Transfer of Podokinetik Adaptation From Stepping to Hopping

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1Department of Clinical Neurosciences and Neuroscience Research Group, The University of Calgary, Calgary, Alberta T2N 2T9, Canada; and 2Balance Disorders Laboratory, Oregon Health and Science University, Beaverton, Oregon 97006

Received 18 July 2001; accepted in final form 16 October 2001

Earhart, Gammon M., G. Melvill Jones, F. B. Horak, E. W. Block, K. D. Weber, and W. A. Fletcher. Transfer of podokinetik adaptation from stepping to hopping. J Neurophysiol 87: 1142–1144, 2002; 10.1152/jn.00588.2001. Following stepping in-place on the surface of a rotating circular treadmill, a subject attempting to step in-place or walk in a straight line across the floor without vision will rotate relative to space. This adaptation, termed podokinetik after-rotation (PKAR), transfers to backward walking following forward walking on the rotating disk. We asked whether adaptation obtained during stepping in-place on the rotating disk would transfer to hopping on both feet. We hypothesized that subjects would demonstrate PKAR during both hopping and stepping, adding support to the hypothesis that PKAR is a centrally mediated adaptation of general locomotor trajectory that is not specific to the form of locomotion used while on the rotating disk. Subjects demonstrated PKAR during both hopping and stepping after stepping in-place on the rotating disk. The time courses of PKAR during hopping and stepping were similar, although the angular velocity amplitude of PKAR was lower in hopping than in stepping. This difference in amplitude suggests an incomplete transfer of PKAR.

INTRODUCTION

After stepping or walking in-place on the surface of a rotating treadmill, a subject asked to step in-place on a stationary surface or walk along a straight line without vision will inadvertently rotate (Weber et al. 1998). This adaptive phenomenon, called podokinetik after-rotation (PKAR), represents a remodeling of the rotational relationship between the feet and the trunk. During podokinetik stimulation (i.e., stepping in-place on a rotating disk), the feet turn relative to the trunk by virtue of their contact with the rotating surface during the stance phase of gait. During PKAR, the walking surface is stationary so that the feet cannot turn relative to space during stance. Rather, the trunk turns over the stationary feet during PKAR (Earhart et al. 2001; Gordon et al. 1995).

Podokinetik adaptation is not specific to the form of locomotion used during exposure to the rotating disk. Following forward walking in-place on the perimeter of a rotating disk, subjects asked to walk forward or backward on firm ground along a straight line with eyes closed produce curved trajectories with similar amplitudes and time constants (Earhart et al. 2001). This indicates that podokinetik adaptation transfers between two forms of locomotion, forward and backward walking. A common feature of forward and backward walking is that the left and right limbs alternate with one another. Is this similarity in interlimb coordination essential for transfer of adaptation?

To address this question, we asked whether adaptation obtained while using out-of-phase interlimb coordination (i.e., stepping in-place) would transfer to a locomotor form that has in-phase interlimb coordination (i.e., hopping on both feet). For stepping, step frequency was controlled at 2 Hz using a metronome. For hopping, subjects self-selected their preferred frequency, which is typically slightly greater than 2 Hz (Farley et al. 1991; Melvill Jones and Watt 1971). We hypothesized that adaptations would transfer from stepping to hopping despite differences in interlimb coordination and frequency, supporting the hypothesis that the podokinetik system controls general locomotor trajectory.

METHODS

Subjects

Participants were seven healthy adult volunteers (5 male, 2 female), 27–78 yr of age. All subjects gave informed consent prior to participation.

Protocol

Each subject participated in two sessions, separated by at least 24 h. In both sessions, the subject completed 30 min of podokinetik stimulation by stepping in-place on the axis of a disk rotating in the clockwise (CW) direction at 60°/s. During this period, step frequency was maintained at 2 Hz through use of a metronome attached to the trunk. At the end of PK stimulation, postadaptation responses were measured over 30 min. In one session, the subject was asked to step in-place, and in the other session the subject was asked to hop in-place on both feet during the postadaptation trials. For postadaptation stepping trials, step frequency was matched to a metronome set at 2 Hz. For postadaptation hopping trials, subjects selected a preferred hop frequency. This frequency was measured by counting the number of hops performed in 10 s and dividing by the sampling period (i.e., 10 s). Postadaptation trials were each of 2-min duration and were repeated at 5-min intervals, starting 0, 5, 10, 15, 20, 25, and 30 min after termination of PK stimulation. Subjects wore a blindfold and earplugs for all postadaptation trials. Subjects were still able to hear the metronome during postadaptation stepping trials, as the metro-
Data collection and analysis

During postadaptation trials, subjects held a very low-friction wheel mounted overhead. This wheel was equipped with a rotary potentiometer used to record each subject’s angular position in space. Position values were differentiated by estimating angular displacement per 10-s intervals to obtain angular velocity measures for PKAR (see individual points in Fig. 1). Velocities in the counterclockwise (CCW) and clockwise directions were assigned negative and positive values, respectively.

For each subject, plots of angular velocity versus time for the first postadaptation trial of each condition (i.e., the data set at time 0 in Fig. 1) were fitted with exponential curves to obtain 2-min rise maxima and rise time constants (see 1st 2 rows in Table 1). Plots of angular velocity versus time across all trials within a condition (i.e., the entire 30-min data set) were fitted with three-parameter exponential decay curves to obtain values for initial velocity, response decay time constant (the length of time over which the PKAR response declined to 1/3 of its original value), and final asymptote for each trial (see rows 3–5 of Table 1). We extrapolated the curves to zero to obtain y-intercept values (row 6 of Table 1). We compared PKAR initial velocity, time constant, and asymptotes between stepping and hopping conditions using paired t-tests (P = 0.05). We also plotted group average angular velocity for each trial versus time. A Friedman repeated measures ANOVA (P < 0.05), followed by Tukey’s HSD post hoc tests, was used to compare average angular velocities between stepping and hopping.

Results

Following stepping in-place on a CW-rotating disk, subjects demonstrated CCW PKAR during both hopping and stepping. The average self-selected hop frequency was 2.21 ± 0.05 Hz (mean ± SD). Step frequency was maintained at 2 Hz through use of a metronome.

DISCUSSION

We observed PKAR during hopping on both feet following stepping in-place on a rotating disk. PKAR during hopping was of similar time course but lower amplitude than PKAR during

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<th>Table 1. Curve fit values</th>
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<tr>
<td>Curve Fit Value</td>
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<tr>
<td>Maximum rise, deg/s</td>
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<td>Rise time constant, min</td>
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<td>Initial velocity, deg/s</td>
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<td>Decay time constant, min</td>
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<td>Decay asymptote, deg/s</td>
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Values are means ± SE. Maximum rise and rise time constant values were obtained by fitting data from the first post-adaptation trial (i.e., trial at time 0) of each condition with an exponential rise to maximum curve. Initial velocity, decay time constant, and decay asymptote were obtained by fitting an exponential decay function across all trials (i.e., the entire 30-min set of data) within each condition. * Significant difference between stepping and hopping (P < 0.05).

The velocity of turning during PKAR was less for hopping than for stepping for all subjects. Figure 1 shows hopping and stepping PKAR from a single subject for each trial. Although the velocity for hopping PKAR is less than that for stepping PKAR, the two responses follow similar time courses. Average values for curve fits like those shown in Fig. 1 are given in Table 1. Note that the y-intercept value for hopping is significantly different from that of stepping, reflecting the difference in PKAR velocities for the two conditions. Initial response velocities and maximum rise values also reflect the differences between hopping and stepping, although these differences were not significant at the P = 0.05 level because of the substantial variability. There were no differences in rise or decay time constants or asymptote values for hopping and stepping. Figure 2 shows the group average angular velocities (±SE) for hopping and stepping over each trial. Average velocity was significantly lower for hopping than for stepping in the trials that began 0, 15, 20, and 25 min after termination of PK stimulation.

![Figure 1](http://jn.physiology.org/)

![Figure 2](http://jn.physiology.org/)
stepping in-place. This is in contrast to previous studies examining transfer of PKAR to backward walking following forward walking on a rotating disk, where backward walking PKAR was of similar time course and similar amplitude to forward walking PKAR (Earhart et al. 2001).

The lesser transfer from stepping to hopping than from forward to backward walking may result from several factors. In forward and backward walking, as well as stepping, the lower limbs alternate with one another. While one limb is in contact with the disk and undergoing a slow clockwise rotation relative to the pelvis, the other limb is lifted and performing a quick compensatory counterclockwise rotation with respect to the pelvis. Thus throughout PK stimulation, the left and right limbs are often turning in opposite directions relative to the pelvis. During walking or stepping PKAR, this relationship is maintained; the trunk turns slowly over the stance limb while the opposite limb performs a quick, compensatory rotation in the opposite direction. Maintenance of out-of-phase coordination may facilitate transfer of PKAR. During hopping, however, the lower limbs are in-phase with one another; both feet are in contact with the disk at the same time and lifted at the same time. The feet must therefore turn in the same direction relative to the pelvis during hopping. This change in interlimb coordination may reduce transfer of adaptation from stepping to hopping. During hopping, each limb may have an inhibitory influence on the other as a result of prior experience, suggesting that the internal representation for PKAR may be primarily concerned with the rotational relationship between the stance foot and the trunk. The lesser transfer of PKAR from stepping to hopping than from forward to backward walking supports the hypothesis that each limb is represented individually and the effects of the two limbs are additive. This is consistent with the results of a previous study showing that one limb can be adapted independently from the other, but information from the two limbs is quickly integrated during PKAR to eliminate differences between the limbs (Earhart et al. 2002).

Differences in the amount of time the feet are in contact with the ground could also influence the amount of turning, as angular propulsion can only be accomplished when the feet are in contact with the surface. During stepping, one foot is always in contact with the surface. During hopping, however, there are periods when neither foot is in contact with the surface. Thus the overall ground contact time is greater for stepping than for hopping. Lesser ground contact time in hopping may contribute to the reduction in turning.

Another difference between forward to backward transfer and stepping to hopping transfer is movement frequency. For forward to backward transfer, step frequency was held at 2 Hz for both directions of walking (Earhart et al. 2001). For stepping to hopping transfer, step frequency was held at 2 Hz, but hop frequency was self-selected and was >2 Hz in six of seven subjects. This dissimilarity in frequency between stepping and hopping could reduce transfer, but we think this is unlikely for two reasons: 1) one subject’s self-selected hop frequency was 2 Hz, matching step frequency, but this subject’s behavior was not different from that of other subjects who hopped at a frequency greater than 2 Hz; and 2) one subject completed an additional session during which hop frequency was held at 2 Hz through use of a metronome, and this resulted in lower PKAR amplitude than when the subject hopped at a self-selected frequency of 2.3 Hz.

An additional factor that could affect hopping PKAR is the influence of the vestibular system on the podokinetic system. Previous studies related the initial rise of PKAR to a gradual decay in vestibular suppression of PK responses. The vestibular signal decays over the first minute of constant rotation as a result of the high-pass filter characteristics of the semicircular canals (Weber et al. 1998). During hopping, however, the jolting experienced during each landing may provide additional vestibular signals not present during stepping or walking, when contact with the ground is relatively smooth. This jolting may also cause near-synchronous activation of joint receptors throughout the body, providing another source of sensory information not present during stepping. These differing sensory consequences of hopping may serve to reduce or mask the transfer of PK adaptation.

These results suggest that PK adaptation transfers from stepping to hopping, but this transfer is less complete than that from forward to backward walking. Transfer may be reduced by disparities between conditions, but can still occur despite dramatic changes in interlimb coordination. Future studies of transfer from running to stepping and hopping may clarify the roles of changes in interlimb coordination, frequency, and sensory consequences on transfer of PK adaptation.

This work was supported by National Institute on Deafness and Other Communication Disorders Grant R01-DC-04082-01A1 and Medical Research Council Grant MA-15639.

REFERENCES


