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Evidence for limb-independent control of locomotor trajectory

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Abstract

After stepping in place on a rotating treadmill, individuals exhibit involuntary turning in the direction opposite treadmill rotation when stepping in place on a stationary surface without vision. This response is called podokinetic after-rotation (PKAR). It remains unclear where the control center for PKAR is located and whether separate, independent podokinetic control centers exist for each lower limb. To better understand neural mechanisms underlying locomotor trajectory adaptation, this study asked whether PKAR transfers between lower limbs. Thirteen healthy adults underwent separate 15-min sessions where one (trained) leg or both legs stepped on the rotating surface. Afterward, all subjects exhibited PKAR during one-legged hopping on a stationary surface, whether hopping on the trained or untrained limb. There were no significant differences in mean turning velocity across conditions. Our results support the absence of independent podokinetic control centers for lower limbs, indicating that a single center may control locomotor trajectory.

Keywords

Locomotion; Adaptation; Podokinetic; PKAR

Introduction

Transfer of adaptations across forms of locomotion or across limbs implies sharing of circuitry between the locomotor forms or limbs, while lack of transfer implies the presence of separate and independent control centers. Previous studies have investigated the transfer of locomotor adaptations to better understand the organization of locomotor circuitry in humans. The rotating treadmill is one tool that has been used to study locomotor adaptations.

The rotating treadmill has been used to provide podokinetic (PK) stimulation, which involves stepping on a rotating surface and turning one's feet in the opposite direction of platform rotation in order to maintain a fixed position of the head and trunk (Earhart and Hong 2006). After PK stimulation, subjects unknowingly turn in circles in the absence of visual cues when stepping on a stationary surface (Weber et al. 1998). This adaptive response, known as

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podokinetic after-rotation (PKAR, Gordon et al. 1995) is thought to represent an adaptive recalibration of the rotational relationship between the trunk and the feet. Strong transfer of PKAR between locomotor forms has been demonstrated (Earhart et al. 2001, 2002a; Earhart 2006). In addition, transfer of this adaptation between the lower limbs was implied when PKAR was expressed during bilateral stepping following unilateral PK stimulation (Earhart et al. 2002b). However, bilateral expression following unilateral stimulation only emerged approximately 15 steps into the response. The delayed transfer of PKAR expression from one limb to another may reflect an interaction between two limb-specific, independent control centers which was dependent on the limbs being used together. Therefore, the design of this former experiment did not definitively determine whether podokinetic adaptation transfers from a trained to an untrained limb when the untrained limb is used in isolation.

To ascertain whether the adaptation transfers from a trained to an untrained limb when the untrained limb is used in isolation, one can examine the post-adaptation response of each limb separately through one-legged hopping, since feedback from one limb during post-adaptation bilateral stepping may confound the overall podokinetic response. The hypothesis that transfer of adaptation responses between control centers for the lower limbs is dependent on subsequent bilateral use is supported by findings from a study examining adaptations induced during one-legged forward hopping on a conventional treadmill (Anstis 1995). In this study, significant aftereffects were seen during post-adaptation hopping for the trained but not the untrained leg when the limbs were only used independently. Further, following one-legged hopping over ground without vision, a leg-specific adaptation was seen when individuals attempted to hop in place on one leg without vision (Durgin et al. 2003). These findings support the idea that adaptations from unilateral conventional treadmill training and over-ground hopping are not transferred between lower limbs, but previous studies have not definitively established if the particular locomotor trajectory adaptations occurring during rotating treadmill training transfer between limbs.

The aim of the present study was to test the hypothesis that locomotor trajectory adaptations do not transfer between limbs, indicating the presence of autonomous control centers for the regulation of locomotor trajectory adaptations in the lower limbs. We used a rotating treadmill to induce locomotor adaptation in one leg (trained), while the other leg (untrained) stepped on a stationary surface. We compared the PKAR effects during one-legged hopping on the trained versus the untrained leg to assess potential transfer between legs. We hypothesized that subjects would not demonstrate PKAR during one-legged hopping on the untrained leg, suggesting the presence of independent control centers for locomotor trajectory of the lower limbs. An additional goal was to compare the effects of unilateral and bilateral PK stimulation on PKAR assessed during one-legged hopping to determine whether bilateral stimulation enhances the PKAR after-effect. If PKAR augmentation is seen following bilateral stimulation, it would suggest either an enhanced output from a common control center or from two separate but linked control centers. If separate, autonomous control centers exist for locomotor trajectory in the two lower limbs, the proposed PKAR augmentation following bilateral stimulation would be less likely. (However, a lack of PKAR augmentation in response to bilateral stimulation would not entirely rule out the possibility of two separate but dependent control centers or one common PKAR control center.) We hypothesized that PKAR during one-legged hopping on the trained limb would be similar following either unilateral or bilateral PK training, in keeping with our hypothesis of separate, independent trajectory control centers for the two limbs.

Materials and methods

Subjects and protocol

We recruited 13 healthy subjects (9 females, 4 males) with a mean age of 25 (± 1.06) years. Written informed consent was provided by all subjects, in accordance with the Human Research Protection Office at Washington University School of Medicine. Subjects participated in two sessions, separated by at least 24 h. In each session, subjects walked in place at their preferred pace for 15 min with one foot on either side of the center axis of a rotating platform (Neuro Kinetics, Inc. Pittsburgh, PA, USA). Prior work has shown that stepping on axis or on the perimeter of the platform yield similar PKAR responses (Earhart lab, unpublished observations). The platform was 122 cm in diameter, and rotated clockwise at 60°/s in all trials. A stationary surface was laid over the left half of the platform, so only the right limb stepped on the rotating disk (turning only the right limb relative to the trunk), while the left limb stepped on the slightly raised stationary surface (Fig. 1a, b).

After 15 min of PK stimulation, PKAR was measured as the individual hopped in place on one leg in the center of the stationary platform while holding onto an overhead low friction wheel and wearing a blindfold and ear plugs. Loosely holding the overhead wheel prevented subjects from drifting or losing balance during hopping in place, but they did not appear to use the wheel to support their weight. Subjects were asked to hop continuously on a specified leg for 2 min at their preferred hop frequency while data were collected. The same procedure was repeated in the second session, except hopping was done on the opposite leg. Subjects were randomly divided into two groups, with one group ($n = 5$) hopping first on the trained (right) leg, while the other group ($n = 8$) hopped on the untrained (left) leg in the first session. All subjects completed the first 2 min of hopping without signs of performance-hindering fatigue.

A subset of the original subjects ($n = 7$, mean age 26 ± 1.90 years, 5 females) returned for an additional session that included bilateral PK stimulation. During this session, subjects walked in place with both feet stepping on the rotating platform for 15 min, followed by 2 min of hopping on one leg (randomly assigned left or right) (Fig. 1c).

Motion analysis

Six reflective markers (20 mm diameter) were placed on subjects (left/right anterior superior iliac spine (ASIS) of pelvis, left/right posterior superior iliac spine (PSIS) of pelvis, sacrum, midway down the anterior aspect of the left thigh). The sacrum and left and right PSIS markers were included to allow for virtual reconstruction of the positions of markers of interest if a marker was briefly obscured during trials. The left thigh marker provided asymmetry in the marker set, clearly distinguishing the left and right sides for later analysis. Three stationary markers were also placed on the floor to facilitate determination of subject orientation in space during data processing. Two floor markers were used in the generation of pelvis positions in space for turning velocity calculations. The positions of each marker were recorded at 100 Hz using an eight camera 3-D motion capture system (Motion Analysis Corporation, Santa Rosa, CA, USA).

Data analysis

The presence of a PKAR response was determined according to the sensory vestibular threshold for detecting turning, which is defined as rotating more than 1–2°/s (Mergner et al. 1993). Parameters assessed during PKAR included average turning velocity (average pelvic angular velocity), maximum turning velocity, and rise time constant. All kinematic data were filtered with a 6-Hz low pass second-order Butterworth filter. The angular velocities of pelvic rotation about the yaw axis during hopping were calculated by taking the first derivative of the pelvis angular position recorded by EVaRT Version 4.4 motion analysis software (Motion Analysis

Corp., Santa Rosa, CA, USA). The angle formed by a line drawn between the two ASIS markers and two of the floor markers was used to define pelvic position. We calculated mean turning velocities during the 2 min of hopping in all post-adaptation periods for each subject. Mean velocities were examined as a summary measure of each participant's response.

For the unilateral training session, mean turning velocities of PKAR were compared between the trained and untrained leg PKAR using paired *t* tests. Mean turning velocity values for the trained leg in the unilateral training condition versus bilateral training condition were also compared with paired *t* tests. We plotted turning velocity over time for each 2-min period of hopping, and the maximum turning velocity and rise time constant for each curve were obtained by fitting with a 2-parameter exponential rise to maximum function [$y = a(1 - e^{-bx})$, where *a* is the maximum velocity and $1/b$ is the rise time constant]. The rise time constant provides information about the typical rise in rotational velocity during the initial 1–2 min of PKAR (Weber et al. 1998). This portion of the PKAR response is thought to be the result of vestibular-somatosensory interactions (Earhart et al. 2004). The maximum turning velocity represents the point at which the PKAR response was the strongest, before the response begins to decay.

Maximum turning velocity and rise time constants were compared between the trained and untrained leg hopping trials, as well as the unilaterally versus bilaterally trained hopping trials, using paired *t* tests. Data plotted in Fig. 1d–f were obtained by calculating mean turning velocity for each consecutive 5-s bin over the 2-min trial. For all tests, significance was set at $P \leq 0.05$.

Results

During post-adaptation hopping on a stationary surface, all subjects turned in the opposite direction of treadmill rotation (i.e., counter-clockwise). Pilot data collected from three subjects demonstrated that individuals who completed baseline hopping on one leg, not preceded by rotating treadmill training, did not exhibit turning. None of the subjects turned more than $1.5^\circ/\text{s}$ (equivalent to $180^\circ/2 \text{ min}$). As a result, the baseline data were not collected from subsequent subjects in this study to minimize fatigue.

Trained versus untrained

Figure 1 displays the average turning velocity over 2 min of hopping for a representative subject on the untrained (Fig. 1d) and trained (Fig. 1e) leg. The subject demonstrated similar turning when hopping on the untrained and trained legs. Across subjects ($n = 13$), there were no differences in mean turning velocity for the untrained or trained leg [Fig. 2a, $t(12) = 1.613$, $P = 0.133$].

There were also no significant differences detected between the maximum turning velocities (obtained via curve fitting; Table 1) observed in the trained versus untrained conditions [$t(12) = 1.495$, $P = 0.161$]. Further, no significant differences were detected in the rise time constants in the trained versus untrained conditions [$t(6) = 1.654$, $P = 0.149$].

Unilateral versus bilateral

Comparisons of hopping on a trained leg following unilateral versus bilateral training for a single subject are shown in Fig. 1e, f. The subject demonstrated similar turning following unilateral and bilateral training. Across subjects there were no differences in mean turning velocity when hopping after unilateral or bilateral training [Fig. 2b, $t(6) = -1.592$, $P = 0.163$].

Similarly, no significant differences were detected between the maximum velocities seen in the bilaterally trained versus unilaterally trained conditions [$t(12) = 0.301$, $P = 0.767$], and no significant differences were detected in the rise time constants in the bilaterally trained versus unilaterally trained conditions [$t(6) = 0.395$, $P = 0.707$]. Table 1 shows the mean average

turning velocity, maximum turning velocity, and rise time constant values for conditions with the full set of participants, as well as the subset of participants that completed bilateral training.

Discussion

Our study shows that locomotor trajectory adaptations, in response to walking on a rotating treadmill, transfer from a trained limb to an untrained limb. The present findings were contrary to our initial hypothesis. We did not expect to see adaptation transfer between limbs, given the lack of transfer demonstrated previously in other treadmill and over-ground paradigms, particularly when the effects on trained and untrained limbs were isolated during assessment of transfer (Anstis 1995; Durgin et al. 2003). It is important to note that evidence against interlimb transfer from the most similar treadmill study is based on data collected from only one subject, and these data show a non-significant trend toward an aftereffect in the untrained limb (Anstis 1995). Results from a study involving one-legged hopping over ground also did not show transfer of adaptation from the trained to the untrained leg (Durgin et al. 2003); however, the trained leg was always tested first, followed by a short period of rest, and then hopping on the untrained leg. Inability to detect an aftereffect in the untrained leg may therefore be due to an experimental design artifact, as similar aftereffects from a bilateral treadmill adaptation experiment have been shown to dissipate within a minute or two following training (Anstis 1995).

In contrast to the aforementioned studies, a previous rotating treadmill study showed that PKAR adaptation transferred from the untrained to the trained leg during bilateral stepping following unilateral treadmill training (Earhart et al. 2002b). However, the design of the present study definitively demonstrates interlimb adaptation transfer without the confound of using the trained and untrained limbs together during assessment of the adaptive aftereffect.

In addition to providing additional evidence of transfer of locomotor adaptations between lower limbs, this study also provides strong support for a central, rather than a peripheral, adaptive mechanism. Prior work examining PKAR has suggested that PKAR may result in recalibration of the “neutral” angular relationship between the feet and the trunk. Given this viewpoint, it has been proposed that PKAR may reflect a peripheral adaptation of the lower limb somatosensory system rather than a central process (Hollands et al. 2007). The present evidence directly refutes this view, as transfer from one limb to another argues against the adaptation occurring at the level of the limb somatosensory system and supports the presence of a central adaptive mechanism.

The present study provides evidence supporting the transfer of locomotor trajectory adaptations between lower limbs, indicating that there are not separate and autonomous control centers for locomotor trajectory adaptation. Instead, we suggest storage of certain locomotor adaptations, including PKAR, may reside in a single, higher control center, above the level of the spinal cord. This would still allow for the presence of independent, limb-specific locomotor control centers at the spinal cord level for other aspects of locomotor control, such as interlimb phasing or postural aftereffects, which do not transfer in split-belt treadmill or moving sled studies, respectively (Jensen et al. 1998; Reisman et al. 2005; Choi and Bastian 2007; Reynolds and Bronstein 2004, 2007). Reisman et al. (2005) suggested that different types of adaptation, such as PKAR and interlimb phasing, are generated and stored using separate processes and systems. If this is the case, the control centers for the production of PKAR locomotor trajectory adaptation would not need to co-exist spatially with those for the interlimb phasing adaptations. Alternatively, our results could be used to argue for the presence of strongly-coupled pattern-generating spinal circuitry for each leg, but this appears to be less likely given the evidence from other locomotor paradigms (Choi and Bastian 2007; Anstis 1995).

This study adds to the literature examining PKAR, but the location of PKAR storage remains unclear. To help elucidate the location of PKAR storage, PKAR has been studied in humans with basal ganglia disease (Hong et al. 2007), bilateral vestibular loss (Earhart et al. 2004), and cerebellar degeneration (Earhart et al. 2002c). Patients with Parkinson's disease display normal PKAR, but individuals with bilateral vestibular loss show an abnormal PKAR aftereffect during the first 2 min of the response, and a majority of patients with cerebellar degeneration show impaired PKAR. As PKAR is still present in all of these patient populations, the typical functioning of each of the damaged structures individually does not appear to be required for PKAR expression or storage. However, the site of PK storage must receive inputs from the cerebellum, as well as the visual, vestibular, and somatosensory systems. Given the evidence from this study and prior work, we hypothesize control of locomotor trajectory adaptations seen in PKAR may be produced at a single higher-level center in the brainstem that is able to influence lower level independent control centers for other locomotor adaptations, such as interlimb phasing and walking direction.

Conclusions and future directions

This study definitively demonstrates the presence of inter-limb transfer of PKAR. Our results, when synthesized with prior work, most strongly support the presence of a single, common, limb-independent control center for locomotor trajectory adaptation. The brainstem has been proposed as the putative location for PKAR storage by other sources (Jurgens et al. 1999; Gordon et al. 2003; Hong et al. 2007), and this is in keeping with our hypothesis of a supraspinal control center for PKAR. This trajectory control center is likely separate from control centers for other locomotor adaptations presumed to reside in the spinal cord. Further investigation of this phenomenon is required to confirm the networks involved and to determine the control center locus for the production of this and other forms of locomotor adaptation. Future work should also examine the impact of PK stimulation on additional variables, such as perception of subjective straight ahead, in order to determine whether PKAR is a locomotor-specific adaptation or if it represents a more global adaptation of the spatial reference frame.

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Fig. 1.

Experimental conditions include unilateral training followed by one-legged hopping on the untrained (a) or trained (b) leg, as well as bilateral training followed by one-legged hopping on either trained leg (c). Untrained limbs are represented with *black feet*, while trained limbs are represented with *gray feet*. Arrows indicate the clockwise direction of treadmill rotation during all training periods. Mean turning velocity from a single subject plotted over the 2 min of hopping on (d) the untrained leg, (e) the trained leg after unilateral rotating treadmill training, and (f) one leg after bilateral rotating treadmill training. PKAR is demonstrated on the untrained limb although it never stepped on the rotating surface, and it was used in isolation from the trained leg

Fig. 2.

a Mean turning velocity during hopping on the untrained or trained leg following unilateral rotating treadmill training ($n = 13$). Inadvertent turning was seen in both conditions, and means did not differ significantly. **b** Mean angular velocity during hopping on the trained leg following unilateral or bilateral rotating treadmill training ($n = 7$). No significant difference was detected between conditions. *Error bars* indicate SEM

Table 1

Mean average turning velocities, maximum velocities, and rise time constants

	Unilateral untrained (<i>n</i> = 13)	Unilateral trained (<i>n</i> = 13)	Unilateral trained (<i>n</i> = 7)	Bilateral trained (<i>n</i> = 7)
Average turning velocity (°/s)	4.57 ± 0.90	6.33 ± 0.91	7.01 ± 1.29	9.38 ± 1.18
Maximum velocity (°/s)	5.59 ± 1.17	7.95 ± 1.41	8.59 ± 2.08	11.02 ± 1.93
Rise time constant (min)	25.84 ± 10.18	29.94 ± 8.01	21.85 ± 8.59	17.61 ± 7.09

The mean average turning velocities, maximum velocities, and mean rise time constants are included for all conditions for the full set of participants (*n* = 13), as well as the subset who completed the second task (*n* = 7). Values are mean ± SEM. There were no significant differences in any of the above variables between conditions