previc 1992).

Correspondence between the amplitude of postural sway and the velocity of visual motion became even more evident when the subjects negotiated a 3° toes-up inclined surface. In this situation, whole body center of mass was observed to first shift forward in response to the physical disturbance and then to produce a backward motion that was clearly modulated by the velocity of the visual scene. Although individual segmental movements did not always respond significantly to the visual field, incremental changes with increasing visual velocity emerged and were even larger when the platform was tilted. The summation of these incremental changes at the head and hip as velocity increased would be expected to modify the ultimate position of the center of mass (Dokka et al. 2009) so that velocity of the visual environment had a stronger and more discriminating influence on motion of the body when the

platform was tilted than when the base of support was stationary. The reduction of sensory conflict by concomitant visual and physical motion has been a mainstay of simulators for promoting the “suspension of disbelief” in crewmembers (Young 1978). Unlike the simulator case, however, the well-defined modulation of body motion with respect to visual field motion occurred at shorter latencies in this study than would be expected from avection response. In addition, the well-defined changes with visual field velocity would suggest that the identification of orientation in space becomes more dependent on (or more heavily weights) the dynamics of the visual field when the base of support was not earth-referenced (Guerraz et al. 2001a, b; Peterka 1995).

The tendency of the body to follow both the direction and amplitude of the visual flow field implies that ambiguity in the information about gravitational vertical provided by the vestibular otoliths (Green et al. 2005; Zupan and Merfeld 2005) promotes a reliance on visual information for identification of vertical orientation. The dependence of the postural response amplitudes on the velocity of the visual field has been reported previously for the segmental kinematics (Dokka et al. 2009; Keshner et al. 2007). Although these behaviors occurred at latencies much shorter than those elicited byvection, we infer from these results that there are shared control pathways for visual influences on postural reactions and the postural sway elicited by an illusion of self-motion. Short latency optokinetic responses elicited by a visual flow field (Miles 1998) have the potential for generating the early postural reactions to a visual flow field. In monkeys, the medial superior temporal (MST) region of the cortex is the earliest stage at which global optic flow is encoded at the level of single neurons

(Tanaka and Saito 1989), and it has been suggested that MST has a central role in compensation for translational disturbances (Busettini et al. 1997) and the computation of heading (Duffy and Wurtz 1995).

Our data also suggest that the visual control of postural sway is pervasive for the alignment of head and ankle orientation with respect to the gravitational vertical. Although the stability of the base of support did not directly affect head angular displacement, increases in the velocity of the visual scene were always accompanied by an increase in the magnitude of head angular displacement. Across the different visual velocities, significant adjustments occurred at the ankle joint with both the stationary and inclined support surfaces implying that the visual inputs contributed to ankle joint stabilization as well. It is of some interest to note that the ankle joint never fully compensated for the 3° tilt of the platform in the dark condition, from which we might infer that proprioception and vestibular information may not accurately identify a vertical orientation in space in the absence of visual feedback.

Our study of postural restabilization reveals that when subjects experienced concomitant disturbances of the visual and proprioceptive/vestibular systems, the initial recovery of vertical orientation in space was very sensitive to the dynamics of the visual field. Such adaptations to an active visual environment, particularly when combined with an unstable base of support, may well have significant impact on the ability to maintain upright stance when negotiating challenging environmental demands, and the absence of this rapid response to visual information may contribute to postural instability.

Acknowledgments This work was supported by National Institute of Health grants DC05235 from the NIDCD and AG26470 from the NIA. We gratefully acknowledge VRCO for supplying CAVE library software.

References

- Bent LR, McFadyen BJ, Merkley VF, Kennedy PM, Inglis JT (2000) Magnitude effects of galvanic vestibular stimulation on the trajectory of human gait. *Neurosci Lett* 279:157–160
- Bent LR, McFadyen BJ, Inglis JT (2004) Is the use of vestibular information weighted differently across the initiation of walking? *Exp Brain Res Experimentelle Hirnforschung* 157:407–416
- Brandt T, Glasauer S, Stephan T, Bense S, Yousry TA, Deutschlander A (2002) Visual-vestibular and visuovisual cortical interaction: new insights from fMRI and pet. *Ann NY Acad Sci* 956:230–241
- Busettini C, Masson GS, Miles FA (1997) Radial optic flow induces vergence eye movements with ultra-short latencies. *Nature* 390:512–515
- Clément G, Jacquin T, Berthoz A (1985) Habituation of postural readjustments induced by motion of visual scenes. In: Igarashi M, Black OF (eds) *Vestibular and visual control on posture and locomotor equilibrium*. Karger, Basel, pp 99–104
- Day BL, Guerraz M (2007) Feedforward versus feedback modulation of human vestibular-evoked balance responses by visual self-motion information. *J Physiol* 582:153–161
- Dichgans J, Held R, Young LR, Brandt T (1972) Moving visual scenes influence the apparent direction of gravity. *Science (New York, NY)* 178:1217–1219
- Dichgans J, Brandt T, Held R (1975) The role of vision in gravitational orientation. *Fortschr Zool* 23:255–263
- Dijkstra TM, Schonher G, Gielen CC (1994) Temporal stability of the action-perception cycle for postural control in a moving visual environment. *Exp Brain Res Experimentelle Hirnforschung* 97:477–486
- Dokka K, Kenyon RV, Keshner EA (2009) Influence of visual scene velocity on segmental kinematics during stance. *Gait Posture* 30:211–216
- Duffy CJ, Wurtz RH (1995) Responses of monkey MST neurons to optic flow stimuli with shifted centers of motion. *J Neurosci* 15:5192–5208
- Fitzpatrick RC, Wardman DL, Taylor JL (1999) Effects of galvanic vestibular stimulation during human walking. *J Physiol* 517:931–939
- Gielen CC, van Asten WN (1990) Postural responses to simulated moving environments are not invariant for the direction of gaze. *Exp Brain Res* 79:167–174
- Green AM, Shaikh AG, Angelaki DE (2005) Sensory vestibular contributions to constructing internal models of self-motion. *J Neural Eng* 2:164–179
- Guerraz M, Bronstein AM (2008) Ocular versus extraocular control of posture and equilibrium. *Neurophysiol Clin* 38:391–398
- Guerraz M, Gianna CC, Burchill PM, Gresty MA, Bronstein AM (2001a) Effect of visual surrounding motion on body sway in a three-dimensional environment. *Percept Psychophys* 63:47–58
- Guerraz M, Thilo KV, Bronstein AM, Gresty MA (2001b) Influence of action and expectation on visual control of posture. *Cogn Brain Res* 11:259–266
- Jahn K, Strupp M, Schneider E, Dieterich M, Brandt T (2000) Differential effects of vestibular stimulation on walking and running. *Neuroreport* 11:1745–1748
- Keshner EA, Dhaher Y (2008) Characterizing head motion in three planes during combined visual and base of support disturbances in healthy and visually sensitive subjects. *Gait Posture* 28:127–134
- Keshner EA, Kenyon RV (2000) The influence of an immersive virtual environment on the segmental organization of postural stabilizing responses. *J Vestib Res* 10:201–219
- Keshner EA, Allum JH, Pfaltz CR (1987) Postural coactivation and adaptation in the sway stabilizing responses of normals and patients with bilateral vestibular deficit. *Exp Brain Res* 69:77–92
- Keshner EA, Kenyon RV, Langston J (2004) Postural responses exhibit multisensory dependencies with discordant visual and support surface motion. *J Vestib Res* 14:307–319
- Keshner EA, Streepey J, Dhaher Y, Hain T (2007) Pairing virtual reality with dynamic posturography serves to differentiate between patients experiencing visual vertigo. *J Neuroeng Rehabil* 4:24
- Kleinschmidt A, Thilo KV, Buchel C, Gresty MA, Bronstein AM, Frackowiak RS (2002) Neural correlates of visual–motion perception as object- or self-motion. *Neuroimage* 16:873–882
- Kluzik J, Horak FB, Peterka RJ (2005) Differences in preferred reference frames for postural orientation shown by after-effects of stance on an inclined surface. *Exp Brain Res* 162:474–489
- Kluzik J, Peterka RJ, Horak FB (2007) Adaptation of postural orientation to changes in surface inclination. *Exp Brain Res* 178:1–17
- Kuno S, Kawakita T, Kawakami O, Miyake Y, Watanabe S (1999) Postural adjustment response to depth direction moving patterns produced by virtual reality graphics. *Jpn J Physiol* 49(5):417–424

- Lackner JR, DiZio P (1988) Visual stimulation affects the perception of voluntary leg movements during walking. *Perception* 17:71–80
- Miles FA (1998) The neural processing of 3-D visual information: evidence from eye movements. *Eur J Neurosci* 10:811–822
- Nashner L, Berthoz A (1978) Visual contribution to rapid motor responses during postural control. *Brain Res* 150(2):403–407
- Peterka RJ (1995) Simple model of sensory interaction in human postural control. In: Mergner T, Hlavacka F (eds) *Multisensory control of posture*. Plenum Press, New York City, pp 282–288
- Previc FH, Mullen TJ (1991) A comparison of the latencies of visually induced postural change and self-motion perception. *J Vestib Res* 1(3):317–323
- Previc FH (1992) The effects of dynamic visual stimulation on perception and motor control. *J Vestib Res* 2:285–295
- Previc FH, Donnelly M (1993) The effects of visual depth and eccentricity on manual bias, induced motion, and vection. *Perception* 22:929–945
- Slobounov S, Tutwiler R, Sebastianelli W, Slobounov E (2006) Alteration of postural responses to visual field motion in mild traumatic brain injury. *Neurosurgery* 59:134–139
- Tanahashi S, Ujike H, Kozawa R, Ukai K (2007) Effects of visually simulated roll motion on vection and postural stabilization. *J Neuroeng Rehabil* 4:39
- Tanaka K, Saito H (1989) Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *J Neurophysiol* 62:626–641
- Thurrell AE, Bronstein AM (2002) Vection increases the magnitude and accuracy of visually evoked postural responses. *Exp Brain Res Experimentelle Hirnforschung* 147:558–560
- van Asten WN, Gielen CC, van der Gon JJ (1988) Postural adjustments induced by simulated motion of differently structured environments. *Exp Brain Res* 73:371–383
- Wiest G, Amorim MA, Mayer D, Schick S, Deecke L, Lang W (2001) Cortical responses to object-motion and visually-induced self-motion perception. *Brain Res Cogn Brain Res* 12:167–170
- Wolsley CJ, Sakallari V, Bronstein AM (1996) Reorientation of visually evoked postural responses by different eye-in-orbit and head-on-trunk angular positions. *Exp Brain Res* 111:283–288
- Young LR (1978) Visually induced motion in flight simulation. AGARD conference proceedings, no. 249, pp 16-1–16-8
- Zupan LH, Merfeld DM (2005) An internal model of head kinematics predicts the influence of head orientation on reflexive eye movements. *J Neural Eng* 2:180–197