Tuning of a Basic Coordination Pattern Constructs Straight-Ahead and Curved Walking in Humans

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Tuning of a basic coordination pattern constructs straight-ahead and curved walking in humans. J Neurophysiol 91: 1524–1535, 2004. First published December 10, 2003; 10.1152/jn.00817.2003. We tested the hypothesis that common principles govern the production of the locomotor patterns for both straight-ahead and curved walking. Whole body movement recordings showed that continuous curved walking implies substantial, limb-specific changes in numerous gait descriptors. Principal component analysis (PCA) was used to uncover the spatiotemporal structure of coordination among lower limb segments. PCA revealed that the same kinematic law accounted for the coordination among lower limb segments during both straight-ahead and curved walking, in both the frontal and sagittal planes: turn-related changes in the complex behavior of the inner and outer legs were captured in limb-specific adaptive tuning of coordination patterns. PCA was also performed on a data set including all elevation angles of limb segments and trunk, thus encompassing 13 degrees of freedom. The results showed that both straight-ahead and curved walking were low dimensional, given that 3 principal components accounted for more than 90% of data variance. Furthermore, the time course of the principal components was unchanged by curved walking, thereby indicating invariant coordination patterns among all body segments during straight-ahead and curved walking. Nevertheless, limb- and turn-dependent tuning of the coordination patterns encoded the adaptations of the limb kinematics to the actual direction of the walking body. Absence of vision had no significant effect on the intersegmental coordination during either straight-ahead or curved walking. Our findings indicate that kinematic laws, probably emerging from the interaction of spinal neural networks and mechanical oscillators, subserve the production of both straight-ahead and curved walking. During locomotion, the descending command tunes basic spinal networks so as to produce the changes in amplitude and phase relationships of the spinal output, sufficient to achieve the body turn.

INTRODUCTION

Locomotion is a complex task that involves the coordinated activation of many muscles. Active muscle forces interact with passive forces resulting from interactive torques, floor reaction forces, and gravitoinertial effects, which act along the multi-segmental body chain (Full and Koditschek 1999; Zajac et al. 2002). Bipedal erect posture complicates walking control further—this locomotor posture is inherently unstable and threatens equilibrium at each step (Capaday 2002). Successful locomotion thus requires a fine coordination among body segments: the CNS must control coordination of the lower limb segments, between the 2 limbs, and between the limbs and trunk, in both sagittal and frontal planes.

Previous investigations have provided insight into how the CNS may cope with the problem of intersegmental coordination, showing that task-dependent reduction of the number of degrees of freedom normally occurs in sensorimotor systems (Bizzi et al. 2000; Gielen and van Bolhuis 1998; Mah et al. 1994; Santello et al. 1998; St-Onge and Feldman 2003). In particular, Lacquaniti and coinvestigators (reviewed in Lacquaniti et al. 2002) described a planar law of intersegmental coordination among lower limb segments during human straight-ahead locomotion, which may emerge from the interaction of spinal neural networks and limb mechanical oscillators (Ivanenko et al. 2003). Such a kinematic law of intersegmental coordination simplifies gait control by reducing the dimensionality of the walking system (Lacquaniti et al. 1999).

During straight-ahead walking, the symmetry of body movements facilitates segment coordination. However, goal-directed locomotion, such as that encountered in everyday life, often requires steering along curved paths. The inherently unstable bipedal gait becomes critical during curved walking, as shown by turning difficulties in aged or diseased people (Chekirda et al. 1971; Ito et al. 1995; Thigpen et al. 2000). During curved walking, adapted changes in trunk movements occur so as to maintain equilibrium against the inertial forces that threaten balance (Courtine and Schieppati 2003a; Imai et al. 2001; Patla et al. 1999). In addition, many temporal and spatial features of the movement of the inner and outer leg become asymmetric. Turn-related adaptations of gait parameters and segmental orientation include divergences in stance duration, stride length, and foot rotations of the inner and outer leg (Courtine and Schieppati 2003a; Hollands et al. 2001), and are mirrored in a subtle, though significant and limb-specific, tuning of leg muscle activity patterns (Courtine and Schieppati 2003b).

Thus preservation of gait coordination represents a major computational challenge during curved walking. How does the CNS organize the appropriate coordination in such a complicated context? Does the same planar law found in straight-ahead walking also apply to walking along a curved path? This is hardly predictable, given that the biomechanical context is drastically modified when turning. The gravitoinertial vector...

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tilts outward (Imai et al. 2001), thereby creating forces along body segments that destabilize balance. Emerging demands in terms of equilibrium control in the frontal plane may disrupt efficient limb and trunk segment coordination in the sagittal plane, and the CNS might favor balance-related activity in the lateral plane with respect to the plane of progression.

Vision is not essential to produce curved walking, although closing the eyes increases the variability of the locomotor trajectory with respect to the required path during straight-ahead walking, and more so during curved walking (Courtine and Schieppati 2003a). This might result from the absence of on-line corrections of the walking trajectory, or on modified segment coordination in the absence of visual input, or both. Indeed, the contribution of vision to segment coordination during walking is not known. It is unlikely that segmental coordination is deteriorated during blindfolded walking because highly common movements involve many lower limb, locomotor-based motions without on-line visual feedback. In the no-vision condition, however, maintenance of equilibrium may require adaptive changes in coordination to compensate for the lack of vision-based postural reference. Is the decreased locomotor accuracy observed while blindfolded a consequence for the lack of vision-based postural reference? Is the decreased locomotor-based motions without on-line visual feedback. In the no-vision condition, however, maintenance of equilibrium may require adaptive changes in coordination to compensate for the lack of vision-based postural reference. Is the decreased locomotor accuracy observed while blindfolded a consequence for the lack of vision-based postural reference? Is this coordination further modified during blindfolded curved walking?

In the present study, we analyzed the coordination among elevation angles of the lower limbs and trunk in both the frontal and sagittal planes, in the aim of testing the hypothesis that common principles govern the production of the locomotor patterns for straight-ahead and curved walking, in the normal and blindfolded conditions.

Methods

General procedures for data acquisition and processing have already been described (Courtine and Schieppati 2003a,b). In the present study, we used the kinematic recordings previously obtained while the subjects performed straight-ahead and curved walking.

Participants

Six healthy male adults (20–54 yr old) volunteered for this experiment. Subjects gave written and informed consent and the study conformed to the Declaration of Helsinki.

Locomotor task

Subjects performed straight-ahead (SA) and curved (turning, TU) walking. The curved path (see Fig. 1) shared the 3 initial meters of the straight path, then described a 4.6 m curve toward the right, and ended with a 2-m straight line. The radius of curvature was 120 cm, thus resulting in an overall change of direction of 220°. The subjects made 10 walks along each path with eyes open (EO) and blindfolded (eyes closed, EC). No specific instructions were given to subjects regarding segment orientation or precise location of the feet with respect to the lines drawn on the floor. Subjects easily performed both walking tasks. For example, the average distance between the actual and required locomotor paths during curved walking was only 6.6 ± 1.2 cm with eyes open and 11.7 ± 3.8 cm when blindfolded (see detailed analysis in Courtine and Schieppati 2003a).

Kinematic recordings

Whole body movements were measured by an automatic video-image processor system (Elite, BTS, Italy) at a rate of 100 Hz. Six video cameras were located around the walking area, creating an acquisition volume of 4 × 4 m (2 m high). Reflective markers (8 mm in diameter) were attached to the skin overlying the following body landmarks: vertex and frontal region of the head; for both hemibodies: the glenohumeral joint, anterior superior iliac spine, great trochanter (GT), knee (K), lateral malleolus (M), and the fifth metatarsophalangeal joint of the foot (F). The lower limb segments of both legs were modeled as an interconnected chain of rigid segments: GT-K for the thigh; K-M for the leg; M-F for the foot. Body displacements were calculated as the midpoint between left (L) and right (R) markers located on the ilium and great trochanter. The resulting point labeled body midpoint (x_L, y_L, z_L) provided a good approximation of the displacement of the center of mass. The trunk segment was defined as the line joining the midpoint between left and right glenohumeral joints and the body midpoint. In addition, the limb axis was for each limb the virtual straight line connecting the lateral malleolus to the great trochanter (Borghese et al. 1996). Kinematics data were filtered with a low-pass FIR filter with automatic bandwidth selection (D’Amico and Ferrigno 1990). It will be noted that each lower limb segment was identified by 2 markers. Therefore the marker coordinate system used is not a full 3-dimensional model. As a consequence, the angular displacements computed are approximations of the true segmental movements.

Coordinate frames

Coordinate frames that describe the motion of the body were defined in hierarchical fashion as described in previous papers (see also Imai et al. 2001). Briefly, the primary coordinate frame was the space-fixed reference frame of the video system (X_S, Y_S, Z_S). The heading at each instant was the angle Φ_h between the linear velocity vector of the body midpoint (x_B, y_B) in the horizontal plane and the X-axis of the space-fixed reference frame

Φ_h = tan^-1(y_B / x_B)

The heading was positive for a right turn (i.e., the direction of the curved path). The sagittal plane (X-axis of body reference frame) matches the heading vector at each moment of the evolving trajectory.
Subsequently, any vector in spatial coordinates was converted to body coordinates through multiplication of the vector by the transformation matrix

\[
T = \begin{bmatrix}
\cos \Phi_b & 0 & \sin \Phi_b \\
0 & 1 & 0 \\
-\sin \Phi_b & 0 & \cos \Phi_b
\end{bmatrix}
\]

This method was used to obtain the coordinates of the different markers in the body-centered reference frame

\[
\begin{bmatrix}
x_T \\
y_T \\
z_T
\end{bmatrix} = T
\begin{bmatrix}
x_i \\
y_i \\
z_i
\end{bmatrix}
\]

where \(x_T, y_T,\) and \(z_T\) represent the transposed coordinates of the \(i\)th marker \((x_i, y_i, z_i)\).

A total of 14 angles were defined on the basis of segmental displacements. Thigh, leg, and foot angles with respect to the direction of gravity (elevation angles) were computed for the 2 limbs, and both in the sagittal and frontal planes. In addition, trunk oscillations in pitch and roll directions were evaluated. The angles of thigh, leg, foot, and trunk (pitch) segments with respect to the direction of gravity in the sagittal plane was evaluated through fast Fourier transformation (FFT). The phase shift \((\Phi)\) between the Fourier harmonics from the elevation angles of adjacent limb segments \(p\) (proximal) and \(d\) (distal) were computed as \(\Phi_p - \Phi_d\) where \(\Phi\) is the phase of the first-order Fourier series component (Bianchi et al. 1998). They were expressed in percentage changes \([\Phi \times (100/2\pi)]\) with respect to the gait cycle duration normalized to 100.

**Principal component analysis**

We used principal component (PC) analysis to quantify the spatio-temporal structure of the intersegmental coordination among body segments (Grasso et al. 1998, 2000). For each set of trial data, the analysis was performed by computing the covariance matrix \(\Lambda\) of the ensemble of time-varying angles \((n = 3)\) over the gait cycle, after subtraction of their respective mean values. The PCs were computed from eigenvalues \(\lambda_i\) and eigenvectors \(U_i\) of \(\Lambda\). The PCs were ordered according to the amount of data variance accounted for by each component

\[
\frac{\lambda_i}{\sum_i \lambda_i}
\]

The number of components required to account for data variance was taken as providing insight into the number of degrees of freedom. In particular, linearity and planarity in angular covariation among lower limb segments quantified the weight of intersegmental coupling. Linearity, which indicates covariation of elevation angles along a line, was evaluated as the variance accounted for by \(PC_1\). Planarity, which reveals covariation of elevation angles within a plane, was evaluated as the variance accounted for by \(PC_1 + PC_2\).

Geometrically, each PC is a linear combination of the time-varying values of the original angles. The contribution of the \(i\)th angle to the \(j\)th PC is given by the coordinate \(U_{ij}\) of the eigenvector \(U_j\) of \(\Lambda\). \(U_{ij}\) corresponds to the cosine of the angle made by the direction of the eigenvector with the positive semiaxis of the angular coordinate of the \(i\)th segment. Theoretically, \(U_{ij}\) can vary from \(-1\) to 1. The larger the contribution of the \(i\)th angle to the \(j\)th PC, the more the eigenvector \(U_j\) will be attracted to the axis of \(i\)th angle coordinates, in which case \(U_{ij}\) will tend to 1 (or \(-1\)). PC analysis was applied to the 3 angles of the lower limb segments in the frontal and sagittal planes, separately for each limb. In the normal walking condition, elevation angles of lower limb segments in the sagittal plane covary along a plane (Borghese et al. 1996); the first 2 PCs account for almost all data variance, and identify the “covariation plane.” A measure of its orientation is given by the third eigenvector, \(U_3\), which is the vector normal to the plane. In particular, the angle between \(U_3\) and the thigh coordinate axis is a parameter that is sensitive to plane orientation changes and that reflects modification of temporal coupling between leg and foot segments (Bianchi et al. 1998). Within the covariation plane, the data points describe a loop (see Fig. 3), whose length and width are quantified from the variance accounted for by \(PC_1\) and \(PC_2\), respectively. A strong linear coupling was detected in all subjects \((r = 0.71 \pm 0.09)\) between the variance accounted for by \(PC_2\) and the angle between \(U_3\) and the thigh coordinate axis \((U_{13})\). However, the slope of the relationship varied among subjects, probably attributable to idiosyncratic body features (Bianchi et al. 1998). As a consequence, \(U_{11}\) was taken as a good estimation of the width of the loop. This measure was referred to as the path loop shape in the result. Note that turn- or limb-related significant differences were equally detected by \(U_{11}\) and \(PC_2\).

PC analysis was also carried out on time-varying angles of trunk and lower limb segments in the frontal and sagittal planes over the time interval of the gait cycle, a set of 14 angles encompassing 13 degrees of freedom. Trunk roll and pitch show a small amplitude of variation with respect to angular oscillations of lower limb segments. This would artificially reduce the contribution of trunk angles to the

**Determination of gait events**

The onset of the gait cycles was determined with respect to the oscillation of the limb axis in the sagittal plane, whose forward angular peaks correspond to heel strikes (Borghese et al. 1996). The stride cycle was the interval between 2 successive heel strikes. Gait cycles labeled “turning” were those for which the change in heading per cycle was >40° (Courtine and Schieppati 2003a). In Figs. 6 and 8, the cycles with smaller changes in heading, associated with transition steps, are also included to emphasize the continuity of the locomotor process. Total duration, stance duration, stride length, and mean velocity of gait cycles were measured.

**Intersegmental coordination**

The temporal coupling between the elevation angles of lower limb segments in the sagittal plane was evaluated through fast Fourier transformation (FFT). The phase shift \((\Phi)\) between the Fourier harmonics from the elevation angles of adjacent limb segments \(p\) (proximal) and \(d\) (distal) were computed as \(\Phi_p - \Phi_d\) where \(\Phi\) is the phase of the first-order Fourier series component (Bianchi et al. 1998). They were expressed in percentage changes \([\Phi \times (100/2\pi)]\) with respect to the gait cycle duration normalized to 100.
determination of each PC. To overcome this problem, each angular waveform was divided by its respective SD after subtraction of its respective mean value. The covariance matrix A was computed on these normalized waveforms. Using this method, all segmental oscillations contribute equally, independently of the amplitude of the raw data—the determination of PCs thus depends on the timing between oscillations and the pattern of coordination between oscillations throughout the movement (St-Onge and Feldman 2003).

Statistical analysis

Statistical differences among directions, body sides, and visual conditions were assessed by computing ANOVAs for repeated measures. Post hoc differences were evaluated by means of the Newman–Keuls test.

RESULTS

The results are divided into 5 parts. In the 1st part, we briefly describe spatial and temporal gait parameters during curved walking. In the 2nd and 3rd parts, we show that the same, basic coordination pattern accounts for the movement of lower limb segments in the mediolateral and sagittal planes during both straight-ahead and curved walking. In the 4th part, we report that the tuning of a coordination pattern is correlated to straight-ahead and curved walking. In the 4th part, we report that the tuning of a coordination pattern is correlated to straight-ahead and curved walking.

Gait features during curved walking

Here we briefly summarize the principal results illustrated in previous studies, before detailing the findings on which this paper is based. A typical example of curved walking is shown in Fig. 1. The mean values (±SD) of general gait features exhibited by the subjects during straight-ahead and curved walking are reported in Table 1, separately for EO and EC conditions. The analysis of foot positions revealed 3 features of curved walking: 1) the inner stride length decreased with respect to outer stride length (average difference 23 cm; see Table 1); 2) the outer and inner feet moved away from (6.7 cm) and closer to (4.8 cm) the body midpoint trajectory, respectively; 3) both feet were rotated toward the inner part of the curved trajectory (17°). The cadence was not significantly affected by curved walking (TU, 0.89 cycle s−1) compared with walking straight-ahead (SA, 0.91 cycle s−1), and was obviously the same for both limbs. In turn, the decrease in stride length of the inner limb reduced the distance covered by the body during the time interval of a gait cycle (17.6 cm per cycle on the average). As a consequence, mean body velocity significantly (P < 0.05) decreased during TU with respect to SA walking. Interestingly, despite unchanged gait frequency, the inner and outer limbs displayed different durations of their stance phase during TU, as well as in comparison to the SA values. Mean values (+SD) of the relative stance duration are reported in the horizontal histograms in the top panels of Figs. 2A and 3A. Stance duration decreased (1.9% of the cycle) when the supporting foot was the outer foot, whereas it increased (1.8% of the cycle) when the supporting foot was the inner one [side × direction effect, F(1,5) = 44, P = 0.001]. The increased duration of the stance phase of the right inner foot (i.e., when it carries the body weight) was accompanied by leaning (roll) of the trunk toward the inner side of the curved trajectory. Conversely, the left foot stance duration was inversely correlated with trunk roll to the contralateral side (i.e., to unloading of the outer limb). A detailed description of gait features during curved walking can be found in Courtine and Schieppati (2003a,b).

Coordination patterns among angles in the mediolateral plane

Figure 2 summarizes the features of lateral oscillations of lower limb segments during SA and TU walking. The time course of the elevation angles of thigh and leg in the frontal plane and of the foot in the horizontal plane, during SA (gray traces) and TU (black) walking, are displayed in the plots of Fig. 2A, from left to right, respectively. No differences were found between left and right limb oscillations for the 3 segments during SA (gray traces) or TU walking, but marked divergences appeared during TU. As a rule, mean limb endpoint positions of the 2 limbs shifted outward with respect to trunk and pelvis (i.e., to the actual locomotor trajectory). Such modifications were the product of an outward shift of the mean spatial position around which thigh and leg oscillated during TU. However, the kinematic templates of both segments barely differed between legs or between the 2 walking trajectories. On the contrary, the feet showed different rotation patterns during curved walking. The amount of inner foot rotation substantially diminished during TU, whereas that of outer foot rotation substantially increased. The change in heading mainly occurred during the outer limb stance phase. Thus the body and the leg were moving away from the outer foot, which would explain why the outer foot rotation angle increased. The inverse reasoning accounts for the changes in inner foot rotation. These turn-related adaptive modifications in angular patterns of lower limb segments were similar between walking with eyes open or closed.

The path loops depicted in Fig. 2B were obtained by plotting mean thigh, leg, and foot elevation angles in the mediolateral
plane one against the other, for each limb and walking direction. In this kind of plot, time is not explicitly represented. The stance phase for both legs corresponds to the bottom of the loop, where data points are very close together, whereas the swing phase corresponds to the upward peak where points are more distant. Time moves anticlockwise along the successive points. The grid corresponds to the best-fitting plane calculated by linear regression. Actually, the path loop tended to cluster around a line. PC analysis confirmed these general observations. Results showed in fact that the first PC accounted for 96% of the data variance over all trials for all subjects in SA walking (see Table 1 and Fig. 2C). This measure was taken as a linearity index in the coupling across segments, and suggests that a single elementary function accounts for displacement of lateral segments during the entire time interval of the gait cycle.

The linearity (see METHODS, Fig. 2C) remained high when walking along the curved trajectory (SA vs. TU, $P > 0.1$), whatever the visual condition ($P > 0.6$). The orientation of the covariation line (the line that fits the points in the 3D graph, not shown in the graphs) is given by the coordinates of the first eigenvector $U_1$, termed $W_{\text{Thigh}}$, $W_{\text{Leg}}$, and $W_{\text{Foot}}$ in Fig. 2D (see METHODS). These values indicate the contribution of the oscillation of each segment to the orientation of $U_1$ (i.e., how much it contributed to the tuning of the coordination pattern). No differences were found between the 2 limbs for $W_{\text{Thigh}}$, $W_{\text{Leg}}$, and $W_{\text{Foot}}$ during SA walking ($P > 0.6$). Instead, the differences were significant during curved walking (TU). The contribution of the thigh angle in shaping the principal component significantly depended on the body side [side $\times$ direction effect, $F_{(1,5)} = 9.7, P < 0.05$]. Post hoc testing revealed that $W_{\text{Thigh}}$ of the inner and outer limbs significantly differed during TU ($P < 0.05$): its values respectively increased and decreased in the inner (37%) and outer limb (38%) with respect to SA. $W_{\text{Leg}}$ remained unchanged in the outer limb but significantly [side $\times$ direction effect, $F_{(1,5)} = 6.7, P < 0.05$] decreased (40%) in the inner limb ($P < 0.05$). No specific effect of vision was detected for any theses parameters ($P > 0.5$). This first analysis shows that a single elementary function captured the features of the movements of the whole limb in
the mediolateral plane, and that this elementary function was
limb-specifically tuned according to walking direction (SA
or TU).

**Coordination pattern among angles in the sagittal plane**

We applied the same analysis to the angular oscillations of
lower limb segments in the heading (sagittal) plane. The results
are reported in Fig. 3, which has the same layout as Fig. 2.
Kinematic templates of thigh, leg, and foot angles of the 2
limbs were remarkably similar whatever the walking direction
(plots of Fig. 3A) or the visual condition (not shown), and were
only shifted in time (see next section of RESULTS). The 4 plots
depicted in Fig. 3B were obtained in the same way as those for
Fig. 2B, by plotting against each other the 3 mean elevation
angles of the lower limb segments. The paths described by the
data points progress in anticlockwise direction for all plots, the
heel strike and toe-off phases corresponding to the top and
bottom of the loop, respectively. The grid identifies the plane
of angular covariation, whose intersections with the cubic wire
indicate the spatial position of the plane.

Table 2 reports the results of the principal component anal-
ysis, both visual conditions pooled. The first PC (PC1) ac-
counted for most of the data variance (87%). Contrary to the
former analysis (angles in the frontal plane), a second compo-
nent (PC2) was now required to account for the entire move-

![Heading Component (sagittal)](image)

FIG. 3. **A**: time course of elevation angles of thigh, leg,
and foot in the heading (sagittal) plane during SA and TU
walking (average values from all subjects). Layout of A
and B is the same as that for Fig. 2. C: percentage variance
accounted for by PC1 plus PC2 (planarity) indicates the
goodness of the covariation of the 3 angles within a plane.
D: mean values (+SD) of plane orientation (U31) and loop
shape (U11) quantify the features of the covariation plane.

**Table 2. Percent variance accounted for by each
principal component**

<table>
<thead>
<tr>
<th></th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>In the medio-lateral plane</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SA Left</td>
<td>95.4</td>
<td>3.5</td>
<td>1.1</td>
</tr>
<tr>
<td>Right</td>
<td>96.5</td>
<td>2.7</td>
<td>0.8</td>
</tr>
<tr>
<td>TU Left</td>
<td>96.3</td>
<td>2.8</td>
<td>0.9</td>
</tr>
<tr>
<td>Right</td>
<td>94.7</td>
<td>4.4</td>
<td>1.0</td>
</tr>
<tr>
<td><strong>In the heading plane</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SA Left</td>
<td>87.5</td>
<td>11.9</td>
<td>0.6</td>
</tr>
<tr>
<td>Right</td>
<td>87.1</td>
<td>12.3</td>
<td>0.6</td>
</tr>
<tr>
<td>TU Left</td>
<td>87.7</td>
<td>11.4</td>
<td>0.9</td>
</tr>
<tr>
<td>Right</td>
<td>85.3</td>
<td>14.0</td>
<td>0.7</td>
</tr>
</tbody>
</table>

Results of principal component analysis performed on angles of thigh, leg and
foot angles in the sagittal or medio-lateral plane. Mean values (±SD) of percent
variance accounted for by PC1, PC2, PC3 are reported for the left and right limbs
during SA and TU, both visual conditions pooled. PC, principal component.
ment variability (>99%). The presence of a nonnegligible PC2 implies that the angles of the lower limb segments in the sagittal plane did not covary along a line as they did in the mediolateral plane, but rather covaried within a plane, termed “covariation plane” (Borghese et al. 1996). PC1 and PC2 identified its spatial position and gave an index of its “planarity.” During both SA and TU walking, the planarity was very high because PC1 plus PC2 accounted for more than 99% of the data variance. Planarity slightly, yet significantly, decreased for both limbs during curved walking [direction effect, F(1,5) = 164, P < 0.001]. Note that planarity also decreased when walking blindfolded [vision effect, F(1,5) = 7.5, P < 0.05], during both SA and TU walking, indicating that the temporal changes of the elevation angles of the 3 segments had less tendency to covary within a plane.

Because the angles covaried within a plane rather than along a line, we quantified both the plane orientation and the shape of the path loop (see METHODS). The mean values of both parameters are reported in the histograms of Fig. 3D. Minor differences between the left and right limbs were detected for both plane orientation and path loop shape in SA walking as evidence of a good coordination among the 6 segments of the 2 limbs. Conversely, there was a divergence in the planar covariation between the inner and outer limbs in TU [side × direction effect, F(1,5) = 31, P < 0.005 for the plane orientation; F(1,5) = 21, P < 0.01 for the loop shape]. First, the plane rotated leftward (2°) and rightward (5°) in the outer and inner limbs, respectively. Second, the width of the path loop increased (10%) and decreased (28%) in the outer and inner limbs, respectively. These adaptive, turn-related changes were similar in both EO and EC conditions.

In the next section, we show that these changes in planar covariation among lower limb segments are the counterpart of turn-related changes in intersegmental coupling that accompany the adaptation of the gait pattern of the inner and outer limbs to curved walking.

**Relationships between the features of the coordination pattern and gait parameters**

The plots of Fig. 4A display the average elevation angles of thigh and leg segments (left) and leg and foot segments (right) computed from all trials and all subjects during TU (with eyes open), for both inner and outer limbs, normalized to the duration of the gait cycles. The sum of the oscillations of adjacent leg segments determined the time course of joint angles (i.e., knee and ankle angles), which is depicted in the plots of Fig. 4B. No differences were found in the phase relationships between each pair of segments for the left and right limbs during SA, but opposite changes emerged during TU [side × direction effect, F(1,5) > 19, P < 0.01 for both thigh–leg and leg–foot phase relationships]. These phase changes were evaluated through FFT analysis (see METHODS), the results of which are summarized in Fig. 4C. The phase difference between adjacent segments decreased (P < 0.05) in the outer limb and increased (P < 0.001) in the inner limb. These changes were more consistent in the inner limb (~3% of cycle duration) than in the outer (~2% of cycle duration), but not statistically different between EO and EC conditions (P > 0.6). As a
consequence of the opposite phase changes between adjacent segments of the 2 limbs, the ankle angle underwent different trajectories in the inner and outer limbs during curved walking as did the knee angle, although to a lesser extent.

Interestingly, the phase relationships between the angles of the lower limb segments in the sagittal plane (i.e., $\theta_{\text{thigh-leg}}$ and $\theta_{\text{leg-foot}}$) were correlated with the features of their angular covariation plane. The left and right panels of Fig. 5A show the relationships between $\theta_{\text{thigh-leg}}$ and loop shape ($U_{11}$) for SA and TU walking, respectively (both visual conditions pooled). Similarly, the relationships between $\theta_{\text{leg-foot}}$ and plane orientation ($U_{31}$) are depicted in the 2 panels of Fig. 5B. All the linear regressions, for both limbs and both walking directions, were highly significant ($r > 0.85$ for all regressions). However, whereas the scatter plot related to the left (open circles) and right (filled circles) limbs during SA are superimposed, those related to the inner and outer limbs moved away from each other during curved walking, as expected on the basis of the changes described above in the intersegmental coordination pattern.

The 2 plots of Fig. 5C depict the relationships between loop shape ($U_{11}$) and stride length, also segregated according to limb and walking direction. During SA walking, stride lengths were similar in the left and right limbs. The range of stride lengths was modest and the relationship was not very consistent. On the contrary, stride lengths of both inner and outer limb differed during curved walking and a relationship between stride length and loop shape emerged. Data points computed for the inner and outer limbs remained clustered along the same regression line, but moved up and down, respectively, during TU.

### Coordination pattern among all body segments

To obtain insight into the coordination pattern among all body segments while walking, we performed a principal component analysis on the angles of thigh, leg, and foot segments of the 2 limbs and of the trunk segment in both the mediolateral and sagittal planes. For each gait cycle, the ensemble of the 14 time-varying, standardized segmental oscillations constituted the data set on which the analysis was carried out.

The histogram of Fig. 6A depicts the percentage of variance accounted for by each principal component (PC) according to the walking direction. Principal component analysis revealed that in this case as well, both straight-ahead and curved walking were low dimensional at the task level. Indeed, the first 3 PCs accounted for more than 90% of the movement variability for all subjects, with the 2 first PCs accounting for 77% of data variance. However, significant differences were found for the first and the second PC between the 2 walking directions [direction effect, $F_{1,5} > 20$, $P < 0.01$ for both statistical tests]. The plot of Fig. 6B shows that the percentage of variance accounted for by $PC_1$ (open circles) and $PC_2$ (filled circles) evolved in opposite directions when increasing the steering tightness. On the contrary, neither vision nor interaction be-
 tween walking and vision significantly affected the percentage of variance accounted for by each PC ($p > 0.2$).

The left and right panels of Fig. 7 display the mean time course of PC1 and PC2, respectively, for each subject, in both visual conditions and for both walking directions. Both PCs show 2 broadly symmetric peaks, the former family of curves being reversed with regard to the latter, a fact that could account for alternate oscillations of the 2 limbs. The shape of each PC was highly reproducible across subjects and between visual conditions. Furthermore, the shape of PC1 and PC2 hardly changed when turning (the thick lines are the average of all SA and of all TU curves). This result indicates that the elementary functions subserving the spatiotemporal patterns of angular oscillations of body segments were almost invariant during straight-ahead and curved walking.

Mathematically, each PC is the weighted linear combination of the 14 body angles. Remarkably, the contribution of each angle to PC1 and to PC2 depended on the actual curvature of the locomotor path. The plots of Fig. 8 show the relationships between the change in heading and the contribution of each angle to PC1 (top) and PC2 (bottom), for a typical subject. To emphasize the continuity of the steering process, we added to this representation the gait cycles that corresponded to the transition from the straight to the curved path—the change in heading associated with these cycles is intermediate between the SA and TU gait cycles. The left and right limbs are represented in the same plot by open and filled symbols, respectively. Roll and pitch trunk angles showed less consistency in their contribution to PC1 and PC2 with the exception of trunk roll contribution to PC1, which slightly increased with steering tightness. This may reflect changes in the timing of trunk roll induced by the phase lag between the 2 limbs during turning (Courtine and Schieppati 2003a). The contribution of the angles of the lower limb segments to PC1 was the same for the left and right limbs when walking SA—open and filled data points are superimposed when the change in heading is near zero, indicating symmetry in the movement of the 2 limbs. The angle contributions to PC2 were more variable, but did not differ between the left and right limb, on average, during SA walking, either. In turn, the relationships computed for the inner and outer limbs, for both PC1 and PC2 contributions, increasingly diverged as steering tightness increased. Changes in the contributions of thigh, leg, and foot angles to PC1 were modest but systematic; the contribution of foot rotations of the inner limb was more pronounced. The contributions of the lower limb angles to PC2 in the mediolateral direction substantially increased and decreased on the inner and outer limb, respectively, when changing walking direction. This may account for the inward rotation of the former and outward rotation of the latter, both necessary to produce a smooth change in heading.

**DISCUSSION**

*Coordination pattern among lower limb segments*

Shen and Poppele (1995) showed that the overall features of limb kinematics in cat stepping may be produced by controlling the relative timing and amplitude among lower limb segment oscillations. Others provided evidence that limb kinemat-
ics in human locomotion may also be controlled by manipulating a limited number of factors (Bianchi et al. 1998; Borghese et al. 1996; Cheron et al. 2001; Grasso et al. 1998, 2000; Ivanenko et al. 2002). These authors identified a few elementary functions among the complex pattern of angular waveforms, which recombine the actual body movement as a linear combination of a basic set of waveforms. They reported that limb segment elevation angles in the sagittal plane covary along a plane common to both stance and swing phases (Lacquaniti et al. 2002). Moreover, tuning of the same basic co-variance pattern adapted limb behavior to various constraints such as speed increment (Bianchi et al. 1998), reversal of walking direction (forward to backward; Grasso et al. 1998), stepping under different load conditions (Ivanenko et al. 2002), or with different postures (bent vs. erect; Grasso et al. 2000). This led to the notion that adaptation of joint angles to the locomotor task may simply be achieved by tuning the relative timing between almost invariant oscillations of the adjacent segments.

In the current study, we report that during curved walking, the kinematic templates of elevation angles of the lower limb segments in the sagittal plane remained roughly unchanged, and that thigh, leg, and foot angles still covaried along a plane, although the spatiotemporal configuration of the force pattern sustaining body progression while maintaining equilibrium is dramatically different during curved walking compared with straight-ahead walking. Such a modification of the mechanical context might disrupt intersegmental coordination. We showed instead that lower limb segments preserve their highly coordinated patterns during curved walking, in both the frontal and sagittal planes, and that the same number of basic elementary functions accounts for the coordination patterns during both straight-ahead and curved walking; but how can we produce curved walking—or, how can a similar control pattern account for the constraints connected with the major changes in biomechanical variables accompanying curved walking?

**Segment oscillations on the sagittal and frontal planes**

Subtle and limb-specific changes in the parameters of coordination seem sufficient to produce the adaptations of limb behavior: tuning of planar covariation reflects both temporal and spatial evolution of limb characteristics for both straight-ahead and curved walking. The continuous changes in timing of segmental oscillations are obvious in the strong linear relationship between planar features and phase relationships among adjacent segments (Fig. 5, A and B). Spatial adaptation of gait parameters is expressed by the linear relationship between planar features and stride length in both limbs (Fig. 5C). In addition, we detected a coordination rule among lower limb segments in the frontal plane: in this case, the oscillations of thigh, leg, and foot segments covary along “a line,” rather than on a plane, during both straight-ahead and curved walking. This is taken as evidence of a simplified coordination in the frontal plane—the dimensionality of the interconnected segmental chain of each lower limb was reduced to one degree of freedom. Interestingly, tuning of the orientation of this “covariation line” captured limb-dependent changes in limb configuration for curved walking, such as opposite shifts of the mean segment orientations of the inner and outer limb. We therefore propose that modulation of 2 basic kinematic laws accounts for the coordinated oscillations of lower limb segments in the sagittal and frontal planes, and that these 2 basic coordination patterns are enough to produce the complex sequence of limb-specific postures that accompany steering of the body in space.

**The role of vision**

Visual input can actually influence locomotion in many ways (reviewed in Rossignol 1996). Our subjects performed both walking tasks with eyes open and blindfolded. Suppression of visual input induced a slight increase in average distance between the required and actual locomotor trajectory during straight-ahead walking, and even more so during curved walking (Courtine and Schieppati 2003a). Being blindfolded may modify segment coordination in subjects, which would in turn explain the decrease in locomotor accuracy. It turned out that no major feature of coordination was modified by the presence or absence of vision: visual flux per se had no significant effect on the coordination patterns among body segments observed during either straight-ahead or curved walking. As such, vision seems not to be directly involved in the building of the intersegmental coordination. The role of vision may be confined to informing higher centers about the orientation and location of the body in the earth-based reference frame, whereas automatic locomotor processes simplify navigation and dynamic equilibrium (see following text), thus allowing smooth progression along complicated trajectories.

**Tuning of spinal neural circuits**

Previous studies also used multivariate statistics as a tool for extracting common factors from muscle EMG patterns during limb movement or locomotion (d’Avella et al. 2003; Davis and Vaughan 1993; Ivanenko et al. 2003). For example, d’Avella et al. (2003) demonstrated that modulation of the amplitude ratio and timing difference of 2 or 3 elementary muscular functions accounts for limb kinematics during kicking in frogs. Basically, principal components can be extracted from both EMG and kinematics variables. The former implies a central control of coordinated muscle activation, whereas the latter suggests that a small set of elementary functions are combined to produce a wide range of motor behaviors, and reduce the effective number of degrees of freedom (Lacquaniti et al. 2002; Poppele and Bosco 2003; Santello and Soechting 1998; St-Onge and Feldman 2003). One possibility is that the patterns of coordinated muscle activation and gait kinematics revealed by factorial analysis are based on the existence of a network producing the automatic spatiotemporal coordination pattern for locomotion. According to an influential scheme, multisegmental motion of mammalian locomotion is the final output of a network of coupled oscillators [the central pattern generators (CPGs)] located within the spinal cord (Grillner 1981), and divided into a flexor and an extensor center, each controlling the activity of synergistic muscles acting around a particular joint (Cheng et al. 1998). The adaptation of intersegmental coordination would be achieved by coupling unit oscillators with a variable phase (Jones et al. 2003; Schoner et al. 1990). No conclusive evidence for the existence of such a spinal locomotor system in humans has been provided so far (Barbeau et al. 1999; Bussel et al. 1996; Dietz et al. 2002; Edgerton and...
Putative supraspinal centers

Drew et al. (2002) showed that the motor cortex of walking cats regulates amplitude and temporal pattern of muscle activity for adapting the gait to environmental demands. They suggested that these task-related adaptations are mediated by spinal interneurons, which generate the basic locomotor rhythm. In this manner, the changes specified by the corticospinal drive may be smoothly incorporated into the locomotor cycle. The same neural process might also account for turn-related gait adaptations in humans because the motor cortex has access to the spinal cord machinery during human walking (Bonnard et al. 2002; Capaday et al. 1999; Christensen et al. 2001). During curved walking, the corticospinal drive would produce the necessary changes in muscle activation of the inner and outer limbs (Courtine and Schieppati 2003b), without interfering with the locomotor rhythm and gait organization. On the other hand, the selection of patterns of associated postural activity might be embedded in the discharge of other pathways. In the cat, the reticulospinal neurons receive collateral projections from the motor cortex and substantially contribute to the production of the motor adjustments during gait modifications (see Prentice and Drew 2001). In humans, different brain-stem nuclei might be responsible for appropriate modulation of locomotion. For example, a dysfunction of pedunculopontine neurons may be important in the pathophysiology of postural and locomotor disturbances in Parkinsonian patients (Pahapill and Lozano 2000), in whom a major unbalance emerges when negotiating changes in the walking direction (Morris 2001; Rogers 1996).

In conclusion, these new data appear to give some insight into the problem of how a complex task such as human navigation in the environment could be implemented. Navigation requires the integration of multiple sensory inputs with the planning of the goal-directed action (Berthoz and Viaud-Delmon 1999). This process is effective if the descending command can be transferred reliably and quickly to the spinal machinery for producing body progression in space. Curved walking is the basis of navigation. In this case, the descending command must not only take into account the existence of a high number of degrees of freedom among the lower limb segments—already presenting a challenge for straight-ahead walking (Bernstein 1967; Poppele and Bosco 2003); it must also control the emerging, balance-threatening torques connected with the change in direction of the body masses. These data also suggest that, although the walking trajectory may not be wholly reproduced when the subject is blindfolded, accurate segment coordination per se during walking does not directly depend on vision. The current findings strongly suggest that fine-tuning of one basic coordination pattern constructs both straight-ahead and curved walking, in normal conditions with and without vision, thereby emancipating higher-order cognitive processes (Bove et al. 2001, 2002) from the motor implementation of navigation.

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