Motor Patterns for Human Gait: Backward Versus Forward Locomotion

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Grasso, R., L. Bianchi, and F. Lacquaniti. Motor patterns for human gait: backward versus forward locomotion. J. Neurophysiol. 80: 1868–1885, 1998. Seven healthy subjects walked forward (FW) and backward (BW) at different freely chosen speeds, while their motion, ground reaction forces, and electromyographic (EMG) activity from lower limb muscles were recorded. We considered the time course of the elevation angles of the thigh, shank, and foot segments in the sagittal plane, the anatomic angles of the hip, knee, and ankle joints, the vertical and longitudinal ground reaction forces, and the rectified EMGs. The elevation angles were the most reproducible variables across trials in each walking direction. After normalizing the time course of each variable over the gait cycle duration, the waveforms of all elevation angles in BW gait were essentially time reversed relative to the corresponding waveforms in FW gait. Moreover, the changes of the thigh, shank, and foot elevation covaried along a plane during the whole gait cycle in both FW and BW directions. Cross-correlation analysis revealed that the phase coupling among these elevation angles is maintained with a simple reversal of the delay on the reversal of walking direction. The extent of FW–BW correspondence also was good for the hip angle, but it was smaller for the knee and ankle angles and for the ground reaction forces. The EMG patterns were drastically different in the two movement directions as was the organization of the muscular synergies measured by cross-correlation analysis. Moreover, at any given speed, the mean EMG activity over the gait cycle was generally higher in BW than in FW gait, suggesting a greater level of energy expenditure in the former task. We argue that conservation of kinematic templates across gait reversal at the expense of a complete reorganization of muscle synergies does not arise from biomechanical constraints but may reflect a behavioral goal achieved by the central networks involved in the control of locomotion.

INTRODUCTION

Movement includes both variable, context-dependent components and repetitive, stereotypical components. The notion of motor pattern applies to the latter (Carter and Shapiro 1984; Das and McCullum 1988; Dean and Cruse 1995; Schmidt 1982; Terzuolo and Viviani 1979). Motor patterns are thought to represent interactions between intrinsic CNS activity [such as that of central pattern generators (CPGs)] and peripheral influences reflecting biomechanical characteristics and sensory afferent activities (see Pearson 1993). Motor patterns are most readily discernible in terms of those movement properties that change the least under several kinds of movement transformations, such as translation and rotation in space, amplitude and time scaling, loading, etc. A number of these properties was described for point-to-point (e.g., reaching) (see Soechting and Flanders 1991) and continuous (e.g., drawing and handwriting) (see Lacquaniti 1989) movements of the arm. Motor patterns of arm movements pertain to the domain of either kinematics or kinetics. In the kinematic domain, the spatial trajectories and velocity profiles both of the hand and of limb joints are conserved (with appropriate scaling in amplitude and time) under wide changes in movement size, speed, and load (Atkeson and Hollerbach 1985; Lacquaniti et al. 1982, 1987; Soechting and Lacquaniti 1981). In the kinetic domain, joint torque (Atkeson and Hollerbach 1985) and muscle activity (Flanders 1991; Flanders and Herrmann 1992; Flanders et al. 1997) profiles can be decomposed in a set of basic waveforms, a weighted combination of which accounts for movements with different speeds and loads.

Reversal of direction represents a special kind of movement transformation that may help to get an insight into the internal representations of motor patterns for some classes of movements. Not every movement can be reversed; for instance, handwriting, hand gesturing, and speech are unidirectional. Reversible movements, on the other hand, may display hysteresis. Thus, in pointing back-and-forth between two spatial loci, the trajectory of both the hand and limb joints may differ considerably in the two movement directions and so do the joint torque profiles and muscle patterns (Atkeson and Hollerbach 1985; Lacquaniti et al. 1986).

Locomotion belongs to the class of reversible movements. Backward (BW) gait was extensively studied especially in the context of theories on the organization of CPGs. Grillner (1981) hypothesized that each limb is controlled by a network of unit burst generators (unit CPGs). Each unit CPG would drive the muscle synergists acting at a given joint (such as the knee flexors or the ankle extensors). The total output pattern of the limb would result from the coupled activity of the different unit CPGs. BW gait could be produced by switching the sign of the phase coupling among unit CPGs controlling different joints of the limb (Grillner 1981).

In lower vertebrates, axial gait is based essentially on a set of antagonistic myotomes whose alternate contractions generate flexion–extension movements. The motor patterns of these species can then be equated to both body kinematics and muscle activity. The corresponding motor patterns of BW gait are simply the time-reversed copy of those of for-
ward (FW) gait (Grillner et al. 1995). In mammals, instead, the nature of the control waveforms that are putatively encoded by the CPGs and that might be time reversed for BW gait was not determined unambiguously (for a review see Zernicke and Smith 1996). The simple solution that both the temporal sequences of muscle activity as well as those of body kinematics reverse in time may be prevented by the multijointed nature of the limbs and by the high degree of anatomic asymmetry of the body in the anteroposterior direction.

In humans, mixed results were reported. The changes of hip angle of BW gait tend to be the time-reversed, mirror copy of those of FW gait, but the changes of knee and ankle angle are not (Kramer and Reid 1981; Thorstensson 1986; Vilensky et al. 1987; Winter et al. 1989). The correlation between the joint torques in the two movement directions also is inhomogeneous (high correlation for the hip and ankle torques and low correlation for the knee torque), whereas the correlation between the joint powers is generally lower than that of the corresponding joint angle or torque (Winter et al. 1989). As for the patterns of muscle activity, Thorstensson (1986) noted marked differences between the two gait directions, whereas Winter et al. (1989) suggested that somewhat similar muscle activation patterns could be used to produce both modes of locomotion, but the temporal cycling of muscle contraction would be reversed.

Here we reexamine the issue of what patterns, if any, are conserved across reversal of gait direction in the human. We consider the elevation angles, in addition to the joint angles, because the former generally are more reproducible than the latter across trials and subjects in FW gait (Borghese et al. 1996; Shen and Poppele 1995). Moreover, the intersegmental coordination of FW gait is defined by a law of planar covariation of the elevation angles of the thigh, shank, and foot that holds during both stance and swing phases (Bianchi et al. 1998; Borghese et al. 1996). Principal component and cross-correlation analysis (Alexandrov et al. 1998; Flanders 1991; Flanders and Herrmann 1992; Mah et al. 1994; Soechting and Lacquaniti 1989) are applied to limb kinematics, ground reaction forces, and electrical muscle activity to reveal the existence of common patterns underlying FW and BW gait.

**METHODS**

General procedures were previously described (Bianchi et al. 1998; Borghese et al. 1996). Kinematic data were obtained by means of the ELITE system (Ferrigno et al. 1990). Four 100-Hz TV cameras were spaced on the recording side of the walkway to enhance spatial accuracy. After three-dimensional calibration, the spatial accuracy of the system was better than 1.5 mm (root mean square). The position of selected points on the side of the dominant lower limb was recorded by attaching the infrared reflective markers to the skin overlying the following bony landmarks (Fig. 1): glenohumeral joint (GH), anterior superior iliac spine (ASIS), posterior superior iliac spine (PSIS), greater trochanter (GT), lateral femur epicondyle (LE), lateral malleolus (LM), and fifth metatarsophalangeal joint (VM). ASIS and PSIS coordinates were averaged to obtain ilium (IL) position. Right: trunk, pelvis, thigh, shank, and foot are the body segments identified by these markers. The elevation angle of each segment in the sagittal plane corresponds to the angle between the segment and the vertical (dashed line).

**FIG. 1.** Schematic illustration of the body geometry. Left: markers placed on one side of the subject were monitored by the ELITE system. From top to bottom: glenohumeral joint (GH), anterior superior iliac spine (ASIS), posterior superior iliac spine (PSIS), greater trochanter (GT), lateral femur epicondyle (LE), lateral malleolus (LM), and fifth metatarsophalangeal joint (VM). ASIS and PSIS coordinates were averaged to obtain ilium (IL) position. Right: trunk, pelvis, thigh, shank, and foot are the body segments identified by these markers. The elevation angle of each segment in the sagittal plane corresponds to the angle between the segment and the vertical (dashed line).

face electrodes from the gluteus maximus (GM), biceps femoris (long head, BF), rectus femoris (RF), vastus lateralis (VL), lateral gastrocnemius (GCL), and tibialis anterior (TA). EMG signals were preamplified (×100) at the recording site, digitized, and transmitted to the remote amplifier via 15-m optic fibers. These signals were band-pass filtered (10-Hz high-pass and 200-Hz low-pass, 4-pole Bessel filters), and sampled at 500 Hz. Sampling of kinematical, force and EMG data were synchronized.

**Protocol**

Experiments were approved by the Ethics Committee of Santa Lucia Institute and conformed with the Declaration of Helsinki on the use of human subjects in research. Seven healthy volunteers (4 females, 3 males, 21- to 36-yr age range, 31-yr mean age) participated after giving verbal informed consent. In one subject EMG was not monitored. Before the recording session, the dominant lower limb of each subject was determined according to standard criteria (Vanden-Abeele 1980). Subjects were instructed to walk barefoot with the arms folded on the chest at a freely chosen, roughly constant speed within the ELITE sampling volume. They were encouraged to vary the speed across trials. To avoid modifications of the natural step length, subjects were asked not to pay
attention whether they stepped onto the force platform. In about one-half of the trials, BW walks alternated with FW walks. In the rest of the experiment, walks were performed in blocks of three to five trials all in one direction, FW or BW.

Data analysis

Trials with appreciable drifts in the speed of the subject (as derived from instantaneous velocity of greater trochanter (GT) marker in the walking direction) were eliminated, as were those lacking complete kinematic and kinetic data. Three-dimensional kinematic data were filtered with an optimal low-pass FIR filter with automatic bandwidth selection (D’Amico and Ferrigno 1990). The body was modeled as an interconnected chain of rigid segments as shown in Fig. 1. The angle of elevation of the ith segment in the sagittal plane with respect to the vertical was computed as \( \alpha_i = \arctan \left( \frac{y_i - y_{i-1}}{x_i - x_{i-1}} \right) \), subscripts \( p \) and \( d \) denoting proximal and distal end points of the segment, respectively, and \( x \) and \( y \) denoting the horizontal and vertical coordinates in the sagittal plane, respectively. Elevation angles are positive in the FW direction relative to the vertical. In addition, relative joint angles between two adjacent limb segments in the sagittal plane were computed from the corresponding elevation angles. Joint angles increase in extension. Stance phase was defined as the interval during which the vertical reaction force exceeded 7% of body weight, gait cycle (\( T \)) was defined as the time interval between two successive maxima in the time series of the limb axis elevation, step length (\( S \)) was the linear translation of GT during \( T \), and average speed was \( V = S/T \). EMGs were numerically rectified and low-pass filtered (to avoid time distortions to avoid tail and phase distortions) by means of a Butterworth filter, with cutoff at 50 Hz. Trials in selected speed ranges were ensemble averaged after time interpolation of the kinematic, kinetic, and EMG data over \( T \) to fit a normalized time base (expressed as percentage of \( T \)). Normalization was obtained by first resampling the original signals at an appropriate rational frequency and then filtering by means of FIR filters. Note that this procedure is unaffected by phase distortions.

The cross-correlation function between pairs of normalized waveforms was computed by means of the following formula that accounts for the signal periodicity \( N \) that is the number of samples in one gait cycle (Challis and Kitney 1990, 1991)

\[
CC_{ij}(t) = \mathcal{F}^{-1} \left[ \frac{\mathcal{F} \{ X_i(t) \} \ast \mathcal{F} \{ X_j(t) \} \} \sqrt{\mathcal{F} \{ X_i^2(t) \} \ast \mathcal{F} \{ X_j^2(t) \} \} } \right]
\]

where \( \ast \) denotes element-by-element scalar product, \( \mathcal{F} \) and \( \mathcal{F}^{-1} \) stand for direct and inverse discrete Fourier transform respectively, \( X_i \) and \( X_j \) denote the two waveforms (after subtraction of the respective means \( X_i \), \( X_j \)). The numerator corresponds to the cross-spectral density from the EMG pair, and it is scaled to the product of total signal power (i.e., the autocovariance at 0 delay, the denominator in Eq. 1) so that the cross-correlation ranges from \(-1 \) to 1. By convention, positive time delays (0–50% of the cycle) indicate a lead of the ith waveform relative to the jth waveform, whereas negative delays (\(-50\%–0\%\)) indicate a lag. The cross-correlation coefficients are significantly different from zero (\( P < 0.01 \)) when they are \( >0.22 \) with \( N-1 \) degrees of freedom (Chatfield 1980).

Co-contraction between pairs of muscles (EMG\(_1\), EMG\(_2\)) over \( T \) was measured by applying a method proposed by Winter (1990) that assesses the percentage overlap area in each EMG pair

\[
\text{Cocontraction} = 2 \cdot \frac{\min \{ \text{EMG}_{i}(t), \text{EMG}_{j}(t) \} dt}{\text{EMG}_{i}(t) dt + \text{EMG}_{j}(t) dt}
\]

where \( \min \) denotes the minimum between two signals at time \( t \).

Principal component analysis

We used principal component analysis to quantify the statistical spatiotemporal structure of the collected signals (Flanders 1991; Glaser and Ruchkin 1976; Soechting and Lacquaniti 1989). Principal component analysis fits a set of data waveforms with a set of principal components in a similar way as Fourier analysis fits a given waveform with a set of sinusoidal components. Unlike Fourier analysis, principal components have a shape that depends on the original data waveforms. Principal components are computed by means of least-square-fitting algorithms and can be rank ordered according to their contribution to the variance of the original set of waveforms. If several common patterns are embedded in the waveforms of the original set, then a linear combination of fewer principal components (less than the total number of data waveforms) yields an accurate fit of the data.

In general, the number of principal components corresponds to the number of waveforms in the original set. The nth principal component is given by

\[
PC_n(t) = (1/\sqrt{\lambda_n}) \sum_{i=1}^{n} u_i X_i(t)
\]

where \( \lambda_n \) is the eigenvalue, \( u_n \) are the eigenvectors, and \( X_i \) is the \( i \)th original waveform. The inverse transformation that yields the original data from the principal component waveforms is

\[
X_i(t) = \sum_{n=1}^{N} \sqrt{\lambda_n} u_n PC_n(t)
\]

The eigenvalues \( \lambda \) and eigenvectors \( u \) are computed by factoring the covariance matrix \( R \) from the set of original signals by using a singular value decomposition algorithm such that

\[
R = U \Lambda U^T
\]

where \( U \) and \( \Lambda \) are the eigenvector and eigenvalue matrices, respectively, and superscript \( T \) denotes matrix transpose. The sum of the eigenvalues is equal to the sum of the variances of the original signal waveforms. Therefore each eigenvalue expresses the percentage of the overall variance accounted for by the corresponding principal component.

Comparison of FW and BW patterns

Several tests were used to compare kinematic and kinetic data between the two tasks. First, a linear regression analysis was performed between the average waveform of a given signal obtained from a set of trials within a selected speed range (0.4–1 ms\(^{-1}\), see RESULTS) in the FW direction and the corresponding average waveform obtained in the BW direction. This test assesses the global similarity between FW and BW patterns. Second, we tried to predict BW waveforms by using a linear combination of appropriately weighted principal components derived from the corresponding FW waveforms. This approach stems from the assumption that FW and BW patterns are comprised of the same basis functions whose amplitude may differ between the two tasks. To perform this test we first computed the principal components of the original FW waveform according to the procedure described in the previous section. We then retained the subset of principal components that account together for \( \geq 99\% \) of the FW data variance. Finally we performed a (least-squares) multiple linear regression of this principal components set on the BW waveforms. We also verified to what extent the results of this procedure depend on the signal bandwidth and data filtering. This was done by performing the same analysis on EMG-rectified data that were low-pass filtered at the same cutoff as that used for the kinematic data.
Intersegmental coordination

In previous work on FW gait (Bianchi et al. 1998; Borghese et al. 1996) it was found that the changes of the elevation angles at the thigh, shank, and foot covary linearly throughout the gait cycle. Here we investigated whether the same law of covariation applies to both FW and BW gait. In each trial we computed the covariance matrix \( A \) of the ensemble of time-varying elevation angles over the gait cycle, after subtraction of their respective mean value. The three eigenvectors \( u_1-u_3 \) of \( A \), rank ordered on the basis of the corresponding eigenvalues, correspond to the orthogonal directions of maximum variance in the sample scatter. The first two eigenvectors \( u_1-u_2 \) lie on the best-fitting plane of angular covariation. The third eigenvector \( u_3 \) is the normal to the plane and defines the plane orientation in the position–space of the elevation angles. For each eigenvector, the parameters \( u_{ij} \) correspond to the direction cosines with the positive semiaxis of the thigh, shank, and foot angular coordinates, respectively.

Statistical analysis

Analysis of variance (ANOVA) designs (Statistica 5.1) were used when appropriate to test for the effect of walking direction on locomotor parameters. Parameters that covaried linearly (as labels. The changes in trunk elevation are limited in both tasks. In FW gait, pelvis, thigh, shank, and foot elevation display the features detailed in previous reports (Bianchi et al. 1998; Borghese et al. 1996). Briefly, all limb segments rotate clockwise during stance and counterclockwise during swing. As for BW gait, the angular changes are the mirror image of those of FW gait: counterclockwise rotations during stance and clockwise rotations during swing.

The ensemble averages (±SD) of 10 trials performed within the 0.4- to 1-ms\(^{-1}\) speed range are plotted in the left and right panels of Fig. 3 for FW and BW gait, respectively. In this and subsequent illustrations, data were interpolated to the gait cycle duration \( T \) before averaging (see Methods), and BW traces were time reversed to make the comparison easy. The time base is expressed as percentage of \( T \), and the mean value was subtracted from the elevation and joint angles. Moreover, we set the amplitude scale of each plot proportionally to the peak-to-peak fluctuation of the corresponding signal so that the width of the SD intervals also is scaled in proportion. The graphs give thereby an indication of the relative reproducibility across the combined range of speeds. The scales for FW and BW trials are the same.

The SD interval of all elevation angles of the limb and of the knee angle is very narrow compared with the dynamic range of the corresponding variable. The variability of hip and ankle angles as well as that of the contact forces are comparatively larger.\(^1\) Once BW waveforms are time reversed, they appear similar to the corresponding FW waveforms. As noted above, the similarity is especially striking for the elevation angles, whereas some discrepancy is apparent in the other kinematic and kinetic variables. The changes of hip angle in BW gait tend to be time reversed relative to that of FW gait; the hip extends during FW stance and flexes during BW stance and

\[^{1}\text{Note that the SD interval of the ankle angle is greater than the sum of the foot and shank SD interval, indicating that part of inter-trial ankle variability does not result from measurement error but from biological variability in that angle.}\]
FIG. 2. Stick diagrams from one forward (FW) trial (left) and one backward (BW) trial (right) performed at comparable speeds (0.85 and 0.86 ms⁻¹, respectively) in subject RG. For each trial, the stick diagrams corresponding to one gait cycle are sampled at 100 Hz and are plotted in position space (x, y coordinates).

FIG. 3. Ensemble averages (±SD) of 10 trials (0.4- to 1-ms⁻¹ speed range) for FW (left) and BW (right) gait in subject RG. The time base is normalized to the duration of the gait cycle, and BW traces are time reversed. Traces from top to bottom are elevation angles of thigh, shank, and foot, joint angles of hip, knee, and ankle, and longitudinal (Fx) and vertical reaction force (Fz). Elevation angles are positive in the FW direction relative to the vertical. Hip and knee angles increase in extension, ankle angle in plantar-flexion. Fx is positive in the FW direction, Fz is positive in the upward direction. The mean value was subtracted from the elevation and joint angles. The schematic stick diagrams at the bottom delimit the stance phase. The horizontal dotted lines indicate body weight.
vice versa during swing. The extent of FW–BW correspondence is somewhat smaller for the knee and ankle angles. Thus the knee undergoes a sequence of flexion, plateau, extension during FW stance, whereas it flexes almost monotonically during BW stance. A similar degree of asymmetry exists for the ankle angle, particularly during swing. Knee and ankle asymmetries between the two gait directions agree with those reported in previous studies (Thorstensson 1986; Vilensky et al. 1987; Winter et al. 1989).

The patterns of the ground reaction forces also differed between the two movement directions. In FW gait, the longitudinal shear force (\(F_x\)) is directed BW during early stance when the heel brakes on the ground and the center of body mass decelerates. \(F_x\) changes monotonically in the FW direction during middle and late stance when the ball and toes push back against the ground and accelerate the body FW. In BW gait, \(F_x\) is directed FW when the toes contact the ground and decelerate the body during early stance, it is close to zero during midstance, and reverts to the BW direction when the heel pushes FW accelerating the body BW during late stance.

In both FW and BW gait, the vertical reaction force (\(F_z\)) exhibits two main peaks when body mass is accelerated upward during the double support phases of early and late stance and a trough during the single support phase of midstance when the body accelerates downward. However, the two peaks are roughly symmetrical in FW gait, whereas in BW gait the first peak caused by loading with body weight is always greater than the second peak caused by the heel push-off. This difference between FW and BW gait was systematic in all experiments. On the average, heel-contact (HC) peak of \(F_z\) was 100.8 \(\pm\) 4.4\% of body weight and toe-off (TO) peak was 105.0 \(\pm\) 6.6\% in FW trials. By contrast, toe-contact (TC) peak was 115.0 \(\pm\) 17.6\% of body weight whereas heel-off (HO) peak was 93.6 \(\pm\) 4.7 in BW trials. In addition, TC peak was significantly greater than HC peak in six out of seven subjects (\(P < 0.01\), unpaired \(t\)-test), and HO was significantly smaller than TO in all subjects (\(P < 0.005\)).

**Pattern reproducibility**

The reproducibility of FW and BW patterns across speeds was quantified in terms of the first principal component (Glaser and Ruchkin 1976) subject by subject. This principal component best fits the whole ensemble of data and resembles the conventional mean when the data structure contains repeated occurrences of a single basic pattern affected by statistical noise. Table 1 reports the percentage of variance accounted for by the first principal component computed by pooling together all trials performed in the 0.4- to 1-ms\(^{-1}\) speed range. On average, for both FW and BW gait, this principal component explains \(>93\%\) of the intertrial variability of all limb elevation angles, the hip and knee angles, and the ground reaction forces. Instead, the first principal component of the ankle angle explains a significantly lower percentage of variance (unpaired \(t\)-test for foot–ankle, \(P < 0.01\)).

**Quantitative comparison of FW and BW patterns**

A linear regression analysis between the ensemble average in the FW direction and the time-reversed average in the BW direction was used to assess the global similarity between FW and BW patterns in each subject. Both averages included all trials within the 0.4- to 1-ms\(^{-1}\) speed range. Figure 4 shows the results for two different subjects. FW and BW data are plotted superimposed (as thick, unfilled lines) and the difference is somewhat smaller for the knee and ankle angles.

In addition, TC peak was signifi-ondantly greater than HC peak in all subjects (\(P < 0.01\), unpaired \(t\)-test), in agreement with the previous observation that BW patterns are more similar to FW patterns when they are expressed in terms of the joint angles. In general the amplitude of BW angles tends to be shorter than that in FW trials (see Table 2).

**TABLE 1.** Percent variance accounted for by the first principal component in the two locomotor directions

<table>
<thead>
<tr>
<th>Variable</th>
<th>FW</th>
<th>BW</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thigh</td>
<td>98.0 (\pm) 2.1</td>
<td>98.4 (\pm) 0.6</td>
<td>NS</td>
</tr>
<tr>
<td>Shank</td>
<td>98.3 (\pm) 1.9</td>
<td>98.9 (\pm) 0.4</td>
<td>NS</td>
</tr>
<tr>
<td>Foot</td>
<td>96.5 (\pm) 3.6</td>
<td>96.8 (\pm) 1.6</td>
<td>NS</td>
</tr>
<tr>
<td>Hip</td>
<td>96.7 (\pm) 2.5</td>
<td>96.7 (\pm) 1.3</td>
<td>NS</td>
</tr>
<tr>
<td>Knee</td>
<td>96.5 (\pm) 3.3</td>
<td>97.9 (\pm) 0.5</td>
<td>NS</td>
</tr>
<tr>
<td>Ankle</td>
<td>89.7 (\pm) 6.8</td>
<td>85.1 (\pm) 8.3</td>
<td>NS</td>
</tr>
<tr>
<td>(F_x)</td>
<td>98.5 (\pm) 2.0</td>
<td>93.0 (\pm) 1.7</td>
<td>(P = 0.05)</td>
</tr>
<tr>
<td>(F_z)</td>
<td>97.8 (\pm) 1.4</td>
<td>96.9 (\pm) 1.1</td>
<td>NS</td>
</tr>
<tr>
<td>GM</td>
<td>44.6 (\pm) 11.3</td>
<td>38.4 (\pm) 6.3</td>
<td>(P = 0.07)</td>
</tr>
<tr>
<td>RF</td>
<td>37.9 (\pm) 14.3</td>
<td>40.4 (\pm) 8.7</td>
<td>NS</td>
</tr>
<tr>
<td>VL</td>
<td>38.4 (\pm) 13.2</td>
<td>39.2 (\pm) 6.2</td>
<td>NS</td>
</tr>
<tr>
<td>BF</td>
<td>45.2 (\pm) 12.3</td>
<td>39.9 (\pm) 5.8</td>
<td>NS</td>
</tr>
<tr>
<td>GCL</td>
<td>51.0 (\pm) 10.7</td>
<td>34.8 (\pm) 10.7</td>
<td>(P = 0.01)</td>
</tr>
<tr>
<td>TA</td>
<td>39.0 (\pm) 13.0</td>
<td>40.1 (\pm) 7.5</td>
<td>NS</td>
</tr>
</tbody>
</table>

Data represented are means \(\pm\) SD from six subjects. Statistical significance of the FW–BW comparison is reported in the Difference column. FW, forward; BW, backward; NS, not significant; \(F_x\), longitudinal shear force; \(F_z\), vertical reaction force; GM, gluteus maximus; RF, rectus femoris; VL, vastus lateralis; BF, biceps femoris; GCL, lateral gastrocnemius; TA, tibialis anterior.

The choice of reversing the timescale may be arguable for comparing the ground reaction forces between the two movement directions. For the sake of comparison, the force patterns could be aligned with the propulsion and absorption of kinetic phases rather than with the kinematic phases. Therefore, in addition to the previous regressions, we also computed linear regressions between FW and BW force patterns in trials running in FW time, aligned with the beginning of the stance phase (when the vertical reaction force exceeded 7\% of body weight). The correlation was higher than that obtained with time-reversed BW patterns for the longitudinal reaction force, but it was lower for the vertical reaction force (on the average, \(r^2 = 0.92 \pm 0.04\) vs. 0.86 \(\pm\) 0.09, \(P < 0.05\) paired \(t\)-test, for \(F_x\), and \(r^2 = 0.89 \pm 0.05\) vs. 0.94 \(\pm\) 0.04 (NS) for \(F_z\), without and with time reversal respectively).
FIG. 4. Ensemble average waveforms from FW trials (thick, unfilled envelopes) and time-reversed average waveforms from BW trials (thin, shaded envelopes) in subject LB (left) and subject DT (right) are plotted superimposed and regressed versus one another. Averages include all trials in the 0.4- to 1-ms−1 speed range. The regression coefficients (r²) are indicated. Subject LB is a 31-yr-old male (1.83 m, 72 kg); subject DT is a 35-yr-old female (1.60 m, 55 kg). The correlation coefficients were significantly higher (P < 0.05) for the thigh, shank, and foot than for hip, knee, and ankle, except for the knee-shank comparison in DT.

We also verified the extent to which FW and BW waveforms can be decomposed in the same set of basis functions. To this end, we tried to reconstruct time-reversed BW waveforms by using a linear combination of appropriately weighted principal components derived from the corresponding FW waveforms (see METHODS). In FW gait, the first 2 out of 10 principal components account together for >99% of the variance of elevation angles and for <93% of joint angles, whereas the same proportion of variance of the reaction forces (99%) requires 4 principal components to be explained. The theoretical BW waveforms predicted by FW principal components are superimposed on the observed BW waveforms in Fig. 5 (thin, shaded envelopes vs. thick, unfilled envelopes, respectively). Data are from the same sub-
TABLE 2. Linear regression between FW and reversed BW patterns

<table>
<thead>
<tr>
<th></th>
<th>b</th>
<th>r²</th>
<th>SEE</th>
<th>SEE%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thigh</td>
<td>0.91 ± 0.13</td>
<td>0.96 ± 0.04</td>
<td>2.21 ± 0.91°</td>
<td>5.9 ± 2.4</td>
</tr>
<tr>
<td>Shank</td>
<td>0.96 ± 0.08</td>
<td>0.95 ± 0.03</td>
<td>4.24 ± 1.60°</td>
<td>6.1 ± 2.5</td>
</tr>
<tr>
<td>Foot</td>
<td>0.84 ± 0.11</td>
<td>0.91 ± 0.04</td>
<td>4.57 ± 1.61°</td>
<td>5.5 ± 1.9</td>
</tr>
<tr>
<td>Hip</td>
<td>1.01 ± 0.14</td>
<td>0.94 ± 0.03</td>
<td>2.12 ± 0.67°</td>
<td>8.9 ± 2.4</td>
</tr>
<tr>
<td>Knee</td>
<td>0.82 ± 0.17</td>
<td>0.90 ± 0.06</td>
<td>4.98 ± 1.62°</td>
<td>8.4 ± 2.8</td>
</tr>
<tr>
<td>Ankle</td>
<td>0.82 ± 0.17</td>
<td>0.71 ± 0.22</td>
<td>3.67 ± 1.31°</td>
<td>13.2 ± 6.2</td>
</tr>
<tr>
<td>Fx</td>
<td>0.83 ± 0.18</td>
<td>0.86 ± 0.09</td>
<td>12.86 ± 5.70 (N)</td>
<td>7.7 ± 3.3</td>
</tr>
<tr>
<td>Fz</td>
<td>0.98 ± 0.13</td>
<td>0.94 ± 0.04</td>
<td>60.71 ± 32.18 (N)</td>
<td>9.2 ± 3.6</td>
</tr>
</tbody>
</table>

Data represented are means ± SD from seven subjects. Slope b, coefficient of determination (r²), standard error of the estimate (SEE), and SEE normalized to the peak-to-peak value of the FW average. The intercept was never significantly different from 0. See Table 1 for definitions.

So far we focused on data obtained at speeds <1 m s⁻¹. Qualitatively similar results hold for higher speeds. Figure 6 shows two trials in FW and BW directions performed at 1.3 m s⁻¹. Once again, the time-reversed changes of the elevation angles in BW direction are similar to the elevation angles in the FW direction, whereas some discrepancy between the two directions is apparent for both the joint angles and the ground reaction forces. In particular, at moderate to high BW speeds, the longitudinal shear force becomes oscillatory during midstance, and the peak of the vertical reaction force at TC becomes pronounced.

Intersegmental coordination

It was previously found in FW gait that the temporal changes of the elevation angles of the limb segments do not evolve independently of each other but they covary along an attractor plane common to both the stance and swing phase (Bianchi et al. 1998; Borghese et al. 1996). We now report that a similar law of intersegmental coordination also applies to BW gait.

Figure 7 shows the gait loops described by plotting the elevation angles of the thigh, shank, and foot one versus the others (three-dimensional position–space). In this kind of plot, time is not represented explicitly. In each panel, several trials in the 0.4- to 1-ms⁻¹ speed range performed by an individual subject are plotted superimposed. For both FW and BW trials, the data points lie close to a plane. The grids correspond to the best-fitting planes, and to their intersection with the cubic wire frame of the angular coordinates. On average, the planar regression accounts for 98.9 ± 0.4% (FW) and 98.1 ± 0.9% (BW) of the data variance over all trials of all subjects.

Fig. 5. Comparison between the BW waveforms predicted by FW principal components (thin, shaded envelopes) and the observed average BW waveforms (thick, unfilled envelopes) in subject LB. The principal components that account together for >99% of the FW data variance were computed and fitted to the BW data by means of (least-squares) multiple linear regression. The r² differences between the pairs thigh-hip, shank-knee, and foot-ankle are significant (P < 0.01).
The orientation of the plane in the three-dimensional space is similar for FW and BW trials in subject DT (bottom panels in Fig. 7) but differs in subject LB (top panels in Fig. 7; LB is the subject with the largest change in plane orientation between BW and FW.) In general, ANOVA on the direction cosines of the normal to the plane (with speed as the covariate) demonstrates very small yet significant changes in plane orientation caused by the reversal of locomotion. On the average, in BW gait $u_{3n}$ changed relatively to FW gait by $3.9^\circ$ ($F_{1,193} = 107.3, P < 0.001$), $u_{3t}$ by $0.1^\circ$ ($F_{1,193} = 4.4, P < 0.05$), and $u_{3s}$ by $3.3^\circ$ ($F_{1,193} = 1.1, \text{NS}$). The subject effect was always highly significant ($P < 0.001$) and so was the interaction between subjects and direction ($P < 0.001$), indicating that the orientation of the plane and its change on the direction reversal were rather idiosyncratic.

Figure 8 shows the thigh-shank and shank-foot cross-correlations for a subject with a significant change in the
plane orientation (subject RG) and a subject with no significant change (subject SM). In both subjects, the BW cross-correlations are roughly the mirror image of the FW cross-correlations around time 0. In FW thigh leads shank (the maximum of cross-correlation falls at 14% of the gait cycle both for RG and SM), whereas it lags behind in BW (by 6 and 14%, for RG and SM, respectively). The maximum of Shank-foot cross-correlation falls at 0% regardless of the task and of the subject.

**EMG patterns**

In contrast to kinematics, the EMG patterns of BW gait were poorly related to those of FW gait. Moreover, both FW and BW patterns exhibited a substantial intersubject variability. Ensemble averages of rectified EMG activity for FW and BW data are plotted superimposed (as thick, unfilled envelopes and thin, shaded envelopes, respectively) in Fig. 9. The data are from the same two experiments as in Fig. 4. The activity patterns of all muscles investigated in BW gait were strikingly different from those of FW gait. (The mean $r^2$ coefficients over all subjects were GM 0.03 ± 0.04, RF 0.06 ± 0.07, VL 0.08 ± 0.09, BF 0.10 ± 0.12, GCL 0.18 ± 0.21, and TA 0.09 ± 0.18.) Thus in FW gait the hip extensor GM showed a burst of activity in early stance (HC), returned toward the baseline activity during midstance, and had a smaller burst in late stance (TO). By contrast, in BW gait, GM activity was maximal during midstance and was close to the baseline during late stance. A similar kind of discrepancy between FW and BW gait was present in RF (a hip flexor and knee extensor) and VL (knee extensor). They were mostly active during early stance and swing in FW gait, whereas they were mostly active during early and midstance in BW gait. BF, a hip extensor and knee flexor, showed some degree of correspondence between FW and BW in subject LB but a much poorer relationship in subject DT. The ankle extensor GCL was mostly active during midstance in FW gait, whereas it was mostly active during early and late stance in BW gait. Finally, the ankle flexor TA was active during early stance and swing phases in FW and during the support phase in BW.

Not only did EMG patterns differ between FW and BW movements but they could even differ substantially among subjects for the same movement direction. Thus, whereas the EMG patterns of GM, RF, and VL were qualitatively comparable in the two subjects of Fig. 9, the patterns of BF, GCL, and TA were quite different. Thus, in FW gait, BF activity was close to the baseline between the burst of early stance and that of
FIG. 8. Cross-correlations between thigh and shank (solid lines) and between shank and foot (dotted lines) are plotted as a function of the percentage of gait cycle for 2 subjects (RG and SM) and 2 directions (FW and BW). Cross-correlations were computed from the ensemble average of the corresponding elevation angles in the 0.4- to 1-ms⁻¹ speed range. BW data were not time reversed so that the actual phase shift can be appreciated. A positive value of cross-correlation at a positive time delay indicates that the 1st segment in the label leads the 2nd, whereas a positive cross-correlation at a negative delay indicates a time lag of the 1st segment relative to the 2nd.

swing in subject LB, whereas the same muscle exhibited a burst of activity in midstance and baseline activity in subject DT. Conversely, in BW swing, BF exhibited a large burst of activity in subject DT but not in subject LB.

The reproducibility of the EMG waveforms is quantified in terms of the first principal component in Table 1. On average, this principal component accounts for ~50% of the EMG variance. Up to 7 principal components out of 10 had to be used to explain 95% of the intertrial EMG variance, and all principal components were necessary to explain ~99% of the variance. This result should be contrasted with the previous observation that the first two principal components explained 99% of the kinematic variability.

We investigated the extent to which FW and BW EMG waveforms can be decomposed in the same set of basis functions by means of the same procedure used for kinematics and reaction forces in Fig. 5 (after verifying that the procedure was affected to a very limited extent by the higher frequency content of the EMG signals; see METHODS). The theoretical BW EMG waveforms predicted by FW principal components are superimposed on the observed BW waveforms in the left panel of Fig. 10. Despite having used all principal components (10) we failed to predict BW waveforms starting from FW ones, as indicated by the lack of correspondence between the two sets of data (note the exception of BF). To verify that this failure was not due to the high intertrial variability of EMG data, we used the same procedure to predict the average EMG FW pattern of subject DT starting from that of subject LB, and we obtained a much better correspondence (Fig. 10, right panel).

EMGs cross-correlations

The previous analysis indicated that the EMG waveforms of BW gait do not resemble those of FW gait. However, it could be that what is common between the two movement directions is not the pattern of activation of individual muscles but rather the pattern of muscular synergies, that is, the time sequence of activation of different muscles. Thus, muscles that behave as antagonists in one gait direction also could be antagonists in the opposite gait direction but with an exchange of the sign of activation; for instance, the activation of knee extensors (VL and RF) in one phase of the FW
gait cycle could be replaced by the activation of knee flexors (BF) in the corresponding phase of BW gait and vice versa. To investigate this simple kind of synergy as well as more complex patterns of muscle synergies we computed the cross-correlation function between pairs of EMG ensemble averages (see Eq. 1), cross-correlations for FW gait and those for BW gait (BW EMGs were time reversed as before) are superimposed in Fig. 11.

The autocorrelations of the indicated muscles are plotted on the diagonal. They were generally very different.
between FW and BW gait (except for VL), confirming the previous observation that the two sets of patterns of activation of individual muscles are poorly related in these two tasks. The new result shown in Fig. 11 is that also the patterns of muscle synergies differ drastically between FW and BW gait. The peaks in the cross-correlations occur at different time delays. For example, BF tends to be reciprocally activated with VL and RF in BW gait, as indicated by the negative cross-correlation value around 0 time delay and by the positive peak at about 50% of the cycle. By contrast, these two sets of muscles tend to be coactivated in FW gait, BF activation leading that of RF and VL by ~20% of the gait cycle (see also Fig. 9). A similar discrepancy between FW and BW cross-correlations characterizes all pairings of muscles, with the following exceptions: RF tends to be coactivated with VL,
and GM tends to be reciprocally activated relative to GCL in both movement directions.

The percentage co-contraction (see Eq. 2) was never significantly different between FW and BW directions for pairs of muscles acting as anatomic antagonists at a given joint (GM–RF, VL–BF, and GCL–TA). The index, however, was greater in BW than in FW for the pair GCL–TA (by 13.3%, \( P < 0.07 \), paired \( t \)-test). Moreover, the index was greater in BW for muscles acting on different joints (RF–GCL, 14.5%, \( P < 0.05 \); VL–GCL, 12.5%, \( P < 0.01 \)) and was lower in BW for the pair GM–TA (13.0%, \( P < 0.05 \)).

**Mean EMG activity over gait cycle**

So far we focused on the time course of the EMG signals. Does also the absolute magnitude of muscle activity differ between FW and BW gait? Figure 12 shows the mean of the EMG over the gait cycle as a function of speed in one subject. Mean EMG increases exponentially with speed in both FW and BW gait. However, at each given speed, EMG activity generally tends to be higher in BW gait than in FW gait. Also, the rate of EMG increment with speed is generally higher in the former than in the latter.

To test statistical differences between FW and BW gait, we first fitted the EMG versus speed relationship with the exponential function indicated in the legend of Fig. 12, subject by subject, muscle by muscle, FW and BW; then we predicted the mean EMG activity at 0.95 m·s\(^{-1}\) (corresponding to the mean BW speed) and finally we performed a paired \( t \)-test between these predicted values for the two gait directions. We found that regressions were always significant and the percentage of variance explained by the fitting procedure was on average 70 and 77% for FW and BW, respectively. On average, GM activity increased in BW relative to FW gait by 94% (\( P < 0.05 \)), RF by 220%, (\( P < 0.01 \)), VL by 135%, (\( P < 0.01 \)), BF by 107%, (\( P < 0.05 \)), GCL by 40%, (NS), and TA by 154% (\( P < 0.01 \)).

**DISCUSSION**

The question we set out to address is what motor patterns are conserved across the reversal of gait direction. Our results indicate that the class of waveforms that changes the
least is that of the elevation angles of the lower limb segments; they undergo a simple reversal in time during BW locomotion compared with FW locomotion. Moreover, the law of planar covariation among the elevation angles of the different limb segments that holds for FW gait (Bianchi et al. 1998; Borghese et al. 1996) also holds for BW gait. Limb kinematics is conserved at the expense of a complete reorganization of the muscle synergies. In the following we argue that the conservation of kinematic templates across gait reversal does not arise from biomechanical constraints but reflects a behavioral goal achieved by the central networks involved in the control of locomotion.

Characteristics of BW gait as compared with FW gait

In general the mechanics of BW gait is different from that of FW gait. In particular, stance is characterized by an inverted plantigrade-digitigrade sequence in the two movement directions. FW stance begins with heel strike and ends at TO, whereas in BW stance the toes contact the ground first and the heel is lifted off the ground last. The anatomic and functional asymmetry of the foot and leg along the anteroposterior axis also imposes different biomechanical constraints on BW and FW gait. At the anterior extremity of the foot, the toes articulate on the metatarsal joints and behave as a deformable support surface, whereas at the posterior extremity the tarsus represents a more rigid segment and articulates with the shank and the leg. Calf and thigh muscles are highly asymmetrical about the frontal plane; the mass and strength of the muscles on the posterior aspect of the calf (triceps surae) and on the anterior aspect of the thigh (quadriceps femoris) are much greater than those of the muscles on the respective opposite side. All these asymmetries may well explain the lack of correspondence of many gait parameters between FW and BW directions.

Thus, in agreement with the conclusion drawn by Thors- tensson (1986), we found that the patterns of muscle activity of BW locomotion bear a poor relation to those of FW locomotion. The foot impact on the ground in early stance is sustained by coactivation of several limb muscles (flexors and extensors at the hip, knee, and ankle) in FW gait, whereas the same event is accompanied by activity in knee extensors and ankle plantar-flexors in BW gait. The main FW thrust is normally provided by ankle plantar-flexors, whereas the main BW thrust is provided by hip and knee extensors. Not only do FW and BW EMG waveforms differ globally but they cannot even be accounted for by a combination of the same basis functions with different weighing factors (as indicated by the principal component analysis). Finally, the lack of correspondence between FW and BW cross-correlations indicates that also the patterns of intermuscular synergies differ drastically between the two movement directions. Thus knee flexors tend to be reciprocally activated with knee extensors in BW gait, whereas they are roughly coactivated in FW gait. Conversely, ankle flexors tend to be reciprocally activated with ankle extensors in BW gait, whereas they are coactivated for extensive periods of BW gait cycle. The magnitude of EMG activity integrated over one gait cycle generally is greater in BW gait than in FW gait (see also Winter et al. 1989), suggesting a greater level of energy expenditure in the former than in the latter gait. In fact, the exponential increment of muscle activity
with speed we observed (cf. Nilsson et al. 1985) is reminiscent of the relationship between the mechanical power or metabolic power and speed (Taylor and Heglund 1982), and a greater level of oxygen consumption in BW gait than in FW gait was previously reported (De Vita and Stirling 1991; Flynn et al. 1994; Minetti and Ardigo 1997). The differences in muscle activity are paralleled by the differences in the ground reaction forces and joint angles between BW and FW gait (see also Thorstensson 1986; Vilensky et al. 1987; Winter et al. 1989).

By contrast, the waveforms of the elevation angles are essentially conserved across the reversal of gait direction, the waveforms of BW gait being almost the mirror image of those of FW gait. The time-reversed BW elevation angles of all limb segments are highly correlated with the corresponding FW angles ($r^2 > 0.90$), and they can be reconstructed faithfully ($r^2 > 0.98$) starting from the first two principal components of the FW angles. Therefore the elevation angles emerge from this study as the templates that more closely match the definition of motor patterns for locomotion given in the INTRODUCTION.

The law of intersegmental coordination that was previously described for FW gait (Bianchi et al. 1998; Borghese et al. 1996) also holds for BW gait. This law consists in the planar covariation of the changes of the thigh, shank, and foot elevation during both stance and swing. This planar covariation is not an obligatory outcome of any movement of the lower limb because it is not associated with either voluntary shaking movements or passive manipulations that replicate cyclic oscillations of locomotion (Grasso et al., unpublished observations). It is therefore most remarkable that the planar law is shared by two walking modes, FW versus BW, that differ drastically between each other in terms of mechanical characteristics and patterns of muscle activity.

Central representations of gait motor patterns

In several animal species, locomotion is controlled by CPGs located in the spinal cord and under the influence of several peripheral and supraspinal signals (Grillner 1981; Grillner et al. 1995; Pearson 1993; Rossignol 1996). Principles of functional organization of the CPGs were proposed according to which the multisegment motion of mammals locomotion would be controlled by a network of coupled oscillators. Each oscillator would drive the flexors or extensors at one joint, and changing the interoscillator phase coupling would generate speed changes and gait transitions. Grillner (1981) further hypothesized that the reversal of gait direction may result from a sign change of the phase coupling between oscillators controlling different limb joints.

This scheme is compatible with these findings if one assumes that CPGs control limb segment motion instead of joint muscles and that they can encode the waveforms of the elevation angles. These could be output in a direct or time-reversed form (such as a motor tape) depending on the gait direction. The cross-correlation analysis also confirmed that the phase coupling among these kinematic patterns is maintained with a simple reversal of the delay on the reversal of walking direction, in agreement with Grillner’s hypothesis (1981). The planar law of intersegmental coordination might derive from the dynamic interaction of segmental oscillators between each other and with limb mechanics. It has been previously shown that the specific orientation of the plane of angular covariation reflects the phase relationships between the elevation angles of the lower limb segments and therefore the timing of the intersegmental coordination (Bianchi et al. 1998). Speed increments are related to a progressive phase shift between the foot elevation and the shank elevation. In this context, phase plays the same role of control variable as that previously hypothesized for the network of CPGs. Shen and Poppele (1995) also argued for a control of the timing of the turning points of the elevation angles during FW locomotion of cats (see Halbertsma 1983). They found that the changes of the elevation angles of all hindlimb segments conform to a common waveform and differ only in the timing and amplitude. In addition, the relative time difference between the turning points of pairs of limb segments scales with the duration of the FW swing (or equivalently gait speed). These laws of intersegmental coordination for gait control are reminiscent of the algorithm that was proposed for the generation of drawing movements of the arm (Soechting et al. 1986; Soechting and Terzuolo 1986). Drawing involves oscillatory changes of the orientation angles of the upper arm and forearm. The phase differences among these angular coordinates define the spatial location of the drawn figure, whereas the phase differences among lower limb elevation angles define the trajectory of the foot in gait.

Role of behavioral goals

It may appear surprising that kinematic waveforms of FW gait are conserved in BW gait at the expense of an increase of muscle activity and (presumably) energy cost. Indeed the traditional view is that locomotion is always performed according to a principle of minimum energy (Alexander 1989; Taylor and Heglund 1982). Instead we found that muscle activity in BW gait is controlled in a subordinate manner with respect to the control of limb kinematics. However, we believe that kinematic waveforms are neither hard-wired in the CPGs nor the only possible motor patterns for gait. The nature of motor patterns probably is flexible and dictated by the behavioral goal to be achieved. Thus Winter (1995; Winter et al. 1989) proposed that also biomechanical variables such as the joint torques and powers should be considered motor patterns reflecting the integrated and final goals of the nervous system.

That behavioral goals may be crucial in the selection of the motor patterns for gait can be inferred by considering the ethological context in which BW gait is performed in different mammals. In cats, for instance, BW gait is often associated with preparation for fight. A change of the geometric shape of the body and limbs relative to the standard shape could be appropriate for conveying to the opponent a message of readiness to fight. On the other hand, preactivation of a set of muscles similar to those used in FW gait could be useful in view of a FW step or jump. In fact, detailed studies in this animal species demonstrated that the instantaneous geometric configurations of the limbs and body in BW gait are essentially
unrelated to those of FW gait (Buford et al. 1990a), whereas the direct patterns of activity of many limb muscles are similar irrespective of walking direction (Buford et al. 1990b; Pratt et al. 1996).

When humans step back, instead, they usually need not change shape of the body and legs. Time reversal of FW kinematics to generate BW steps could then follow from a principle of conservation of geometric shape. Walking style represents a complex Gestalt whose significance encompasses both the mechanical requirements of gait (such as equilibrium, progression, speed, and energy) as well as the expressive and emotional aspects of life (Bianchi et al. 1998; Thomas 1940). Although the reversal of gait direction does not seem to violate the locomotor Gestalt of lower limb movements, other task constraints, such as walking steepest, may well do so (see Trank et al. 1996).

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