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Abstract

Previous studies demonstrated a leaning after-effect (LAE) following standing or walking on an inclined surface consistent with a long-lasting, somatosensory memory for body orientation relative to the surface. Here, we asked whether providing a brief visual reference during LAE resets postural orientation to the new visual reference. The results showed that subjects immediately return to upright when eyes were opened briefly during the post-incline period. However, the subjects also immediately resumed leaning after closing their eyes again following 20 s of eyes open. The duration of LAE was not influenced by 1 or 2 brief periods of vision. Also, the amplitude of the lean following the brief vision period was often larger than when subjects had their eyes closed for the entire post-incline period. These results suggest a powerful somatosensory memory contribution to postural orientation in space that is not eliminated or recalibrated with brief exposure to a visual reference.

Introduction

Upright standing posture with respect to vertical requires central integration of visual, somatosensory, vestibular, and graviceptive inputs to adapt to changes in sensory conditions. These sensory inputs must be integrated and interpreted with respect to a stable frame of reference, or set point, for the task (Gurfinkel et al. 1995).. Recent work by Kluzik et al. (2005, 2007) has shown the body-to-support surface relationship is a particularly important reference for the CNS internal representation of postural orientation. This relationship between standing posture and the support surface orientation in space acts on global, whole body control and is subject to adaptive modification. Following standing on an inclined surface, most individuals demonstrate a post-incline leaning after-effect (LAE) in which they lean to maintain a similar trunk to support surface orientation as experienced during the upright standing on an incline. LAE occurs whether subjects experience stance or walking on an incline with either the eyes open or eyes closed. However, subjects do not lean when standing on a flat surface after experience on an incline when a visual reference is available. The present study investigates whether provision of a brief visual reference in the midst of ongoing LAE eliminates the somatosensory memory and quickly resets the postural system to a new vertical body orientation.

Visual information is known to be an important reference for postural orientation (e.g., Berthoz et al. 1975; Lestienne et al. 1977; Soechting & Berthoz 1979; Clement et al. 1985). Studies that have manipulated visual information during adaptive after-effects have revealed at least two qualitatively different phenomena. A stable visual reference can cause complete cancellation, or dumping, of optokinetic after-nystagmus (OKAN) and post-rotatory nystagmus (Cohen et al. 1977; Waespe and Schwarz 1986). Alternatively, vision may have the effect of canceling an after-effect while a visual reference is present, and the after-effect may resume again once vision is removed. This has been demonstrated for podokinetic after-rotation

(PKAR), in which subjects unintentionally turn in circles after walking on a rotating surface (Jürgens et al. 1999; Falvo et al. 2009).

The difference in effects of a visual reference on after-effect may be related to the source of the stimulus. OKAN is solely caused by vision (see Cohen et al. 1977) and post-rotatory nystagmus by vestibular stimulation, whereas somatosensory experience is the basis for the establishment of PKAR (Weber et al. 1998; Jürgens et al. 1999). LAE, like PKAR, is also primarily dependent upon somatosensory experience for its establishment, so we hypothesized that providing visual information would cancel LAE when vision was present, but that LAE would resume once vision was removed.

Methods

Participants

The experimental protocol was approved by the Institutional Review Board at Oregon Health & Sciences University and was performed in accordance with the 1964 Helsinki Declaration. Prior to testing all subjects provided written informed consent. Eleven people (6 men and 5 women, mean (±SD) age 30.9 ± 8.4 years) participated in this study. However, only nine subjects were included in the analysis, as two subjects did not demonstrate LAE responses.

Experimental setup

Subjects stood with each foot on a separate force platform (see Kluzik et al. 2005 for more details) with malleoli aligned to the axis of pitch rotation. Foot placement on the force platforms was constant across trials. The visual environment was standardized using an artificial surround composed of an arrangement of horizontal and vertical stripes that varied in width and

tone (see Peterka 2002). Subjects wore headphones and listened to an audio book to distract them from focusing on their posture and to mask background noise. Questions about the story were asked afterward to ensure that participants focused on the story. An easily audible beeper was located next to the subject to indicate time to open or close the eyes. Eye-lid movements were observed with a video camera located above the visual surround so the experimenter could monitor eye movements during the trials and ensure that subjects were responding appropriately to the beeper.

Procedure

Each trial consisted of 8.5 min of quiet stance on the force platforms. For all trials, inclination of the platforms was zero for the first minute and then changed to a 5°, toes up position at a rate of 1°/s (Fig. 1a). This 5° inclination was maintained for 2.5 min, after which the platform returned to a horizontal position at a rate of 5 deg/s. Subjects continued to stand on the horizontal surface for another 5 min. Four experimental conditions were tested in 9 trials. There was at least 1 h between each trial, during which subjects walked (including stair climbing) in order to wash-out possible after-effects.

The four conditions altered the presence and duration of available visual input (Fig. 1b). In the Control No Vision trials (CNV, 2 trials), subjects kept their eyes closed during the entire trial. CNV corresponded to the experimental trials in Kluzik et al. (2005), measuring the complete LAE response. In the Control Vision trials (CV, 2 trials), the eyes were opened 10 s after the platform returned to a horizontal position and remained opened for the rest of the trial. (The maximal leaning peak was always within the 10 s of eyes closed that immediately followed return of the platform to a horizontal position.) In the other vision conditions, vision was available for one, Vision 1 (V1, 3 trials) or two, Vision 2 (V2, 2 trials) periods of 20 s. Three

trials of V1 were administered, rather than two, as our primary interest was the V1 trials examining the effects of a single period of vision on LAE. Inclusion of three rather than two trials of V1 in the analyses does not change the results reported herein. Subjects opened and closed their eyes upon sounding of a beeper located on their shirt and were allowed to practice responding to the beeper prior to beginning any trials. Before each trial, subjects were told how many beeps could be expected. The 9 trials were subdivided into three test days, mostly on alternating days with a maximum of 4 trials per test day. To ensure that similar control trials were not tested in 1 day, the nine trials were ordered rationally. Test day order as well as trial order per test day was randomized.

Data Analysis

Four ground reaction force vectors were measured by four strain gauges in each force platform with a sample frequency of 100 Hz. From these data, anterior–posterior center of pressure (CoP) was calculated. The CoP evolution was low-pass filtered with a 4th order Butterworth filter with a cut-off frequency of 0.1 Hz.

To determine how visual information affected the leaning behavior, the peak amplitude of each period of leaning, duration of each period of leaning, and the overall duration of leaning were measured from the CoP displacements. Peak amplitude for each lean was defined as the most anterior position of the COP obtained during a particular period of leaning. Duration of each period of leaning was defined by determining the onset and offset times of a leaning response. Baseline values were defined as the average COP position during the first 60 s of standing with eyes closed on a flat surface. Onset of leaning was defined as the point in time when the COP moved anteriorly more than 2SD above baseline, and offset was the time when

COP position returned to within 2 SD of baseline. For CNV and CV trials, only one peak and one lean duration were calculated as there was only one period of leaning in each trial of these conditions. For V1 trials, two period of leaning were present as the subject leaned first upon returning to a flat position from a toes up position, returned to near vertical upon opening the eyes, and then leaned again upon closing the eyes. For V2 trials, three peaks were present as there were two instances of opening and then closing the eyes. As such, for V1 and V2 trials, for each period of leaning we determined peak amplitude and duration of each lean. Finally, for each condition, we also determined overall duration of the entire LAE response across the trial from onset of the first lean to offset of the final lean.

One-way repeated measures ANOVAs were used to test for differences in peak amplitude, duration of each lean, and total duration of LAE response across visual conditions. In addition, paired t-tests were used to compare peak amplitudes of leaning for the second lean of V1 and the second and third leans of V2 to the corresponding COP values at equivalent times in the CNV condition. For example, peaks of the second leans in V1 and V2 were compared to CNV values 20 s earlier than the time of these second peaks to account for the 20 s period of eyes open that intervened in the V1 and V2 trials. The peak of the third lean in V2 was compared to the CNV value 40 s earlier than this third lean of V2 to account for the two 20 s period of intervening eyes open in the V2 trials. All statistical analyses were conducted using NCSS software with $P = 0.05$ (Hintze 2007). Paired t-tests were Bonferroni corrected to account for multiple comparisons, with significance level set at $P = .016$ for each paired t-test.

Results

All subjects demonstrated LAE and visual information had a significant effect on the LAE response. Upon opening the eyes, subjects quickly returned to a near vertical position. Once

subjects opened their eyes and maintained eyes open, they remained in an upright position for the rest of the trial. During brief exposure to visual references in the V1 and V2 conditions, however, all subjects immediately resumed leaning upon closing their eyes again, often leaning farther than they would have if they had kept their eyes closed (Fig. 2).

Amplitude of Leans

Across all conditions, peak amplitude for the first bout of leaning was similar, attesting to the consistency of repeated LAEs (Fig. 1c). Amplitude of the subsequent LAE peaks in the V1 and V2 trials, however, was significantly smaller than the first lean, reflecting the exponential decline of the leaning after-effect across time ($P < 0.001$, Fig. 1c).

Peak Lean Values Relative to Control No Vision Condition

Recovery of post-incline leaning upon resumption of eyes closed exceeded the amount of lean at an equivalent time during trials not interrupted by visual input (Fig. 1c and d). The peak amplitudes of the second leans in V1 and V2, as well as the third lean in V2, were all significantly higher than corresponding COP position values in the CNV trial ($P < 0.005$). Peak amplitude for the second lean of V1 was 90.6 ± 6.6 mm compared to a value of 62.7 ± 4.8 mm at the matched time in CNV. Peak amplitude for the second lean of V2 was 102.1 ± 10.3 mm compared to a value of 55.3 ± 12.0 mm at the matched time in CNV. Peak amplitude for the third lean of V2 was 87.9 ± 6.1 mm compared to a value of 57.4 ± 10.9 mm at the matched time in CNV.

Duration of Leans

Opening the eyes in the midst of a LAE and then closing them again did not significantly alter the course of the lean. The total duration of the LAE response from onset of the first lean to offset of the final lean was not significantly different between CNV, V1, and V2 conditions (Fig. 1d).

Maintaining eyes open in the CV condition (Fig. 1d) resulted in significantly shorter overall duration of leaning than all other condition ($P < 0.05$). In fact, the duration of individual leans for all conditions in which the eyes were opened was significantly shorter than in CNV condition when the eyes remained closed for the entire trial ($P < 0.001$, Fig. 1d). This reflects the rapid return to a vertical position each time the eyes were opened.

Discussion

Visual information resulted in a rapid elimination of leaning after-effects but leaning after-effects resumed as soon as vision was removed again. These results are consistent with a powerful somatosensory memory contribution to postural orientation in space that is not eliminated or recalibrated with brief exposure to a visual reference.

The resumption of LAE with eye closure after a brief period of reorientation to vision excludes the notion that visual information is critical for this postural adaptation. That is, periods of visual information do not result in an altered interpretation of somatosensory information. Vision may serve as an extrinsic reference frame for proprioceptive verticality but does not recalibrate the proprioceptive set point for postural orientation.

It is noteworthy that recovery of leaning upon removal of vision was somewhat greater than leaning in trials lacking vision. The origin of this overshoot upon elimination of vision is unknown. In contrast to a study by Nashner and Berthoz (1978), this overshoot does not seem to

be a consequence of a temporary stop in the decay of LAE as the interjections of periods of vision did not result in prolongation of the LAE response. The time course of the LAE was not affected by one or more periods of reorientation to visual vertical. High inertial forces due to a rather fast recovery to a leaning orientation might contribute to the overshoot.

The striking effect of vision on LAE suggests that during periods of vision, individuals immediately switch from an alignment based upon proprioceptive memory of the relationship between the trunk and the support surface to an alignment based upon actual visual vertical (Kluzik et al. 2005). Upon removal of vision, subjects return to postural alignment based on the memory of proprioceptive vertical experienced during the conditioning period of standing (or walking) on the incline (Kluzik et al. 2007b). It is not clear why individuals align to this memory of proprioceptive vertical rather than aligning to current vestibular vertical or to the now horizontal support surface. This may relate to individual inherent preferences for different sources of sensory input (Kluzik et al. 2005). Since we intentionally selected only individuals who demonstrated strong LAE, the participants all likely relied heavily on proprioceptive, kinematic information for postural alignment, rather than kinetic forces under the feet (Kluzik et al. 2005). It is worth noting that LAE as described here may only occur in response to toes up platform tilt following which the aftereffect is a forward lean. Toes down platform tilt in healthy individuals results in much smaller backward lean, likely as a result of the physical limitations of the base of support (Schweigart and Mergner 2008).

We hypothesized that the LAE was due to a somatosensory memory, rather than visual or vestibular memory so that the interjection of a period of visual input would not result in a dumping of the response as has been seen with optokinetic after-nystagmus and vestibular nystagmus (Cohen et al. 1977; Waespe and Schwarz 1986). These phenomena, based,

respectively, upon visual and vestibular memory, are distinct from the LAE, which relies upon proprioceptive memory. LAE also appears to be distinct from leans induced via galvanic vestibular stimulation, which occur in the frontal plane when the head is not turned and only occur in the sagittal plane when the head is turned to the side (Popov et al. 1986).

Our previous studies showed that the adaptive mechanisms underlying LAE regulate the relationship of the trunk to the surface inclination, rather than acting more locally at the level of the ankle joint (Kluzik et al. 2005, 2007a and b). Podokinetic after-rotation is also thought to represent a recalibration of the relationship between the trunk and the surface (Weber et al. 1998). In fact, the recovery of the LAE was similar to the recovery of podokinetic after-rotation following a brief visual interjection (Jürgens et al. 1999; Falvo et al. 2009). Podokinetic after-rotation, like LAE, likely relies upon proprioceptive memory involving orientation of the foot to the trunk in yaw space. This seems an interesting similarity in postural and locomotor adaptive control mechanisms, especially since LAE can be observed not only after standing on an incline but also after stepping on an incline (Kluzik et al. 2007b). Future work directly comparing LAE and podokinetic after-rotation responses in the same individuals may help to further elucidate the potentially shared mechanisms underlying postural and locomotor adaptive responses.

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Figure 1. Illustration of the platform positions (a), conditions examined (b), as well as peak amplitudes (c) and durations (d) of leaning for different periods of each condition. (A) In every condition, the platform was horizontal (0°) for 1 min, then tilted to 5° where it stayed for 2.5 min before returning to a horizontal position. (B) Conditions from top to bottom: Control No Vision eyes closed during entire trial, Control Vision eyes are opened 10 s after the platform returns to horizontal and remain open during the rest of the trial, Vision 1 10 s after the platform returned to horizontal the eyes were opened for a period of 20 s and then closed for the rest of the trial, Vision 2 similar to Vision 1 except the eyes were opened for two 20 s periods spaced 30 s apart. In Panels C and D, the first, second, and third leans as appropriate for each condition are shown. The total duration of all periods of leaning summed is shown in D and designated as "total". * = significantly different from 1st leans of all conditions, # = significantly different from Control No Vision. Values are means ± SEs.

Figure 2. Illustration of average responses of three individual subjects in the various conditions. Each column depicts responses from a single subject across conditions, while rows depict responses across subjects within a condition. The top row shows Control Vision vs. Control No Vision responses (panels A1–A3), the middle row shows Vision 1 vs. Control No Vision responses (panels B1–B3), and the bottom row shows Vision 2 vs. Control No Vision responses (panels C1–C3). All graphs show anterior/posterior center of pressure versus time, with positive values reflecting anterior movement of the center of pressure.

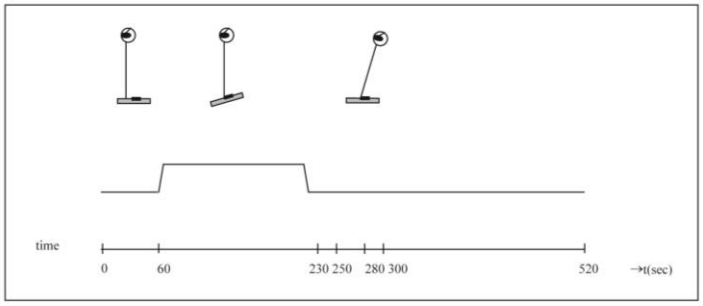
Table 1. Peak Amplitude, Timing, and Duration of LAE Responses

Condition	Peak Amplitude (mm)	Time of Peak (s)	Duration (s)	Corresponding CNV Value
Control No Vision	125.3 ± 2.9	221.5 ± 4.0	199.6 ± 23.0	N/A
Control Vision	124.0 ± 2.9	222.1± 4.0	75.6 ± 20.8†	N/A
V1 (1st peak)	123.9 ± 3.0	222.1 ± 3.9	19.6 ± 20.8†	N/A
V2 (1st peak)	125.2 ± 2.9	220.4 ± 3.9	23.5 ± 24.4†	N/A
V1 (second peak)	90.1 ± 6.6*	284.0 ± 4.4*	76.3 ± 23.0†	62.7 ± 4.8†
V2 (second peak)	102.1 ± 10.3*	270.9 ± 5.4*	16.5 ± 30.9†	55.3 ± 12.0†
V2 (third peak)	87.9 ± 6.1*	320.8 ± 5.0*^	35.3 ± 26.1†	57.4 ± 10.9†
V1 Overall	N/A	N/A	134.3 ± 29.2	N/A
V2 Overall	N/A	N/A	134.7 ± 33.1	N/A

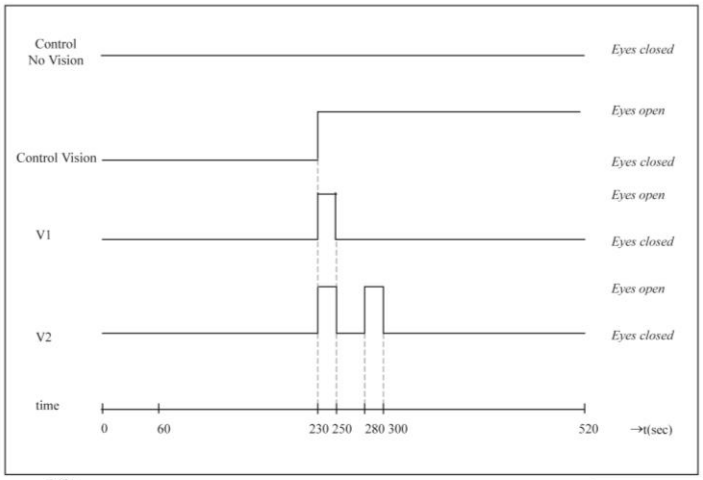
Values are means ± SEs.
* = significantly different from CNVa, CVa, V1a, and V2a
^ = significantly different from V1b and V2b
† = significantly different from CNVa

Figure 1

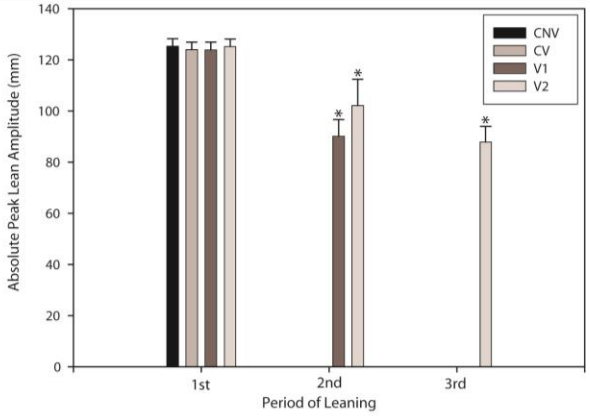
A



B



C



D

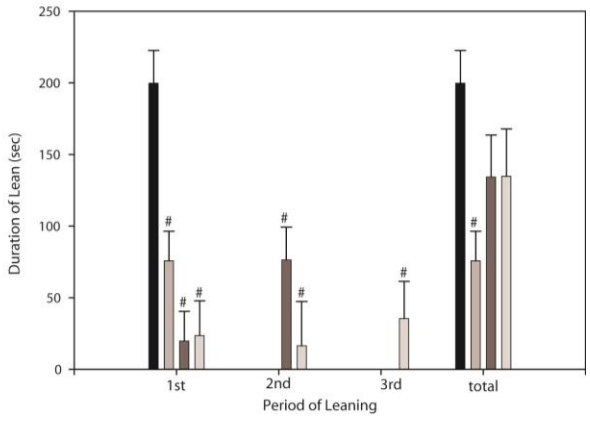
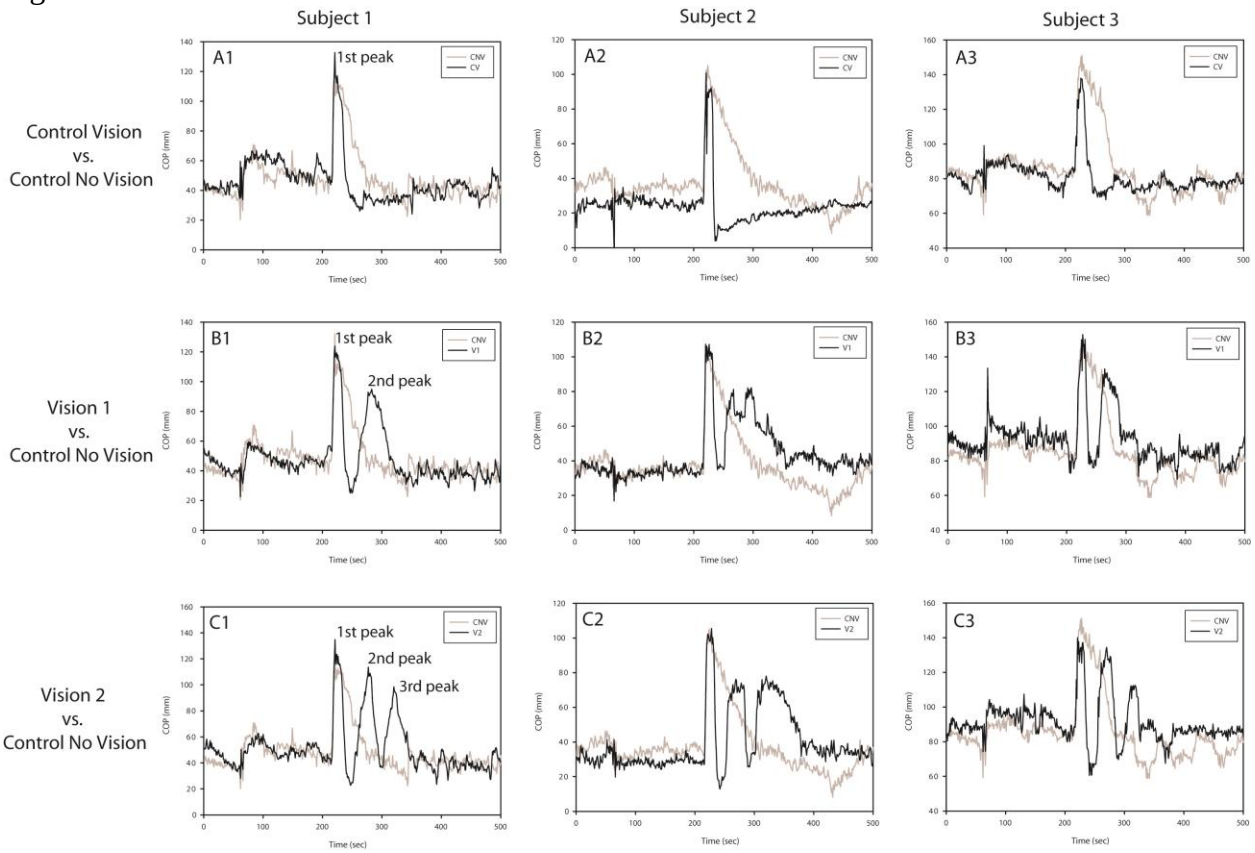


Figure 2


Subject 1
Subject 2
Subject 3
Control Vision
vs.
Control No Vision
Vision 1
vs.
Control No Vision
Vision 2
vs.
Control No Vision
A1
A2
A3
B1
B2
B3
C1
C2
C3
1st peak
2nd peak
3rd peak
CNV
CV
V1
V2
COP (mm)
Time (sec)