INTRODUCTION

Successful locomotion relies on the ability to adjust locomotor output to meet a variety of environmental conditions and behavioral goals. Several features of locomotion can be changed to accommodate the multitude of situations encountered. For example, one can change the direction of locomotion and walk forward or backward as desired. Comparisons of forward and backward walking suggest that kinematic profiles for forward walking are reversed during backward walking (Grasso et al. 1998; Thorstensson 1986). Motor patterns for forward and backward walking support the hypothesis that backward walking may be produced using muscle synergies similar to those of forward walking, although the order of muscle activation within synergies is reversed for the two directions of walking (Buford and Smith 1990; Winter et al. 1989). Kinematic and myographic evidence indicates that forward and backward walking may be controlled by common neural circuitry.

In addition to changes in direction, one can also adjust relationships between sensorimotor elements of locomotor control and perception of movement. Following forward walking on the perimeter of a rotating disk, subjects generate curved walking trajectories when asked to walk forward in a straight line without vision (Gordon et al. 1995). Subjects have no knowledge of this turning, termed podokinetic after-rotation (PKAR), as they perceive that they are indeed walking along straight paths. PKAR does not depend on a sensory conflict between somatosensory information indicating that the feet are turning and visual information indicating that one is stationary with respect to the environment. Subjects exposed to a rotating disk in the presence of a rotating visual surround, a situation in which both somatosensory and visual sources indicate movement, demonstrate PKAR despite a lack of conflict between sensory inputs (Jürgens et al. 1999). Rather, PKAR suggests a remodeling of the somatosensory signals regarding the relationship between trunk rotation with respect to the feet and the perception of trunk rotation relative to space (Weber et al. 1998).

Our goal in this study was to determine whether, following an adaptive podokinetic (PK) stimulus presented in the context of forward walking, PKAR would be expressed similarly in both forward and backward walking. In light of previous studies reporting similarities between forward and backward walking patterns, we hypothesized that forward walking PK stimulation would result in PKAR during backward, as well as forward, walking. Demonstration of PKAR during backward walking following a forward-walking adaptive stimulus would support the hypothesis that the two forms of locomotion share common circuitry. It would also suggest that adaptations in-
duced through the PK system represent a general adaptation of locomotor trajectory control, rather than a remodeling specific only to the form of locomotion used during the adaptive stimulus.

METHODS

Subjects

Eleven healthy volunteers, 7 male and 4 female, participated in this study. Subjects ranged in age from 19 to 78 yr old. All subjects gave informed consent prior to participation in the study.

Protocol

Each subject participated in two experimental sessions, one to test forward walking and one to test backward walking. The direction of walking for each subject’s first session was randomly selected to reduce the potential for order effects. A cadence of 2 Hz was maintained during the entirety of both sessions through use of a metronome attached to the trunk. Each session consisted of control trials, a 30-min period of PK stimulation, and postadaptation trials. Subjects wore a blindfold and earplugs for all control and postadaptation trials but not for the period of PK stimulation. Trials were each 2 min in duration.

Forward Walking Session. Each subject performed three control trials during which they were asked to walk straight forward across the floor of a large, quiet television studio with a clear space of approximately 15 m × 20 m. Subjects were then exposed to the adaptive PK stimulus: 30 min of forward walking-in-place on the perimeter of a 76-cm-diam disk rotating at 60°/s in a clockwise direction. After this adaptation, blindfolded subjects were transported by wheelchair to the studio and asked to walk forward in a straight line across the floor. Six postadaptive trials, A1–A6, were performed at 5, 10, 15, 20, 25, and 30 min after termination of the adaptive stimulus. Between trials, and while still blindfolded, subjects were seated in a wheelchair and moved to a different, unknown starting location for the next trial.

Backward Walking Session. The backward walking session was the same as the forward walking session except subjects walked backward during the three control trials and the six postadaptive trials.

Data collection and analysis

As subjects walked, the position of the right foot was marked on the floor with chalk at 10-s intervals. To mark these positions, an experimenter followed each subject closely but made no physical or verbal contact with the subject. For forward walking, the experimenter walked behind the subject and marked the position of the heel, as this was the portion of the foot that made initial contact with the ground. For backward walking the experimenter again trailed the subject (requiring the experimenter to stand facing the backward-walking subject) and marked the position of the toe, as this was the portion of the foot that made initial contact with the ground. For all trials, the experimenter stayed in direct linear alignment with the subject to reduce the potential for directional cues. In addition, subjects wore a blindfold and earplugs, reducing the likelihood that visual or auditory cues influenced subject behavior.

Trajectories for each trial were measured in polar coordinates using a large compass rose and a tape measure (Gordon et al. 1995). Polar plots of trajectories were produced using Sigmaplot 5.0 (SPSS, Richmond, CA). Angular velocities were calculated by measuring the angle between two successive segments of the plot and dividing by the time between measures (i.e., 10 s). Clockwise and counterclockwise angular velocities were assigned positive and negative values, respectively.

We considered the possibility that the vestibular response to real rotation at the start of a trial might result in lower PKAR angular velocities at the beginning of a trial, while higher velocities may be reached by the end of a trial after attenuation of the vestibular signal due to continued rotation. Plots of each angular velocity measurement versus time within the trial were fitted with exponential growth curves to obtain maximum values and rise time constants. Although there was a trend toward increasing angular velocity as a trial proceeded, eliminating the first half of each trial and analyzing only the second minute produced results very similar to those obtained using all the measurements. Thus average angular velocities were calculated using the entire 2 min of data from each trial. Statistical comparisons of forward walking to backward walking values were performed using Friedman repeated measures ANOVAs (P = 0.05).

Mean angular velocities across subjects were plotted versus the start time of each trial (e.g., start time for A1 was 5 min, for A6 was 30 min). These plots were fitted with three-parameter exponential decay functions to determine the initial velocity, time constant of response decay, and a final asymptote value for each direction of walking. Curve fits were extrapolated to zero to obtain y-intercept values for each.

RESULTS

Following 30 min of forward stepping on a disk rotating clockwise (CW) at 60°/s, subjects demonstrated counterclockwise (CCW) podokinetic after-rotation whether tested walking forward or backward. During PK stimulation the left leg was the inner limb and the right leg the outer limb with respect to the center of disk rotation. This relationship was maintained when subjects walked CCW during forward PKAR. However, during backward walking this relationship was reversed. Subjects walked CCW during backward PKAR, with the right lower extremity as the inner and the left as the outer limb relative to the center of rotation.

Figure 1 illustrates the locomotor trajectories for forward walking (Fig. 1A) and backward walking (Fig. 1B) in the same subject for trials recorded 10 min after cessation of the adaptive PK stimulus. Note that the paths taken for the two directions of walking are similar, both turning in the CW direction. Average angular velocities (°/s) for the two trials illustrated were $-7.2 \pm 0.30$ (mean ± SE) and $-6.5 \pm 0.24$ for forward and backward walking, respectively.

Average angular velocities across all subjects are presented for forward and backward conditions in Fig. 2. Note that control values are low, indicating that subjects walked fairly straight paths prior to PK stimulation. For both forward and
backward PKAR, the highest angular velocities were obtained for trial A1, recorded 5 min after cessation of the PK stimulus. Mean velocity for A1 was significantly greater for forward than for backward walking. From the A1 peak, values gradually declined, although some effect was still apparent at A6, recorded 30 min after PK stimulus offset. Values obtained by fitting data with exponential decay curves were similar for forward and backward walking (Table 1).

In addition to the features of each trial as a whole, we examined patterns of angular velocity changes within each trial to determine whether there were differences between forward and backward walking. Figure 3 shows the angular velocities measured across the 2-min duration of forward and backward A1 trials from the same subject. Note that in both forward and backward PKAR, there is a trend toward increasing angular velocity as the 2-min trial progresses. This is similar to the 1- to 2-min rise described previously for the PKAR response (Weber et al. 1998). Rise times and maxima of trials A1–A6 for forward and backward walking are given in Table 2. The maximum value for A1-forward was significantly greater than that of A6-backward, but no other significant differences were noted for maxima across trials or conditions. There were no significant differences in rise time across trials or between forward and backward conditions.

TABLE 1. Exponential decay curve values

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Forward Walking</th>
<th>Backward Walking</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial velocity, deg/s</td>
<td>−6.46</td>
<td>−4.46</td>
</tr>
<tr>
<td>First-order asymptote, deg/s</td>
<td>−2.66</td>
<td>−1.41</td>
</tr>
<tr>
<td>Decay time constant, min</td>
<td>13.9</td>
<td>20.9</td>
</tr>
<tr>
<td>Y-intercept, deg/s</td>
<td>−8.3</td>
<td>−5.6</td>
</tr>
<tr>
<td>Goodness of curve fit (R²)</td>
<td>0.98</td>
<td>0.97</td>
</tr>
</tbody>
</table>

Values were obtained by fitting group data for forward and backward walking with exponential decay curves.

FIG. 2. Average angular velocity ± SE for forward and backward walking conditions. Control values are low, indicating that subjects walked relatively straight prior to PK stimulation. Conditions A1–A6 were recorded at 5-min intervals, starting with A1 recorded 5 min after PK stimulus offset and ending with A6 recorded 30 min after PK stimulus offset. * Significant difference between forward and backward (P < 0.05).

FIG. 3. Angular velocity measures taken each 10 s for the forward and backward A1 trials of a single subject. For both walking directions, values tend to increase as the trial proceeds. Plots like these were fitted with exponential growth curves to yield the data presented in Table 2.

DISCUSSION

PKAR: an adaptive process?

An adaptive process has three defining features: acquisition, retention, and transfer (Schmid and Jeannerod 1985). Prior reports of PKAR have demonstrated acquisition, i.e., a change in response that occurs as the result of a period of stimulation (Gordon et al. 1995; Weber et al. 1998). Retention, the persistence of a modified response after a period of rest, has also been documented. PKAR can persist for several hours following stimulation even when subjects sit quietly for periods of 25–30 min between trials (Weber et al. 1998). These results suggest that PKAR may be an adaptive process, as two of the three defining features have been noted. The present study illustrates transfer, the expression of a modified response in a situation different from that used to produce the changes. We report PKAR during backward walking following PK stimulation during forward walking. This result, in combination with those of prior studies, supports the hypothesis that PK modification is an adaptive process characterized by acquisition, retention, and transfer.

Implications of PKAR transfer from forward to backward walking

We noted substantial PKAR during backward walking following forward PK stimulation. Anstis (1995), however, re-

<table>
<thead>
<tr>
<th>Condition</th>
<th>Forward Maximum, deg/s</th>
<th>Backward Maximum, deg/s</th>
<th>Forward Rise Time Constant, s</th>
<th>Backward Rise Time Constant, s</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1</td>
<td>−8.12 ± .61</td>
<td>−5.89 ± .72</td>
<td>13.25 ± 3.39</td>
<td>16.77 ± 5.31</td>
</tr>
<tr>
<td>A2</td>
<td>−7.03 ± .56</td>
<td>−5.19 ± .84</td>
<td>17.31 ± 5.36</td>
<td>13.63 ± 2.74</td>
</tr>
<tr>
<td>A3</td>
<td>−5.52 ± .89</td>
<td>−4.80 ± .74</td>
<td>13.57 ± 1.13</td>
<td>16.87 ± 2.78</td>
</tr>
<tr>
<td>A4</td>
<td>−4.78 ± .74</td>
<td>−3.55 ± .57</td>
<td>12.48 ± 1.65</td>
<td>13.97 ± 5.08</td>
</tr>
<tr>
<td>A5</td>
<td>−4.54 ± .93</td>
<td>−4.40 ± .74</td>
<td>26.22 ± 5.33</td>
<td>26.13 ± 5.99</td>
</tr>
<tr>
<td>A6</td>
<td>−4.88 ± .95</td>
<td>−3.49 ± .80</td>
<td>13.23 ± 2.12</td>
<td>20.58 ± 5.09</td>
</tr>
</tbody>
</table>

Values are means ± SE.
ported no transfer of linear translation aftereffects from one leg to the other leg after hopping on a linear treadmill. Differences between our results and those of Anstis may result from several factors. In the present study, both legs were exposed to the adaptive stimulus and the direction of locomotion was changed, whereas only one leg was exposed to the stimulus in Anstis’ study. Additionally, the circuitry for control of hopping on one leg may not overlap substantially with the circuitry controlling hopping on the other leg. There is much evidence, however, supporting the possibility that common network elements may control forward and backward walking (Duyssens et al. 1996; Eilam and Shefer 1992; van Deursen et al. 1998).

Transfer of PKAR from a forward-walking stimulus condition to a backward-walking postadaptive condition provides additional support for this potential sharing of circuitry. Transfer of PKAR across different forms of locomotion also suggests that the PK system may be a general control system for locomotor trajectory. As such, adaptations obtained during one form of locomotion would result in changes to trajectory for all other forms of locomotion. Based on this hypothesis, one would predict that PK adaptation during forward walking would also influence the trajectory of forward running and skipping. We were not able to test these forms of locomotion due to limitations in the space available for overground locomotor testing and concerns about subject safety.

PKAR transfer from forward to backward walking conditions provides interesting insights into the parameters being regulated by the PK system. The relationship of the two legs to the center of rotation was not maintained across the two directions of locomotion, as the left limb was the inner leg during forward walking but the outer leg during backward walking. As such, the left leg moved through a shorter distance than the right leg during forward walking, but through a larger distance than the right leg during backward walking. Despite this change, we propose that the direction of relative rotation between the trunk and feet was preserved regardless of the direction of locomotion. During PK stimulation with the disk rotating CW (Fig. 4A), the feet rotate to the right relative to the space-stable trunk by virtue of their contact with the rotating disk during stance, i.e., when the foot is firmly planted on the support surface. When a normal subject walks CCW overground in either the forward or backward direction (Fig. 4B), the feet again rotate to the right relative to the trunk, although in this case the feet are space-stable during stance and the trunk rotates leftward relative to the feet. This relative rotation of the feet with respect to the trunk can be verified by slowly walking forward and backward in a CCW direction around a curved path. This same rotation of the feet with respect to the trunk is true for an adapted subject performing PKAR in the CCW direction. Thus the relative rotation between the feet and the trunk was similar for PK stimulation, forward PKAR, and backward PKAR. These results suggest that the PK system is primarily controlling relative rotation between the trunk and feet, rather than relationships between the two limbs. Remodeling of the relationship between trunk rotation and the feet has been proposed previously as the mechanism for PKAR (Jürgens et al. 1999; Weber et al. 1998). Control of trunk-in-space with respect to the support surface is also consistent with recent models of postural orientation that hypothesize an internal representation of surface in space resulting from a combination of vestibular and somatosensory information (Mergner and Rosemeier 1998).

**Comparison of overground PKAR to in-place PKAR**

Most previous experiments examining PKAR have involved postadaptive tests of stepping-in-place on the turntable, rather than tests of overground locomotion. The clear advantage to this in-place testing is that data can be collected for longer periods of time, as room size is not a limiting factor. But is this in-place PKAR a reasonable fascimile of overground PKAR? Our results for forward overground PKAR are similar to those for forward, in-place PKAR in terms of first-order asymptote and decay time constant values (Weber et al. 1998). Our results are dissimilar in terms of y-intercept, which had a magnitude of 8.3°/s in the present study but 16.0°/s for in-place PKAR (Weber et al. 1998). This difference is not surprising considering the differences in the adaptation paradigms used. In the present study subjects walked on the perimeter of a 76-cm disk rotating at 60°/s, whereas subjects in Weber et al. (1998) walked over the center axis of the disk rotating at 45°/s. Walking on the perimeter involves backward passive motion of both legs, outer more than inner, whereas walking over the axis involves forward motion of one leg and backward motion of the other. Additionally, we began sampling 5 min after PK stimulus offset, while Weber et al. (1998) began sampling immediately. Despite these differences, we observed similar effects. As such, we think that similar phenomena are being measured in overground and in-place testing of PKAR.
Vestibular-podokinetic interactions

Angular velocities tended to increase in value across the 2-min period of each trial. We were able to fit these rises with exponential growth curves, supporting previous reports of an exponential rise in PKAR response over the first 2 min. This rise is thought to reflect vestibular-podokinetic interactions, with vestibular inputs suppressing PK responses in a decaying manner over the first 2 min of stepping before peak PKAR velocity is obtained (Weber et al. 1998). Our values for rise time constants are quite similar to those calculated previously for healthy subjects and subjects with unilateral vestibular loss (Weber, Fletcher, Melvill Jones, and Block, unpublished data). Additionally, elimination of the first several data points in each trial resulted in very little change in the mathematical results of analyses conducted. It is clear that substantial interactions between vestibular and podokinetic systems occur (Melvill Jones et al. 2000), but the extent to which vestibular influences suppress PKAR in the first minutes of the response is unclear based on current data. This may be clarified by studies of PKAR rise characteristics of subjects with bilateral vestibular loss.

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REFERENCES