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RESEARCH ARTICLE

Podokinetic stimulation causes shifts in perception of straight ahead

John T. Scott · Corey A. Lohnes · Fay B. Horak · Gammon M. Earhart

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Abstract Podokinetic after-rotation (PKAR) is a phenomenon in which subjects inadvertently rotate when instructed to step in place after a period of walking on a rotating treadmill. PKAR has been shown to transfer between different forms of locomotion, but has not been tested in a non-locomotor task. We conducted two experiments to assess effects of PKAR on perception of subjective straight ahead and on quiet standing posture. Twenty-one healthy young right-handed subjects pointed to what they perceived as their subjective straight ahead with a laser pointer while they were recorded by a motion capture system both before and after a training period on the rotating treadmill. Subjects performed the pointing task while standing, sitting on a chair without a back, and a chair with a back. After the training period, subjects demonstrated a significant shift in subjective straight ahead, pointing an average of 29.1 ± 10.6° off of center. The effect was direction-specific, depending on whether subjects had trained in the clockwise or counter-clockwise direction. Postures that limited subjects' ability to rotate the body in space resulted in reduction, but not elimination, of the effect. The effect was present in quiet standing and even in sitting postures where locomotion was not possible. The robust transfer of PKAR to non-locomotor tasks, and across locomotor forms as demonstrated previously, is in contrast to split-belt adaptations that show limited transfer. We propose that, unlike split-belt adaptations, podokinetic adaptations are mediated at supraspinal, spatial orientation areas that influences spinal-level circuits for locomotion.

Keywords Orientation · Posture · Pointing · Adaptation

J. T. Scott
Department of Biology, Washington University in St. Louis, St. Louis, MO 63105, USA

C. A. Lohnes · G. M. Earhart (✉)
Program in Physical Therapy, Washington University in St. Louis, School of Medicine, Campus Box 8502, 4444 Forest Park Blvd., St. Louis, MO 63108, USA
e-mail: earhartg@wusm.wustl.edu

F. B. Horak
Department of Neurology, Oregon Health & Science University, Portland, OR, USA

G. M. Earhart
Department of Anatomy & Neurobiology, Washington University in St. Louis, School of Medicine, Campus Box 8502, 4444 Forest Park Blvd., St. Louis, MO 63110, USA

G. M. Earhart
Department of Neurology, Washington University in St. Louis, School of Medicine, Campus Box 8502, 4444 Forest Park Blvd., St. Louis, MO 63110, USA

Introduction

Several studies have shown that, after training on a rotating circular treadmill, an individual asked to step in place or walk forward without vision will inadvertently rotate. This adaptive response, called podokinetic after-rotation (PKAR, Weber et al. 1998), is robust and transfers across different speeds, directions, and forms of locomotion and from one lower limb to the other (Earhart et al. 2001, 2002; Earhart 2006; McNeely and Earhart 2010). The generalization of PKAR is in sharp contrast to other treadmill-induced adaptations, such as adaptations acquired during split-belt treadmill walking. A split-belt treadmill has two belts, one for each lower extremity, such that the belts can be moved independently at different speeds and in different directions. Split-belt studies have shown limited or no transfer of locomotor adaptations across speeds, directions, or from one limb to the other (Choi and Bastian 2007; Vasudevan and Bastian 2010). The distinct differences between the rotating and the split-belt treadmill after-effects raise questions about the nature of the control systems regulating these adaptations. Although a locomotion-induced adaptation, PKAR appears to perhaps be more analogous to adaptations that occur following standing or stepping on a stationary, inclined surface (Kluzik et al. 2005, 2007a, b).

Kluzik et al. (2005, 2007a, b) reported that standing or stepping on an inclined surface caused subjects to subsequently lean when standing on a horizontal surface without vision. The direction and amplitude of the after-effect were related to the direction and amplitude of the incline and brief periods of vision only temporarily suppressed the response (Earhart et al. 2010). They concluded that the leaning after-effect results from an adaptive change to the set point for postural control and that the central nervous system regulates posture through control of whole-body variables. This was supported by the finding that global variables such as the alignment between the trunk and surface were influenced more strongly than local variables such as the position of the ankle joint.

PKAR, like the leaning after-effect, is dependent upon the direction and speed of rotating treadmill stimulation and is only temporarily suppressed by brief periods of visual input (Weber et al. 1998; Falvo et al. 2009). The strong parallels between leaning after-effects and PKAR suggest that PKAR may also operate at the level of global, whole-body variables regarding orientation in space, as has been proposed for leaning after-effects. While the effects of rotating treadmill training have been well documented for locomotor behaviors, only two studies have assessed the effects of such training on quiet stance posture. Quiet standing posture is the orientation of the body segments when a participant is in a comfortable standing position with arms at the sides. Hollands et al. (2007) noted changes in quiet stance posture, but the posture was assessed by having subjects stop and stand still for brief intervals in the midst of a longer period of stepping in place that was used to assess the effects of PKAR on locomotion. Stevens and Earhart (2006) did not note any effect of PKAR during quiet stance assessed immediately after rotating treadmill training prior to any stepping and concluded that PKAR may only play a role in dynamic tasks or only be expressed during or following dynamic stepping behavior.

The aims of the present study are to examine, for the first time, effects of PK stimulation on subjective straight ahead (Exp. 1) and how perception of external space relative to the body relates to postural orientation of body segments in standing and sitting (Exp. 2). We hypothesized that PK stimulation, like post-incline leaning after-effects, would cause a shift in perception of straight ahead as we think that PKAR operates at the level of global variables that influence not just locomotion, but also other tasks.

Methods

To address the aims of this work, we conducted two separate experiments. Details of each experiment are presented separately for clarity.

Experiment 1

To determine how PKAR affects perception of straight ahead while standing.

Subjects and protocol

Eleven healthy, right-handed subjects participated in Experiment 1 (age 26.4 ± 4.5; 4 men, 7 women). Informed consent was obtained in accordance with University policy. Each subject stood facing a wall with feet aligned on marks on the floor that were 12 cm apart and with the heels 305 cm from the wall. Each subject was then blindfolded and asked to raise the arm to shoulder height and point toward the wall to a position located at shoulder level and directly in line with the midline of the feet while holding a laser pointer. This point directly in line with the midline of the feet was defined as the center and given a value of zero. Ten such pointing trials were performed, and the final pointing position was recorded for 2 s per trial using motion capture. In addition, the points indicated by the laser pointer were manually marked by an experimenter on a large sheet of paper hanging on the wall.

Upon completion of 10 pointing trials, each subject trained for 15 min over the axis of a rotating treadmill turning at 60°/s in either the clockwise ($n = 5$) or counterclockwise ($n = 6$) direction as determined via random assignment. Subjects were told to maintain a fixed heading throughout the training period, keeping the head and trunk oriented toward a point directly ahead of them while the legs continuously stepped underneath the head/trunk unit. All subjects were able to follow these instructions and maintain a fixed heading during training. Although subjects were not blindfolded during the training period, they were prevented from seeing the marks indicating where they had pointed on previous trials. At the end of the 15 min of training, subjects immediately placed their feet in the appropriate starting position, donned the blindfold and again performed 10 pointing trials as described previously. Upon completion of the pointing trials, subjects were asked to indicate whether they thought they were successful in pointing straight ahead to the center point and whether they had any perception of changes in postural alignment.

Data collection and analysis

Kinematic data were recorded at 100 Hz using an 8-camera motion capture system (Motion Analysis Corporation, Santa Rosa, CA). Markers were placed bilaterally just anterior to the tragus of the ear, on the anterior superior iliac spine, acromion process, posterior aspect of the calcaneus, and head of the first metatarsal. A marker was placed on subject's right radial styloid. Subjects wore tight fitting clothing to assist with data collection.

Paired *t* tests were used to compare angular positions of body segments before versus after the training period. We specifically investigated the angles of the head, (upper) trunk, pelvis, and arm relative to the foot and the angles between the head and trunk, head and pelvis, trunk and pelvis, and trunk and arm. Statistical analyses were performed using Sigma Stat (Systat Software Inc.) and were Bonferroni corrected to account for multiple comparisons. As such, the threshold for significance for each individual' *t* test was set at $p \leq 0.006$. Paired *t* tests were also used to compare the average pointing position before when compared to after training, as determined by the location pointed to with the laser pointer.

Experiment 2

To determine how sitting posture affects perception of straight ahead during PKAR.

Subjects and protocol

A different sample of ten healthy, right-handed subjects (age 25.5 ± 4.9; 3 men, 7 women) participated in the second phase of the study, and informed consent was obtained in accordance with University policy. Subjects in Experiment 2 completed 3 different days of testing. All test days were identical in terms of tasks performed, but differed with respect to the position in which the tasks were performed. On one day subjects did the tasks in standing as in Experiment 1, on another day subjects performed the tasks while sitting in a chair with no back, and on another day they performed the tasks while sitting in a chair with a back. Order of the different session-days was randomized and a post hoc statistical analysis confirmed that order or presentation had no significant effect on pointing performance ($F = 0.47$, $p = 0.63$). On each day, subjects were first asked to stand or sit quietly with their arms at their sides, and this initial posture (Pre-Training 1) was recorded for 10 s. Subjects then performed 10 trials of pointing as described in Experiment 1. Subjects then again stood or sat quietly with arms at their sides, and posture (Pre-Training 2) was again recorded for 10 s. This second Pre-Training condition, which was not included in Experiment 1, was added to Experiment 2 to make sure that simply standing and pointing did not result in any changes in posture.

Subjects then trained on the rotating treadmill at 60° per second in the clockwise direction for 15 min as described previously. Once again, all subjects were able to follow instructions and maintain a fixed heading during training. Upon completion of the 15 min of rotating treadmill training, subjects completed another block of trials that included one 10-s trial in a quiet position with arms at the sides (Post-Training 1), 10 pointing trials, and another trial in a quiet position with arms at the sides (Post-Training 2). This second Post-Training condition, which was not included in Experiment 1, was added to Experiment 2 to determine how quiet standing posture changed after rotating treadmill training and whether it changed further after a series of pointing trials. Upon completion of the pointing trials, subjects were asked to indicate whether they thought they were successful in pointing straight ahead to the center point and whether they had any perception of changes in postural alignment.

Data collection and analysis

Kinematic data were collected as detailed in Experiment 1. For all measures, one-way RM ANOVAs with position (standing, sitting without back, sitting with back) and time (pre or post) were used to determine significant differences. Tukey–Kramer post hoc tests were used to make subsequent pairwise comparisons as appropriate.

Results

Experiment 1

Perception of straight ahead

Prior to training, all subjects pointed in the same region, showing a slight left-of-center bias prior to any exposure to the rotating treadmill (Fig. 1a). Following the training period, all subjects demonstrated a shift in pointing that was specific to the direction of treadmill training. Those who trained on the clockwise-rotating treadmill pointed to the left of straight ahead by $31.6 \pm 10.4°$; $p < 0.05$, and those who trained on the counterclockwise-rotating treadmill pointed to the right of straight ahead by $26.4 \pm 10.9°$; $p < 0.05$. The magnitude of the effect was not significantly different in the clockwise and counterclockwise directions ($p = 0.73$).

There were also significant changes in the yaw plane angular positions of many segments. The head, trunk, and pelvis all rotated over the feet (Fig. 1b; Table 1). (Note that angular change values presented in Table 1 were obtained

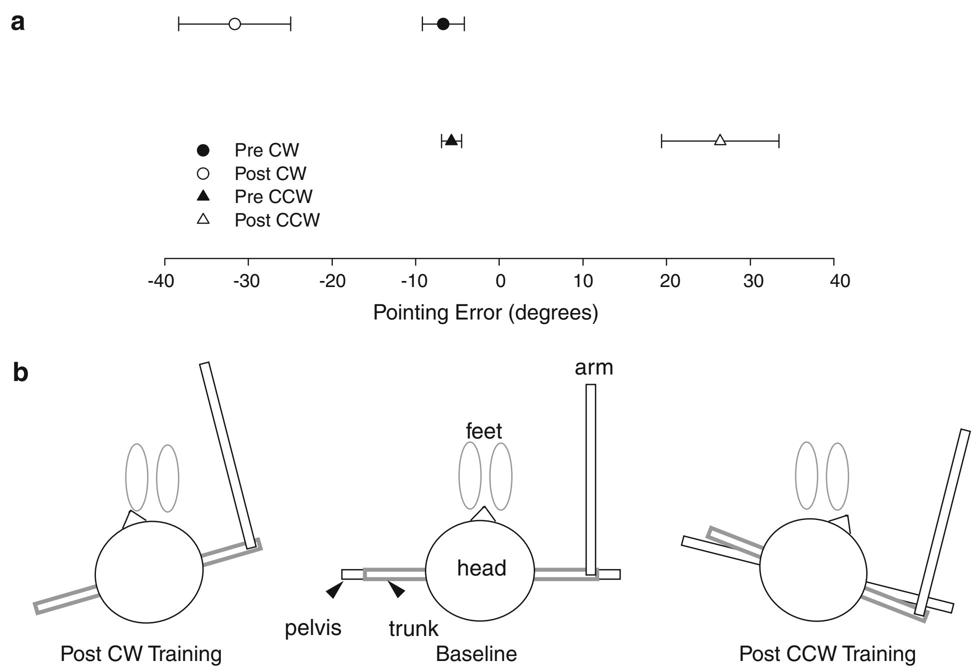

Fig. 1 Illustration of change in straight ahead pointing position **a** before (*filled symbols*) and after (*open symbols*) training on the rotating treadmill in the clockwise (CW, *circles*) or counterclockwise (CCW, *triangles*) direction in Experiment 1. Values are means ± SDs. Stick figures **b** illustrate positions of the head, trunk, pelvis, and arm at baseline (*center*) and after CW (*left*) and CCW (*right*) training

by taking the additive inverse of all data from the counterclockwise training group so that we could combine data from the clockwise and counterclockwise training groups.) In addition, trunk rotation relative to the pelvis increased, with a near significant ($p = 0.007$) increase in head rotation relative to the pelvis. The position of the pointing arm with respect to the trunk also changed slightly, but significantly.

Table 1 Summary of changes in kinematic variables for Experiment 1

Angle	Average change (°)	p value
Head-Foot	24.7 ± 14.4	<0.001*
Trunk-Foot	18.9 ± 11.4	<0.001*
Pelvis-Foot	13.1 ± 8.7	<0.001*
Arm-Foot	13.1 ± 14.7	0.014
Head-Trunk	3.3 ± 5.8	0.085
Head-Pelvis	9.2 ± 9.1	0.007
Trunk-Pelvis	3.4 ± 2.0	<0.001*
Trunk-Arm	2.6 ± 2.0	0.001*

Values are means ± SDs

* Significant difference between pre- and post-training trials at Bonferroni corrected values of $p = 0.006$

Experiment 2

Effect of standing versus sitting on perception of straight ahead

Similar to Experiment 1, subjects pointed slightly left of center prior to rotating treadmill training. This was true regardless of whether subjects were standing or sitting. After rotating treadmill training, subjects showed significant shifts in pointing for all conditions (Fig. 2a). The shift in pointing was largest for standing ($p < 0.001$), followed by sitting on a chair without a back ($p = 0.001$), and was least in sitting on a chair with a back but was still significant ($p = 0.037$). The shift in pointing was significantly larger for standing than for sitting with a back ($p < 0.0005$) or without a back ($p < 0.0005$). The shift in pointing during sitting without a back was significantly larger than for sitting with a back ($p = 0.014$).

Kinematic results from the standing condition were similar to Experiment 1, with significant increases in rotation of the head, trunk, and pelvis over the feet, as well as the head and trunk relative to the pelvis, after training (Table 2). There was also again a significant change in the pointing arm to trunk angle. The two sitting conditions had the effect of eliminating rotation about certain body segments compared with the standing condition, especially the rotation of the pelvis over the feet, the trunk over the feet, and the trunk over the pelvis. In sitting without a back, head rotation relative to the feet was significant, but no other angles changed significantly. In sitting with a back support, there were no significant changes in any of the individual angles examined, despite significant changes in perception of straight ahead.

The changes in head-to-foot ($p < 0.0005$), trunk-to-foot ($p < 0.0005$), and pelvis-to-foot ($p < 0.0005$) angles were significantly greater for standing than for either sitting condition. Changes in arm-to-foot angle were also larger for standing than for sitting without a back ($p = 0.022$) or

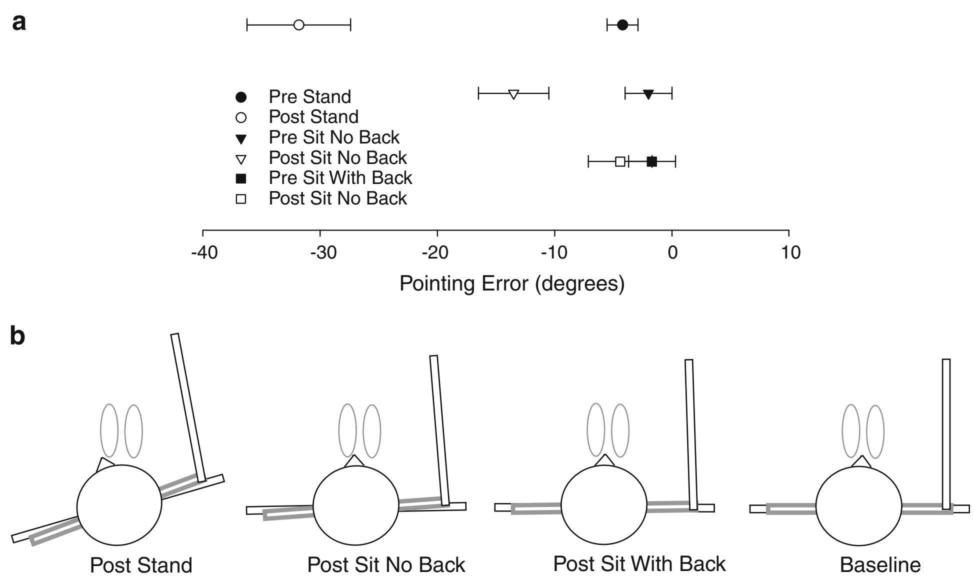

Fig. 2 Illustration of change in straight ahead pointing position **a** before (*filled symbols*) and after (*open symbols*) training CW on the rotating treadmill and pointing from standing (*circles*), sitting with no back (*triangles*), or sitting with a back (*squares*). Values are means ± SDs. Stick figures **b** illustrate positions of the head, trunk, pelvis, and arm in standing, sitting with no back, sitting with a back, and at baseline (*left* to *right*)

Table 2 Summary of changes in kinematic variables for Experiment 2

Angle	Average change (°)		
	Standing	Sitting without back	Sitting with back
Head-Foot	24.0 ± 9.7 (<0.001)*	6.7 ± 4.6 (0.004)*	2.6 ± 5.1 (0.137)
Trunk-Foot	20.5 ± 10.6 (<0.001)*	4.2 ± 4.8 (0.023)	0.8 ± 4.1 (0.542)
Pelvis-Foot	16.2 ± 8.8 (<0.001)*	1.1 ± 5.0 (1.00)	−0.2 ± 5.3 (0.898)
Arm-Foot	10.0 ± 11.9 (0.026)	1.4 ± 2.9 (0.163)	0.8 ± 2.9 (0.407)
Head-Trunk	−1.3 ± 3.4 (0.267)	−0.6 ± 2.0 (0.423)	1.2 ± 1.8 (0.079)
Head-Pelvis	6.6 ± 5.5 (0.005)*	0.9 ± 4.1 (0.442)	1.4 ± 1.9 (0.039)
Trunk-Pelvis	4.3 ± 2.9 (0.001)*	1.7 ± 2.6 (0.090)	1.3 ± 1.6 (0.302)
Trunk-Arm	−6.4 ± 5.3 (0.004)*	−2.2 ± 4.0 (0.114)	−0.5 ± 2.7 (0.589)

Values are means ± SDs (*p* value)

* Significant difference between pre- and post-training

with a back ($p = 0.015$). There were no differences between the two sitting conditions for any of these measures. The changes in head-to-trunk, trunk-to-pelvis, and trunk-to-arm angles were significantly larger for standing than sitting with a back ($p = 0.013$ for head-to trunk, $p= 0.001$ for trunk to pelvis, $p = 0.005$ for trunk-to-arm), but not for standing vs. sitting without a back or between the two sitting conditions. There were no differences in head-to-pelvis angle for any of the conditions.

Table 3 provides quiet stance positions before (Pre-Training 1, Pre-Training 2) and after (Post-Training 1, Post-Training 2) rotating treadmill training. These data differ from the data already presented because they were collected during quiet standing with the arm at the side. Pre-Training 1 is the group average baseline posture in the standing condition with the arm at the side. Pre-Training 2 is the quiet standing posture with the arm at the side after the subject completed 10 pointing trials but before training on the treadmill. Post-Training 1 is the standing posture just after the training period but before completion of any additional pointing trials. Post-Training 2 is the posture with the arm at the side after completion of 10 additional pointing trials. One-way repeated measures ANOVAs revealed statistically significant differences between the postures. There were no significant differences between Pre-Training 1 and Pre-Training 2. Post-Training 1 showed a significant change in the angle of the foot relative to the pelvis, head, and trunk when compared to both Pre-Training 1 and Pre-Training 2. Post-Training 2 showed a significant increase from Post-Training 1 in the same three angles.

For both Experiments 1 and 2, all subjects felt as if they were successfully pointing straight ahead to the center point on the wall. Subjects did not report any perceived change in their posture across the experiments. Subjects were surprised, upon removal of the blindfold, to see that they were standing in an unusual postural alignment and surprised to learn that they had not successfully pointed to the center.

Table 3 Summary of Quiet Stance Variables

Angle	Average angle (°)			
	Pre-Training 1	Pre-Training 2	Post-Training 1	Post-Training 2
Head-Foot	85.4 ± 11.2$^{‡,◇}$	84.3 ± 13.6$^{‡,◇}$	97.6 ± 13.6 $^{*,†,◇}$	110.2 ± 16.4*,†,‡
Trunk-Foot	85.4 ± 8.2$^{‡,◇}$	85.2 ± 11.1$^{‡,◇}$	93.6 ± 9.6$^{*,†,◇}$	105.6 ± 11.4*,†,‡
Pelvis-Foot	85.2 ± 9.7$^{‡,◇}$	83.5 ± 12.2 $^{‡,◇}$	91.6 ± 10.6$^{*,†,◇}$	101.6 ± 13.1*,†,‡
Head-Trunk	4.8 ± 3.0	4.5 ± 2.5	5.9 ± 4.2	6.7 ± 4.8
Head-Pelvis	4.3 ± 1.6$^{◇}$	3.6 ± 2.4$^{◇}$	7.1 ± 5.2	9.4 ± 5.9*,†
Trunk-Pelvis	3.2 ± 1.9$^{◇}$	3.5 ± 1.5$^{◇}$	3.2 ± 1.8	5.3 ± 2.4*,†

Values are means ± SD

* Significant vs. Pre-Training 1

† Significant vs. Pre-Training 2

‡ Significant vs. Post-Training 1

◇ Significant vs. Post-Training 2

Discussion

This is the first report of the effect of rotating treadmill training on the perception of subjective straight ahead (SSA). It is also the first to examine the effects of rotating treadmill training on postural orientation in sitting, compared to standing. Both studies support the hypothesis that turning after-effects of walking on a rotating surface are due to a change in the central nervous system earth orientation reference for straight ahead.

Effects of PK stimulation on subjective straight ahead

We noted significant changes in pointing direction following rotating treadmill training. The change came from a combination of rotation about multiple body segments that appeared to summate to give the overall effect of rotated arm trajectory with respect to feet orientation on the surface. Most of the change came from head, trunk, and pelvis rotation over the feet, with smaller changes occurring elsewhere. Restriction of postural rotation in one or more of these body segments by sitting with or without back support resulted in progressive reductions, but not complete elimination, of the pointing effect. In all conditions, the arm-to-trunk angle showed a change in the opposite direction of the PKAR effect. This counter-rotation of arm-to-trunk angle may represent a compensation to shift the arm back toward straight ahead to counteract the trunk and pelvis rotation present after PK stimulation, but it was not large enough to fully compensate for the body rotation.

Subjective straight ahead has been described as a dynamic construction that directly depends upon past experience regarding our sensorimotor interaction with the environment (Dupierrix et al. 2009). It relies on integration of visual, vestibular, and proprioceptive inputs (Karnath et al. 1994). We know that PKAR also relies upon these same inputs. In the present experiments, and in other published work on PKAR, the influence of vision is eliminated via use of a blindfold. If vision is permitted, it temporarily suppresses PKAR, but PKAR resumes unchanged when visual inputs are again removed (Falvo et al. 2009). The vestibular system has its strongest influence in the first 1–2 min as subjects begin to turn during active stepping PKAR, but yaw plane–related vestibular influences decline once a steady rate of turning is reached (Earhart et al. 2004). In the standing and sitting tasks in the present study, the role of the vestibular system was likely minimal as yaw plane rotations were small and slow and were not perceived by participants.

The lack of perception of the segment rotations is interesting, as the relative rotational relationships of the head, trunk, and pelvis to the feet were clearly shifted. The changes noted in the present study are in keeping with those of Hudson et al. (2005) who noted rapid sensorimotor recalibrations when the feet were passively rotated via a platform while the subject was asked to point with the trunk toward targets. Subjects in that study made adaptive changes in their trunk position to counteract the rotation of the platform, but were unaware of the altered motion of the body in space. These authors propose that the trunk to feet relationship is the critical variable that drives the adaptive response. The head-on-trunk signal has also been proposed to play an important role in generation of the egocentric reference frame (Karnath et al. 1993). In the present study, the relationship of the head to the trunk did not change, and this may explain why subjects continued to point toward the midline of their rotated head/trunk segment rather than pointing in the direction that was truly straight ahead relative to foot position. However, previous work examining pointing while the shoulders were held fixed and the feet slowly rotated under the trunk showed that subjects used the current representation of the perceived trunk position in space, rather than trunk midline, to determine the relationship between egocentric and exocentric reference frames (Wright et al. 2007). This transformation of exocentric coordinates to egocentric coordinates is a critical step in determining the pattern to be used in order to point toward perceived straight ahead (Soechting and Flanders 1989).

Inputs from neck proprioceptors also clearly participate in the elaboration of egocentric space, as vibration of neck musculature can cause shifts in subjective straight ahead (Strupp et al. 1999; Ceyte et al. 2006). Subjective straight ahead is also known to be shifted in individuals with chronic yaw rotation of the head relative to the trunk as a result of cervical dystonia (Müller et al. 2005). Changes in perception of subjective straight ahead induced by podokinetic stimulation and/or cervical dystonia likely have a different mechanism than the shifts in SSA noted in individuals with spatial neglect following stroke. Shifts in SSA after stroke appear to involve translational changes in the frontal plane rather than rotational changes in the yaw plane (Saj et al. 2008; Honoré et al. 2009).

Effects of PK stimulation on quiet standing posture

Based on the data from the four quiet stance recordings, there is evidence that PKAR has an impact on postural alignment in yaw, even in the absence of a dynamic pointing task. Immediately after rotating treadmill stimulation, there were clear differences in quiet stance posture even before subjects actively pointed. This is consistent with the observations of Hollands et al. (2007) but contrasts with Stevens and Earhart (2006). It appears that engagement in a dynamic pointing task may influence quiet standing posture, as shown by larger body rotations following pointing than observed prior to pointing. This gradually increasing postural rotation may be related to the participation in the dynamic pointing task and/or related to a response ramp up over time that may occur even in the absence of a dynamic task. A similar ramping up of the stepping rotation effect is observed over the first 1–2 min when subjects attempt to step in place after rotating treadmill stimulation and then show a gradual decay in the response over time (Weber et al. 1998).

Our results demonstrate that PKAR is not specific to locomotion but also influences postural alignment in both standing and sitting, suggesting that PKAR may represent a change in a global postural control variable such as spatial reference frame, rather than a local variable that is specific to the lower limbs. This could explain the robust transfer of PKAR across different forms of locomotion (Earhart et al. 2001, 2002; Earhart 2006). A similar change in a global postural control reference frame has also been proposed to underlie after-effects of leaning following standing or stepping on an inclined surface (Kluzik et al. 2005, 2007a, b). These processes likely rely upon an internal model where the representation of the foot in space may be based upon information about the head in space, the head relative to the trunk, and the trunk relative to the feet (Mergner et al. 1993).

Insights into neural control of PKAR

The demonstration of transfer of PKAR to other forms of locomotion, and now also to standing and sitting tasks, is in sharp contrast to split-belt treadmill adaptations that have been shown to be very task-specific. Split-belt adaptations do not transfer between limbs, are specific to the form of locomotion used during training, and are also specific to the speed at which training takes place (Choi and Bastian 2007; Vasudevan and Bastian 2010). As such, the circuitry for split-belt adaptations has been proposed to reside at the level of the spinal cord and to contain specific networks for forward walking, backward walking, the left limb, and the right limb (Choi and Bastian 2007).

In contrast, we propose that podokinetic adaptations occur at a level above the spinal cord by affecting spatial orientation for posture and perception. While the PKAR process likely involves a network of supraspinal structures, it is clear that a major contributor to PKAR must be an area where vestibular, somatosensory, and visual inputs as well as cerebellar inputs are received and integrated, as all are known to influence PKAR responses (Jürgens et al. 1999; Hong et al. 2007; Falvo et al. 2009; Earhart et al. 2004). This control center may regulate a global variable regarding spatial reference frame, with adaptations of this reference frame then influencing a multitude of networks in the spinal cord via descending pathways. This could account for the effects of PKAR on various forms of locomotion and also explain how podokinetic stimulation influences standing and sitting postures as well as perception of subjective straight ahead.

The specific nature of the global variable being adjusted and the mechanism for its adaptation remain unclear. One possibility is that PKAR is mediated by a velocity storage mechanism similar to that for optokinetic after-effects (Raphan et al. 1979). If this is the case, one would expect shifts in perception of subjective straight ahead to be related to rotating treadmill training velocity. It is presently unclear whether this is the case, though it is known that turning velocity during stepping PKAR is correlated with training velocity, with typical peak PKAR velocity being roughly 1/3 that of the training velocity (Weber et al. 1998). Another possibility is that the variable being adapted is the relative rotation of the trunk to the feet, as has been proposed previously. If this is the case, one would expect shifts in subjective straight ahead to be independent of treadmill training velocity and instead related to the amount of rotation between the trunk and the feet during the training period. Studies where cadence was manipulated during PKAR suggest, however, that for stepping PKAR velocity, the main determinant is training speed rather than amount of trunk to foot rotation occurring during training (Earhart and Horak 2004).

The specific loci for the mediation of adaptive responses to podokinetic stimulation also remain unclear. Previous work has postulated that one key locus may be located in the brainstem, and more specifically within the pontomedullary reticular formation, midline vestibular nucleus, or mesencephalic locomotor region (Hong et al. 2007). The present results expand our understanding of the global effects of PKAR and lead us to consider additional sites in cerebral cortex that have been implicated in the control of egocentric reference frame and perception of subjective straight ahead (Colliot et al. 2002). Imaging evidence based upon vestibular and optokinetic stimulation paradigms used to induce shifts in subjective straight ahead implicates several perisylvian cortical areas (Bottini et al. 2001). These areas include the insular, retroinsular cortex, parietal cortex, temporoparietal junction, and somatosensory area II. These sites are known to receive the specific sources of information that contribute to generation of an internal representational egocentric reference frame that influences perception of subjective straight ahead (Hatada et al. 2006). As such, we hypothesize that a network of structures, including brainstem and cortical regions, may contribute to the PKAR phenomenon as well as other adaptive responses, such as the leaning after-effect, that involve recalibration of spatial orientation.

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