Published in final edited form as:

Somatosens Mot Res. 2008 September ; 25(3): 188–193. doi:10.1080/08990220802384759.

Podokinetic after-rotation in a simulated reduced gravity environment

Michael J. Falvo¹, Fay B. Horak², and Gammon M. Earhart^{1,3,4}

¹Program in Physical Therapy, Washington University School of Medicine, Saint Louis, MO, USA

²Neurological Sciences Institute, Oregon Health and Science University, Beaverton, OR, USA

³Department of Anatomy & Neurobiology, Washington University School of Medicine, Saint Louis, MO, USA

⁴Department of Neurology, Washington University School of Medicine, Saint Louis, MO, USA

Abstract

Stepping in place on a rotating platform for a period of 15 minutes induces an adaptive response, podokinetic after-rotation (PKAR), which causes a blindfolded individual to inadvertently rotate when attempting to step in place on the floor. The purpose of this investigation was to determine whether lower extremity load receptors were involved in this adaptation. As load receptor input is critical for locomotion, we hypothesized that manipulating load via body weight support (BWS) would influence PKAR. Eleven healthy female volunteers performed 15 minutes of stepping in place on a rotating treadmill (stimulation), followed by 10 minutes of stepping in place (response) without vision on a stationary surface. Response and stimulation periods were with 50% body weight support (BWS) and without body weight support (NoBWS) in all four possible combinations (BWS-BWS, NoBWS-NoBWS, BWS-NoBWS, and NoBWS-BWS). Conditions were randomly assigned to all subjects and performed on four separate occasions at least 48 hr apart. During the 10-min PKAR response period, trunk angular velocity was calculated and plotted versus time, and exponential models were applied to the data to obtain curve-fit parameters for each condition. Despite the manipulations of BWS, no significant differences were found for any parameter value ($p = 0.13$ – 0.98). BWS applied during stimulation only, response only, or during both stimulation and response does not appear to influence PKAR. This suggests that load receptors may not play a critical role in mediating adaptive changes in locomotor trajectory control in response to walking on a rotating surface.

Keywords

Podokinetic after-rotation; load receptor; body weight support

Introduction

Visual, vestibular, and somatosensory information provide cues necessary to control locomotor trajectory (Earhart and Horak 2003). Somatosensory inputs are of particular importance when navigating curved paths or making turns in order to provide input regarding rotation of the trunk relative to the feet. This bottom-up somatosensory regulation is mediated by the

Correspondence: Gammon M. Earhart, Washington University School of Medicine, Program in Physical Therapy, Campus Box 8502, Saint Louis, MO 63108. Tel: 314-286-1425. Fax: 314-286-1410. E-mail: E-mail: earhartg@wustl.edu.

Declaration of interest: The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

podokinetic control system (Weber et al. 1998). To better understand the influence of afferent input on the adaptive control of locomotor trajectory, many investigations have used the rotating circular treadmill paradigm (Earhart et al. 2001, 2002a, 2002b; Hong et al. 2007; Wong et al. 2007). In this model, individuals perform a period of active countercircling, i.e., podokinetic (PK) stimulation, whereby they step in place relative to space on a rotating disc. Following a period of PK stimulation, individuals unintentionally rotate themselves when asked to step in place on a stationary disc without vision. This inadvertent turning phenomenon is referred to as *podokinetic after-rotation* (PKAR; Gordon et al. 1995; Weber et al. 1998) and may be considered an adaptive response (after-effect) reflecting adaptation of the rotational relationship between the trunk and feet (Earhart and Horak 2003).

Adjustment of intersensory interactions is necessary for transition between changing environmental conditions (e.g., walking on a moving treadmill then walking in place), and it appears that these after-effects are elicited in both dynamic and static conditions. For example, following standing on an inclined surface, healthy individuals demonstrated postural after-effects when returning to standing on a horizontal surface such that they maintained the same body-to-surface relative alignment or forward lean (Kluzik et al. 2005). Recently, it has also been demonstrated that these kinesthetic after-effects are present following stepping on an inclined surface as well (Kluzik et al. 2007).

Prior research indicates that PKAR is not specific to local peripheral adaptation, but induces an adaptive after effect of locomotor trajectory involving structures throughout the central nervous system (Earhart and Horak 2003). However, it remains to be established what parts of the somatosensory system mediate this adaptive after-effect of locomotor trajectory. Previously, we speculated that afferent inputs from the hip may be significant, as the hip is the primary site of yaw rotations of the lower extremity during PK stimulation (Wong et al. 2007). As such, we investigated whether a period of kneeling PK stimulation, as compared to the standard stepping PK stimulation, would produce an equivalent PKAR after-effect. We found very little transfer of PKAR from kneeling to stepping, suggesting hip afferent information is not a major contributor to this adaptive response (Wong et al. 2007). These findings have led us to hypothesize that additional afferent inputs, such as load receptors, may be of greater influence in determining the adaptive after-effect of locomotor trajectory.

Early investigations inducing weightlessness in both space (Clement et al. 1985) and water immersion (Dietz et al. 1989) have indicated that visual and vestibular sensory input alone cannot account for the influence of gravity on upright stance. Therefore, *gravity-dependent* (i.e., load) receptors have been shown to be critical in determining the position of the body's center of mass within the base of support during upright stance (Dietz et al. 1992). Presumably, this afferent input may be of equal importance to navigate curved paths and execute turns. Although load receptor significance has been noted during normal locomotion (for review, see Dietz and Duysens 2000), it has not yet been considered within the rotating circular treadmill paradigm. The question asked here is whether manipulating load receptor input, via body weight support, will influence PKAR. We hypothesized that a direct relationship exists between load receptor input and adaptive after-effects of locomotor trajectory, and expected PKAR responses to be attenuated when body weight support was provided either during or after walking in place on a rotating surface.

Methods

Subjects

Eleven healthy female volunteers (ages 24.6 ± 4.6 years, 162.1 ± 4.1 cm, 61.9 ± 4.8 kg, mean $\pm$ SD) participated in this investigation. The protocol described herein was approved by the Washington University School of Medicine Human Research Protection Office, and informed

consent was obtained from all volunteers prior to any testing. This experiment complied in all ways with the Declaration of Helsinki.

Protocol

Each subject completed four separate experimental sessions, performed at least 48 hr apart. Each session began with a 15-min PK stimulation followed by a 10-min PKAR response. The durations of stimulation and response were chosen based on previous research (Hong et al. 2007). During PK stimulation, subjects stepped in place on a treadmill (Neurokinetics, Inc., Pittsburgh, PA, USA) that rotated clockwise at 60 deg sec^{-1} . Subjects were instructed to maintain a constant body position in space by fixating on an eye level visual spot located at a distance of 3.1 m. Following PK stimulation, the treadmill was stopped, and subjects were provided a blindfold and earplugs to eliminate and attenuate external visual and auditory cues, respectively. Subjects then began the 10-min PKAR period, where they were instructed to step in place to the cadence of a metronome ($120 \text{ steps} \cdot \text{min}^{-1}$) which was attached high on the torso such that it was clearly audible. Furthermore, they were instructed to maintain a fixed heading while holding an overhead freely moveable frictionless wheel. This transition from PK stimulation to PKAR response was less than 1 min.

Experimental sessions differed in whether PK stimulation, PKAR response, or both were performed with body weight support (BWS) or without (NoBWS). This created four different conditions, as shown in Table 1. These conditions were randomly assigned via a computer generated program. For example, in the BWS—NoBWS condition, PK stimulation was performed with BWS, which was subsequently removed for the PKAR response. BWS was provided through a harness system that was attached to an overhead support along the vertical axis of the rotating disc. This support could be lowered and raised in order to accommodate individual subjects. Through these adjustments, we determined the height that provided approximately 50% BWS for each subject. These settings were determined at the first experimental session by having subjects stand on a scale placed in the center of the treadmill while outfitted in the harness. This 50% level of BWS has been used elsewhere in gait retraining for rehabilitation purposes and was arbitrarily chosen for this investigation. Individual settings were recorded and reproduced for subsequent experimental sessions. Attached at the end of this support was a frictionless wheel on which subjects were able to comfortably place their hands during the stimulation and response periods.

Data acquisition

Four reflective markers (20mm diameter) were placed on each subject's trunk on the bilateral acromions, sternal notch, and right scapula. Three additional markers were fixed to the floor in a triangular configuration. Kinematic data were collected at 60 Hz using a 3-D motion capture system (Motion Analysis Corporation, Santa Rosa, CA, USA) equipped with eight ceiling-mounted Hawk digital cameras that are accurate to 0.25 mm. Data were collected only during the 10 min of PKAR response.

Data analysis

Trunk position relative to the floor markers was used to calculate trunk angular velocity in the horizontal plane during the PKAR response. Trunk angular velocity was plotted against time individually (Figure 1) and averaged across conditions (Figure 2). Plotted values of velocity were averaged within 5-sec bins. For each plot, two functions were fitted: (a) a two-parameter exponential rise function, $y = a(1 - e^{-bx})$, fitted to the first 2 min of data, yielding values for maximum velocity and rise time constant, and (b) a three-parameter exponential decay function fitted to the data points from 2–10 min, $y = y_0 + ae^{-bx}$, yielding values for initial velocity, asymptote, and decay time constant. Each of the curve fit parameter values were compared across conditions via a one-way repeated measures analysis of variance. In the case of a

significant finding, Bonferonni pairwise comparisons were made. Data met the assumptions of normality and sphericity via the Kolmogorov-Smirnov test and Mauchly test, respectively. All data are presented as mean $\pm$ SD. Statistical significance was established at $p \leq 0.05$ prior to analyses, and all analyses were performed using SPSS (v14; SPSS Inc., Chicago, IL, USA).

Results

Regardless of experimental condition, all subjects exhibited PKAR (Figure 2). Subjects reported they were unable to detect whether they were actually rotating in space or in which direction they were moving during the 10-min response period of PKAR.

Figure 1 depicts representative plots of PKAR angular velocity vs. time for a single subject across the four different conditions. As illustrated in Figure 1 from top to bottom, peak velocities for each condition were 8.82, 9.35, 7.56, and 8.78 deg sec⁻¹, respectively. For the same subject, average velocities were 3.77, 4.11, 4.09, and 4.11 deg sec⁻¹. Please note that these peak and average velocities represent raw data obtained that are represented in the accompanying figures and are different from the curve-fit parameters discussed below and found in Table 2.

Individual curve-fit parameters were obtained from each subject and were averaged for each condition. These group average values are presented in Table 2. Whether BWS was applied during PK stimulation, the PKAR response period, or both, no significant differences were found for any PKAR curve-fit values ($p = 0.13$ – 0.98). The composite plots of average PKAR responses across all subjects are illustrated in Figure 2 with 95% confidence interval (CI) error bars.

Discussion

This is the first investigation to consider the potential contributions of load receptors to PKAR. Adaptive after-effects of locomotor trajectory were present and similar across all BWS conditions, suggesting that load receptor afferent input does not appear to substantially influence PKAR responses.

Ivanenko et al. (2002) investigated the influence of ground reaction forces on lower limb kinematics in a reduced gravity environment. Subjects performed straight-line treadmill walking under several levels of BWS from 0–95% body weight. As expected, the kinetic parameters (e.g., ground reaction force, EMG) changed considerably across conditions, but lower limb kinematics remained accurately controlled. Authors suggested that even minimal contact forces sensed during BWS are sufficient to maintain normal foot trajectory. While imprudent to make a direct comparison to our investigation, it is interesting to note that trunk kinematics (e.g., trunk angular velocity) remained consistent across all four experimental conditions in our study. Averaged across conditions, maximum and average velocities ranged from 7.8–8.9 deg sec⁻¹ and 4.4–5.7 deg sec⁻¹, respectively. In the present experiment, the contact forces in all conditions were sufficient to maintain foot rotation relative to the trunk during PK stimulation. This relative rotation has been hypothesized to drive the adaptive after-effects of locomotor trajectory (Earhart et al. 2001). If it is the relative rotation between foot and trunk that is critical, this could also account for the reduced PKAR response when PK stimulation was performed in kneeling where there was no foot contact with the floor, and thus no rotation of the foot relative to trunk (Wong et al. 2007).

While the subjects recruited for this investigation were young, healthy females, it has been suggested that older adults and individuals with Parkinson disease (PD) have reduced load receptor sensitivity that may contribute to gait impairments (Dietz and Colombo 1998). These authors investigated the influence of body unloading (75, 50, and 25% body weight) on lower

leg muscle activation (EMG) in individuals with PD, age-matched controls, as well as young healthy subjects. They noted that load sensitivity existed on a continuum such that individuals with PD were least sensitive followed by age-matched controls, and young subjects were the most sensitive. The present investigation did not include individuals with PD or age-matched controls, nor did it measure lower leg muscle activation, but the former did not include any kinematic measures. Recently in our lab, we compared the rotational velocity of PKAR in individuals with PD and matched controls (Hong et al. 2007). No significant differences were observed between groups, suggesting that PK adaptation is similar. Similarly, Hong et al. (2007) also compared younger versus older subjects and found no differences in PKAR across age groups. As such, we would not expect the results obtained in our present experiment to differ in older subjects or in subjects with PD.

Although this data does not support our hypothesis that load receptors are important for locomotor trajectory, this investigation does contribute to our understanding of PKAR. Previously, it has been demonstrated that adaptive after-effects of locomotor trajectory transfers from forward to backward walking, stepping to hopping, running to walking, and from one limb to the other (Earhart et al. 2001, 2002a, 2002b; Earhart 2006). The PKAR response or adaptive after effect of locomotor trajectory continues to be robust in the present investigation as well. Regardless of whether PK stimulation and PKAR response were performed with BWS, NoBWS, or a combination (i.e., BWS-NoBWS or NoBWS-BWS), PKAR was present and similar across conditions. This suggests that PKAR not only generalizes to a variety of locomotor tasks, but also to a variety of loading and unloading conditions.

There are several ways in which to enhance this preliminary study. For example, lower extremity EMG assessment as well as additional levels of BWS would enhance comparisons to other literature (e.g., Dietz and Colombo 1998) and advance our understanding of the utility of load receptors in formation and adaptation of locomotor trajectory. Furthermore, consideration of the additional afferent inputs (e.g., plantar surface of foot, joint receptors, and muscle spindles) is warranted.

In conclusion, creation of a simulated reduced gravity environment (i.e., 50% BWS) in order to manipulate load receptor afferent input does not appear to specifically influence PKAR. Similar adaptive after-effects of locomotor trajectory were induced when the reduced gravity environment, or BWS, was applied during PK stimulation only, during the PKAR response only, or during both stimulation and response. This suggests that load receptors do not play a critical role in mediating adaptive changes in locomotor trajectory control in response to walking on a rotating surface.

Acknowledgments

The authors would like to thank Joshua Funk for his assistance in data collection and the creation of figures. The project described was supported by NIH grants T32HD007434, 1R01DC04082, and 1K01HD048437. The content does not necessarily represent the official views of the NIH.

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Figure 1.
Scatter plots of trunk angular velocity versus time for PKAR across conditions for a single subject.

Figure 2. Scatter plots of trunk angular velocity versus time for PKAR across conditions and group averaged. 95% confidence interval error bars are plotted for each data point.

Table I

Experimental conditions.

Condition	PK stimulation (15 min)	PKAR response (10 min)
BWS-BWS	BWS	BWS
BWS-NoBWS	BWS	NoBWS
NoBWS-NoBWS	NoBWS	NoBWS
NoBWS-BWS	NoBWS	BWS

BWS = 50% of body weight supported; NoBWS = no body weight support.

Table II
PKAR curve-fit values (data are presented as mean $\pm$ SD).

Function parameter	BWS-BWS	BWS-NoBWS	NoBWS-NoBWS	NoBWS-BWS	p Value
Initial velocity (deg/sec)	8.1 $\pm$ 1.3	7.1 $\pm$ 2.3	8.0 $\pm$ 2.5	6.93 $\pm$ 2.1	0.13
2-min rise time constant (min)	0.3 $\pm$ 0.2	0.3 $\pm$ 0.2	0.2 $\pm$ 0.3	0.3 $\pm$ 0.2	0.98
Maximum velocity (deg/sec)	12.5 $\pm$ 7.2	11.2 $\pm$ 3.7	17.2 $\pm$ 17.5	11.1 $\pm$ 6.6	0.49
Decay time constant (min)	9.7 $\pm$ 13.3	10.45 $\pm$ 12.7	16.7 $\pm$ 24.7	7.6 $\pm$ 7.7	0.76
Asymptote (deg)	1.3 $\pm$ 6.8	0.9 $\pm$ 3.1	0.5 $\pm$ 4.3	1.4 $\pm$ 3.6	0.96

Conditions are labeled based upon the body weight support provided during training on the rotating treadmill and during measurement of the after-effect. For example, BWS-NoBWS indicates that body weight was supported during training but was not supported during the after-effect.