Interactions Between Posture and Locomotion: Motor Patterns in Humans Walking With Bent Posture Versus Erect Posture

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Human erect locomotion is unique among living primates. Evolution selected specific biomechanical features that make human locomotion mechanically efficient. These features are matched by the motor patterns generated in the CNS. What happens when humans walk with bent postures? Are normal motor patterns of erect locomotion maintained or completely reorganized? Five healthy volunteers walked straight and forward at different speeds in three different postures (regular, knee-flexed, and knee- and trunk-flexed) while their motion, ground reaction forces, and electromyographic (EMG) activity were recorded. The three postures imply large differences in the position of the center of body mass relative to the body segments. The elevation angles of the trunk, pelvis, and lower limb segments relative to the vertical in the sagittal plane, the ground reaction forces and the rectified EMGs were analyzed over the gait cycle. The waveforms of the elevation angles along the gait cycle remained essentially unchanged irrespective of the adopted postures. The first two harmonics of these kinematic waveforms explain >95% of their variance. The phase shift but not the amplitude ratio between the first harmonic of the elevation angle waveforms of adjacent pairs was affected systematically by changes in posture. Thigh, shank, and foot angles covaried close to a plane in all conditions, but the plane orientation was systematically different in bent versus erect locomotion. This was explained by the changes in the temporal coupling among the three segments. For walking speeds >1 m s⁻¹, the plane orientation of bent locomotion indicates a much lower mechanical efficiency relative to erect locomotion. Ground reaction forces differed prominently in bent versus erect posture displaying characteristics intermediate between those typical of walking and those of running. Mean EMG activity versus erect posture displaying characteristics intermediate between those of walking and those of running. Mean EMG activity was greater in bent postures for all recorded muscles independent of the functional role. The waveforms of the muscle activities and muscle synergies also were affected by the adopted posture. We conclude that maintaining bent postures does not interfere either with the generation of segmental kinematic waveforms or with the planar constraint of intersegmental covariation. These characteristics are maintained at the expense of adjustments in kinetic parameters, muscle synergies and the temporal coupling among the oscillating body segments. We argue that an integrated control of gait and posture is made possible because these two motor functions share some common principles of spatial organization.

INTRODUCTION

The issue of the relationship between posture and locomotion is of great theoretical and experimental relevance (see Burleigh et al. 1994; Lacquaniti et al. 1997; Massion 1992; Mori 1987; Winter 1991; Zernicke and Smith 1996). Neurophysiological studies indicate that the control of posture and locomotion are interdependent at many different levels of the CNS, from the motor cortex to the basal ganglia, the brain stem, and the spinal cord. Thus basal ganglia are connected reciprocally with ponto-mesencephalic structures (the pedunculopontine nucleus) belonging to the mesencephalic locomotor region (an area known to modulate spinal locomotion oscillators) (Shik and Orlovsky 1976), on the one side, and with the axial motor cortex, on the other side. These structures participate in the preparation and initiation of locomotion by providing the appropriate spatial frameworks necessary to incorporate postural adjustments in the locomotion process (Garcia-Rill 1986; Grasso et al. 1999). Also when specific areas in the hypothalamus or the brain stem are stimulated, changes in posture are triggered just before step initiation (Mori 1987; Mori et al. 1978, 1983, 1989). Interactions between pathways controlling posture and gait exist even at the level of spinal premotor interneurons (Jankowska and Edgley 1993). In sum, it has been suggested that the "activation of setting mechanisms in the level of postural muscle tone and that of the spinal stepping generator are not separate phenomena" (Mori 1987).

If the interrelationship between posture and locomotion is well recognized, the implications vis-à-vis the issue of the motor pattern generation are not well understood (see, however, Zernicke and Smith 1996). In particular, it is not clear whether or not the setting of different task-dependent postural configurations of the body should affect the waveforms of the basic motor patterns that are rhythmically output during walking. This question hinges on the more general problem of the nature of the control waveforms output by central locomotor networks (see Lacquaniti et al. 1999; Zernicke and Smith 1996).

It is generally thought that the multisegment motion of mammals locomotion is controlled by a network of coupled oscillators (central pattern generators or CPGs) (see Grillner 1981; Pearson 1993; Rossignol 1996). Although it often is assumed that CPGs control patterns of muscle activity, an equally plausible hypothesis holds that they control patterns of limb segment motion instead (Bianchi et al. 1998b; Borghese et al. 1996; Grasso et al. 1998; Shen and Poppele 1995). This hypothesis is based on the following observations (for a review, see Lacquaniti et al. 1999). In walking the waveforms of limb segment angular motion are much simpler and more consistent than the corresponding waveforms of muscle activity, both in man (Borghese et al. 1996; Grasso et al. 1998) and
cat (Shen and Poppele 1995). Moreover the temporal changes of the elevation angles of the lower limb segments do not evolve independently of each other, but they are tightly coupled together (Bianchi et al. 1998b; Borghese et al. 1996). When the elevation angles are plotted one versus the others, they describe a regular loop constrained close to a plane, common to both the stance and swing phase. The specific orientation of the plane of angular covariation reflects the phase relationships between the elevation angles of the segments and therefore the timing of the intersegmental coordination. The phase delay shifts systematically with increasing speed both in man (Bianchi et al. 1998b) and cat (Shen and Poppele 1995). Because in man this phase-shift is correlated with the net mechanical power output over a gait cycle (Bianchi et al. 1998b), we hypothesized that the control of kinematic phase can be used by the nervous system for limiting the overall energy expenditure with increasing speed (Bianchi et al. 1998a). Finally, we observed that a reversal of the direction of walking from forward to backward involves the same waveforms (time-reversed) of the elevation angles as in forward gait, with a simple reversal of the delay in the phase coupling between limb segments, at the expense of a reorganization of the patterns of muscle activity (Grasso et al. 1998).

How does a change in walking posture affect these locomotor patterns? Although we normally walk with an erect posture, we can as easily walk stooped (as it happens in a low tunnel). Here we compared normal erect walking (regular, RE) with two different styles of bent walking, namely knee-flexed walking (KF) and knee-flexed plus trunk-flexed walking (KT). RE walking is a unique feature of human locomotion (nonhuman primates normally walk with a bent posture). Its evolutionary history indicates highly specific adaptations of the skeletal and muscular apparatus (Crompton et al. 1998; Spoor et al. 1994). Also, erect posture is mechanically efficient in humans because the center of body mass vaults over the supporting limb like an inverted pendulum, thereby limiting energy expenditure by means of an exchange of the forward kinetic energy with the gravitational potential energy (Cavagna et al. 1977). Maintaining KF and KT posture while walking may interfere with the pendulum mechanism. McMahon et al. (1987) showed that in subjects running knee-flexed, reaction moments acting on the knee are increased and the effective vertical spring stiffness of the legs is decreased relative to normal running. We introduced condition KT in addition to KF to assess the specific role of trunk orientation in the generation of locomotor patterns. In fact it has been proposed that the trunk may act as a reference in the control of posture and movement (Darling and Miller 1995; Massion et al. 1997; Mouchonino et al. 1993). This role then could be disrupted when the trunk is flexed.

In looking for the effects of changes of walking posture on the locomotor patterns, we keep in mind that there exist inevitable mechanical consequences of a bent posture. In particular, KF and KT walking must involve an offset in the mean value of several kinematic and kinetic variables as compared with RE walking. For instance, because the legs are flexed, the mean elevation angles of the limb segments in the former tasks will be generally different from those measured in the latter task. Also the mean level of muscle activity will be increased because of the reduced mechanical advantage of bent limbs (Biewener 1990). With regard to the issue of locomotor pattern generation, however, the key point concerns the waveform of the kinetic and kinematic signals rather than their mean value. According to our previous hypothesis, locomotion is controlled in a kinematic space (see Lacquaniti et al. 1999). If so, one would expect that the changes in posture should leave the kinematic waveforms essentially unchanged. The interrelationship between posture and locomotion should manifest itself instead on the phase delay between the motion of different limb segments; that is, the control parameter that is set centrally according to the specific task demands. (As we noted in the preceding text, the phase delay varies as a function of changes in walking speed or reversal of walking direction.) An additional implication of our hypothesis is that the conservation of kinematic templates across changes in body posture can occur only at the expense of a reorganization of muscle patterns and synergies.

**Methods**

General procedures have been previously described (Bianchi et al. 1998b; 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 (3D) calibration, the SD spatial accuracy of the system was better than 1.5 mm (Bianchi et al. 1998b). 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 landmarks: gleno-humeral joint (GH), anterior superior iliac spine (ASIS), posterior superior iliac spine (PSIS), greater trochanter (GT), lateral femur epicondyle (LE), lateral malleolus (LM), and fifth metatarso-phalangeal joint (VM). VM marker was placed on the shoe after verifying the correspondence on the bare foot. ASIS and PSIS coordinates were averaged to obtain ilium (IL) position. The body was modeled as an interconnected chain of rigid segments: GH-IL for the trunk, IL-GT for the pelvis, GT-LE for the thigh, LE-LM for the shank, and LM-VM for the foot. The limb axis was defined as GT-LM.

Ground reaction forces were recorded at 500 Hz by means of a monocomponent force platform (0.6 × 0.4 m, Kistler 9281B), placed approximately at the center of the walkway. EMG activity was recorded by means of surface electrodes from the greater trochanter (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 kinematic, 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. Five healthy volunteers (2 females, 3 males, 21–36 yr age range) participated after giving informed consent. Before the recording session, the dominant lower limb of each subject was determined according to standard criteria (Vanden-Abeele 1980). All subjects proved to be right-dominant. Before the experiment, we asked our subjects to adopt static KF and KT postures on the force platform and computed the instantaneous position of the center of pressure of the net reaction forces during 20-s records (which were repeated 2 times). Fifteen seconds of steady state data were averaged to obtain the mean anteroposterior displacement of the center of pressure relative to RE condition, which was 0.38 ± 0.48 and 0.43 ± 0.66 cm (mean ± SD) forward for KF and KT, respectively. This small displacement is not statistically significant.
Subjects then were instructed to walk (with their shoes on) 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. Because no additional constraints were used, the speed range overlapped but did not coincide exactly in different experiments. To avoid modifications of the natural step length, subjects were asked not to pay attention whether or not they stepped onto the force platform. Walks were performed in one of the three different postures (RE, KF, and KT), randomly alternated from trial to trial.

Data analysis

Three-dimensional kinematic data were filtered with an optimal low-pass FIR filter with automatic bandwidth selection (D’Amico and Ferrigno 1990). The angle of elevation of the 1th segment in the sagittal plane with respect to the vertical was computed as \( \alpha = \arctan((x_d - x_p)/(y_d - y_p)) \), subscripts p and d denoting proximal and distal endpoints of the segment, respectively, and x and y the horizontal and vertical coordinates in the sagittal plane, respectively. Elevation angles are positive in the forward direction relative to the vertical (i.e., when the distal marker falls anterior to the proximal). 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) as the linear translation of GT marker during T, and average speed as \( V = ST \). Stance phase was defined as the interval during which the vertical reaction force exceeded 7% of body weight. The maximum elevation of the limb axis slightly precedes the heel touch-down (Borghese et al. 1996). Different trials from each subject were ensemble-averaged after time-interpolation of the kinematic data over T to fit a normalized 1,000-points time base. Postural geometry was measured by taking the mean, maximum and minimum value of the elevation angle of each segment over T. The x, y coordinates of the location of the center of body mass (CM) are computed as the mean of x, y coordinates of the respective centers of mass of seven body segments: the H.A.T. plus the thigh, shank and foot of the right and left limbs. H.A.T. is comprised of head, folded arms, trunk, and pelvis and is assumed to be one rigid link (corresponding to GH-GT segment) (see Winter 1991). The center of mass of each of these segments was derived from anthropometric measurements taken on the subject and the geometric models based on the gamma-scanner method (Zatsiorsky et al. 1990). Motion of the side of the body contralateral to the recording one was estimated by time-shifting the recorded data by T/2, under the assumption of symmetrical gait (Bianchi et al. 1998b).

EMGs were rectified numerically and low-pass filtered (in both time directions to avoid tail and phase distortions) by means of a Butterworth filter, with cutoff at 25 Hz. Cross-correlation functions (CCF) between pairs of muscles were computed as previously described (Grasso et al. 1998).

Intersegmental coordination among the lower limb segments (thigh, shank, and foot) was evaluated starting from elevation angle waveforms both in the time domain (1) and in position space (2).

1) Because of the periodic structure of the elevation angle waveforms over the gait cycle (Bianchi et al. 1998b; Borghese et al. 1996), we decomposed such waveforms into their Fourier series components. The series was truncated at the 10th harmonic which had a frequency corresponding to the highest low-pass cutoff frequency in the data series.

The amplitude transfer ratio (\( C_{pd} \)) and phase shift (\( \Phi_{pd} \)) between the corresponding Fourier harmonics from the elevation angles of adjacent limb segments p and d were computed, respectively, as \( A_d/(dA_p) \) and \( \Theta_d - \Theta_p \) where \( A_d \) and \( \Theta_p \) are the amplitude and phase respectively of the kth order Fourier series component.

2) The intersegmental coordinate was evaluated in position space as previously described (Borghese et al. 1996). Briefly, the changes of the elevation angles of the thigh, shank, and foot covary linearly throughout the gait cycle. The thigh-shank-foot 3D loops describe paths that can be fitted by a plane that is computed by means of orthogonal regression (Bianchi et al. 1998b; Borghese et al. 1996). In each trial, we computed the covariance matrix \( \mathbf{R} \) of the ensemble of time-varying elevation angles over the gait cycle, after subtraction of their respective mean value. Eigenvalues \( \lambda \) and eigenvectors \( \mathbf{u} \) are computed by factoring the covariance matrix \( \mathbf{R} \) from the set of original signals by using a singular value decomposition algorithm such that

\[
\mathbf{R} = \mathbf{U} \mathbf{A} \mathbf{U}^T
\]

where \( \mathbf{U} \) and \( \mathbf{A} \) are the eigenvector and eigenvalue matrices, respectively, and \( \mathbf{T} \) denotes matrix transpose. The sum of the eigenvalues is equal to the sum of the variances of the original signal waveforms. The three eigenvectors \( \mathbf{u}_1 \) of \( \mathbf{R} \), rank-ordered on the basis of the corresponding eigenvalues, correspond to the orthogonal directions of maximum and minimum variance in the sample scatter. The first two eigenvectors \( \mathbf{u}_1 \) lie on the best-fitting plane of angular covariance. The third eigenvector \( \mathbf{u}_3 \) is the normal to the plane and defines the plane orientation in the position-space of the elevation angles. For each eigenvector, the parameters \( \mathbf{u}_x \), \( \mathbf{u}_y \), and \( \mathbf{u}_z \) correspond to the direction cosines with the positive semi-axis of the thigh, shank and foot angular coordinates, respectively. The direction cosines of the plane normal provide a measure of the orientation of the plane. In particular, \( \mathbf{u}_3 \) denotes the direction cosine with respect to the thigh axis.

Results

General gait parameters

Walking flexed was performed easily in both KF and KT conditions. The subjects had no difficulty in maintaining that posture for the few seconds required to walk the 10-m path. We analyzed a total number of 463 gait cycles at speeds within the range \( 0.2 \pm 0.2 \) m s\(^{-1}\). The range of speeds \( 0.5 \pm 1.5 \) m s\(^{-1}\) was represented evenly across subjects and conditions.

The well-known monotonic increase of step length with walking speed was not significantly affected by postural geometry. The slopes of the intrindividual regression lines were \( 0.43 \pm 0.11 \) m per 1 m s\(^{-1}\) speed increment, \( 0.33 \pm 0.38 \) for RE, KF, and KT, respectively (the intercepts were \( 0.75 \pm 0.09 \) m, \( 0.84 \pm 0.41 \), \( 0.83 \pm 0.37 \)). However the scatter was larger for KF and KT than for RE (correlation coefficients were \( 0.97 \pm 0.02 \), \( 0.85 \pm 0.10 \), and \( 0.69 \pm 0.38 \), respectively). Repeated-measures ANOVA across the three conditions yielded nonsignificant outcomes for the comparisons between regression parameters from the three conditions. On average, the duration of the stance phase was \( \sim 60\% \) of the gait cycle in all conditions (61.9 ± 3.9%, 62.1 ± 2.7%, and 62.8 ± 2.6% for RE, KF, and KT, respectively) and decreased with increasing speed (on average by 6.5% of gait cycle duration per 1 m s\(^{-1}\)). The latter relationship was less consistent in KF and KT than in RE.

Geometric postural features

Figure 1 (top) shows stick-diagram series from one subject walking at approximately the same speed (\( \sim 1 \) m s\(^{-1}\)) with the three different postures. As implied by the task, postural geometry differs drastically across the three conditions. In KF and KT, the lower limbs are flexed and the trunk is tilted, more so in KT. The vertical oscillations of the trunk and pelvis segments are less pronounced in KF and KT than in RE. The position of the CM is displaced forward and downward in KF.
and more so in KT so that it tends to lie outside of the body. (CM in the 1st stick diagram from each of the 3 series is displayed as a \( F \) in Fig. 1). Note that the hip is raised above the supporting foot in midstance like an inverted pendulum in RE but that it remains level or is even lowered in midstance in KF, a situation closer to that occurring in running than in normal walking. On the other hand, the trajectory described by the foot tip is similar across the three postures. Figure 1, bottom, shows the instantaneous location of the CM as a function of time from the gait cycles displayed in the top. The prominent oscillation typical of regular gait is dampened drastically in KF, indicating that the impact shock with the ground is attenuated by the lower limb joints. The decrease in the oscillation of the CM in KF relative to RE was more evident at higher speeds.

Table 1 reports the mean value (over the gait cycle, from all trials of all subjects) of the elevation angles of each limb segment in the sagittal plane, and the mean value of the length of the limb axis. The mean orientation of the body segments changed according to the instructions. Thus in bent postures, the trunk was flexed anterior, the thigh was elevated in the forward direction, and the shank in the backward direction in comparison with erect posture. The changes in these parameters were not independent of each other. The mean elevation of the trunk and thigh changed in a correlated manner across all subjects and postures, as did thigh and shank (\( r = -0.73 \) and 0.77, respectively). As expected, the mean limb length was significantly shorter in KF and KT than in RE (\( F_{1,460} = 194.3, P < 0.001 \), with no difference between KF and KT, Scheffe’s post hoc test).

**Kinematic waveforms**

Figure 2 shows the average waveforms (\( \pm SD \), data from all trials and subjects) of the elevation angles in the three conditions. These waveforms are plotted versus normalized time, expressed as a percentage of gait cycle duration. The elevation angle of the trunk and pelvis changed little during the gait cycle. All other elevation angles displayed the typical biphasic shape, which has been described thoroughly in previous articles (Bianchi et al. 1998b, Borghese et al. 1996, Grasso et al. 1998). Briefly, the lower limb segments rotate backward during stance and forward during swing.

The new finding is that the segmental kinematic waveforms have a very similar shape in the three conditions (RE, KF, and KT) even though they may differ in offset or amplitude. The SD bands are rather narrow but more so in the RE condition. Table 2 shows the correlation coefficients (mean \( \pm SD \), data from all subjects) computed between the individual average waveforms of each experimental condition. The correlation was always very high, confirming that the shape of the elevation angle waveforms was maintained across the three walking conditions in all subjects.

Figure 3 shows the range (\( \pm SD \)) of the values of the elevation angles during one gait cycle for the different tasks. For all limb segments, the overall extent of the angular excursion changed only slightly.

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**TABLE 1. Mean elevation angle for the recorded body segments and limb axis length**

<table>
<thead>
<tr>
<th>Segment</th>
<th>RE</th>
<th>KF</th>
<th>KT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trunk</td>
<td>1.4 ± 3.4</td>
<td>−12.8 ± 9.3</td>
<td>−54.5 ± 12.7</td>
</tr>
<tr>
<td>Pelvis</td>
<td>13.5 ± 5.4</td>
<td>10.9 ± 5.8</td>
<td>6.9 ± 6.9</td>
</tr>
<tr>
<td>Thigh</td>
<td>1.2 ± 3.4</td>
<td>22.1 ± 5.3</td>
<td>28.1 ± 3.6</td>
</tr>
<tr>
<td>Shank</td>
<td>−15.2 ± 3.2</td>
<td>−31.5 ± 5.4</td>
<td>−27.7 ± 8.2</td>
</tr>
<tr>
<td>Foot</td>
<td>48.7 ± 6.2</td>
<td>46.2 ± 8.6</td>
<td>49.6 ± 8.2</td>
</tr>
<tr>
<td>Limb axis</td>
<td>754 ± 59</td>
<td>665 ± 50</td>
<td>651 ± 38</td>
</tr>
</tbody>
</table>

Values are means ± SD. Angles are in degrees. Limb axis length is in mm. RE, regular walking; KF, knee-flexed walking; KT, knee- and trunk-flexed walking.
Intersegmental coordination—time domain

The first two harmonics of the Fourier series expansion account together for >95% of the experimental variance of each kinematic waveform (Table 3), and the shape of the reconstructed waveforms faithfully reproduces the main features of the original ones. The first harmonic alone explains most (>70%) of the original waveform variance.

| TABLE 2. Correlation coefficients between elevation angle waveforms |
|---------------------------------|-----------------|-----------------|
|                               | Thigh           | Shank           | Foot            |
| RE-KF                          | 0.87 ± 0.05     | 0.98 ± 0.01     | 0.98 ± 0.01     |
| RE-KT                          | 0.94 ± 0.04     | 0.95 ± 0.04     | 0.98 ± 0.03     |
| KF-KT                          | 0.94 ± 0.08     | 0.98 ± 0.02     | 0.95 ± 0.06     |

Values are means ± SD. n = 5.

Figure 4 shows the average time-normalized waveforms of thigh, shank, and foot elevation angles from one subject. To superimpose all traces on the same scale, the mean value was subtracted from each one. The time changes of thigh elevation lead those of shank elevation (the time delay between the 2 minima is indicated by the shaded areas in the figure). However, the time lead is consistently shorter in KF and KT than in RE. In contrast, the amplitude of segmental excursions does not vary substantially across the three conditions.

The amplitude transfer ratio ($G$) and the phase shift ($\Phi$) between pairs of adjacent lower limb segments (thigh-shank and shank-foot) was quantified by means of harmonic analysis (see METHODS) and is shown in Fig. 5 for the first harmonic (mean ± SD, from all subjects). One-way ANOVA showed that the changes of the two gains across conditions were marginally significant (0.01 < $P$ < 0.05 and $P = 0.05$ for $G_{ts}$ and $G_{sf}$, respectively). The difference between RE and KT was
significant, whereas KF could not be distinguished from either RE or KT (Scheffe’s post hoc test). The relative increase of \( G_{sf} \) means that the amplitude of foot movements relative to that of the shank tended to increase in bent postures relative to the erect posture. The opposite tendency is showed by \( G_{ts} \).

For the phase shifts \( \Phi_{ts} \) and \( \Phi_{df} \), the changes from RE to KF and KT were prominent and highly significant \((P < 0.0001)\). In RE, the first harmonic of the thigh elevation waveform led consistently that of shank elevation \((by \, 53.3 \pm 5.1^\circ, \text{corresponding to} \, 14.8 \pm 1.4^\circ \, \text{of} \, T) \) and the shank led slightly the foot \((by \, 15.2 \pm 10.8^\circ, 3.1 \pm 1.2^\circ \, \text{of} \, T) \). In KF the phase shift between the thigh and shank dropped \((to \, 15.2 \pm 10.8^\circ, 4.2 \pm 3.0^\circ \, \text{of} \, T) \) and the shift between shank and foot increased approximately twofold \((27.6 \pm 6^\circ, 7.7 \pm 1.7^\circ \, \text{of} \, T) \).

Ratios and phase shifts for the second harmonic displayed little changes across the conditions for the shank-foot pair, whereas for the thigh-shank pair only KF differed from either RE or KT \( \text{(which were similar to each other)} \). Higher harmonics contributed little to the original waveform shape, and gain and phases between adjacent segments were related inconsistently to the walking condition.

### Planar covariation of limb elevation angles

We have found previously that in normal erect posture the temporal changes of the elevation angles of the limb segments covary along a plane common to both the stance and the swing phase \((\text{Bianchi et al. 1998b, Borghese et al. 1996, Grasso et al. 1998})\). We now report that a planar law holds consistently that of shank elevation \((by \, 53.3 \pm 5.1^\circ, \text{corresponding to} \, 14.8 \pm 1.4^\circ \, \text{of} \, T) \) and the shank led slightly the foot \((by \, 15.2 \pm 10.8^\circ, 3.1 \pm 1.2^\circ \, \text{of} \, T) \). In KF the phase shift between the thigh and shank dropped \((to \, 15.2 \pm 10.8^\circ, 4.2 \pm 3.0^\circ \, \text{of} \, T) \) and the shift between shank and foot increased approximately twofold \((27.6 \pm 6^\circ, 7.7 \pm 1.7^\circ \, \text{of} \, T) \).

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### Patterns of contact forces with the ground

Figure 8 shows the time-normalized vertical \((\text{top})\) and longitudinal \((\text{bottom}, \text{anterior force is positive})\) ground reaction forces for the speed range \(0.5-1.5 \, \text{m s}^{-1}\) from 11 trials of the same subject as in Fig. 1. In RE the time course of vertical forces exhibits the classical pattern, with two
main peaks (one in early stance and the second one in late stance) separated by a trough in midstance due to partial unloading from the contralateral limb (see Borghese et al. 1996; Winter 1991). The first peak and the trough become more pronounced with increasing speed. By contrast, in KF and KT the profile of vertical forces tends to be monophasic, with peaks and trough much less pronounced than in RE. Moreover this pattern does not vary with increasing speed as much as in RE (the slopes and $r$ coefficients of the regression line relating the walking speed to the peak force are $109 \pm 25 \text{ N m}^{-1} \text{s}$, $r = 0.81$ for RE, $40 \pm 10 \text{ N m}^{-1} \text{s}$, $r = 0.77$ for KF, and $41 \pm 25 \text{ N m}^{-1} \text{s}$, $r = 0.53$ for KT). The amplitude of the plateau in bent postures is lower than the two peaks displayed in RE especially at higher speeds.

As for the longitudinal reaction force, in RE it exhibits an ordered amplitude increase with speed both in the deceleration (after heel touch-down) and the acceleration (before toe take-off) phase ($r = 0.94$ for the peak force vs. speed linear regression). In KF and KT, this force has a lower peak amplitude than in RE and the profiles are much more variable across trials ($r = 0.46$ and 0.41 for KF and KT, respectively). Also the stance phase duration displays a less consistent relation with speed as compared with RE. The linear regression between stance percent duration and speed yielded the following parameters: slope $= -6.9\%$ per $1 \text{ m s}^{-1}$, $-7.2$ and $-8.2$ for RE, KF, and KT; intercept $= 65.6, 68.7$, and $68.5\%$, for RE, KF, and KT; correlation coefficients $= 0.91, 0.83$, and 0.61 for RE, KF, and KT.

**EMG activity**

Figure 9, left, shows the EMG ensemble average of 10 gait cycles from one subject walking at $1 \text{ m s}^{-1}$ in each of the three conditions. In all examined muscles, the mean activity tended to be greater in KF and KT than in RE. GM mean integrated EMG over the gait cycle increased 117 and 230% from RE to KF and KT, respectively, RF increased 271 and 174%, VL 418 and 189%, BF 152 and 460%, TA 72 and 35%, and GCL 278 and 145%. Not only the mean amplitude but also the pattern of activity differed across conditions. RF displayed prominent activity in the early swing phase of KT condition compared with RE. BF displayed a prominent activity during the stance phase of KF and even more so in KT, whereas in RE this muscle is typically active during the swing phase mainly. Task-dependent changes in the activity profile also were observed in the other tested muscles. As a consequence, the squared correlation coefficients between postural conditions tend to be lower than those computed for the corresponding
changes in the elevation angles (right). This was true for all subjects.

Not only the patterns of activation of individual muscles but also the time sequence of activation of different muscles, or muscle synergies, varied substantially as a function of body posture. To quantify this kind of synergies, we computed the CCF between pairs of EMG ensemble averages. The CCFs for the three tasks are superimposed in Fig. 10. The patterns of muscle synergies differ across conditions as indicated by the different shape of the CCF. For instance, in RE and KF the peak in the pair RF-VL occurs at ∼0% of the gait cycle, indicating agonistic activity. By contrast, in KT the peak occurs at ∼40% lead, indicating quasi-antagonistic activity in these two muscles. Most other pairings of muscles exhibit significant time shifts in either the maximum or the minimum of the CCF in KT and KT conditions relative to the RE condition. This is shown by the scatter plot of these values in Fig. 11. Several data points (13/30 and 18/30 for the maximum condition. This is shown by the scatter plot of these values in Fig. 11. Several data points (13/30 and 18/30 for the maximum

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**DISCUSSION**

**Kinematic waveforms**

The purpose of the present study was to verify how walking with a bent posture affects the generation of gait motor patterns. In bent postures (KF and KT), the lower limbs and the trunk are flexed as compared with the erect posture (RE). In spite of the drastic changes in postural geometry, the oscillations of each limb segment relative to the vertical are very similar across different postures.

The adaptation of the intersegmental coordination to the different postures is achieved by changing the phase delays between the motion of different limb segments. Thus the phase lead of thigh oscillations relative to shank oscillations is systematically shorter with bent postures than with an erect posture, whereas the phase lead of the shank relative to the foot oscillations is longer in the former than in the latter. As a result, there is an approximately constant phase décalage (of ∼20° corresponding to ∼5% of the gait cycle) between adjacent limb segments in the proximal-to-distal direction in bent walking. The behavior of a flexed lower limb then can be equated to that of a rolling wheel with the pivot corresponding to the knee joint.

Somewhat similar results have been reported previously in the comparison of level walking versus crouched walking in cats (Trank et al. 1996). (The latter is an attitude typical of stalking behavior in this species.) The profiles of hindlimb kinematics were rather similar between the two forms of locomotion either for the hip, knee, ankle, or the metatarso-phalangeal joint angles (see Fig. 3 of Trank et al. 1996) in spite of prominent changes in their mean values and ranges of excursion. The timing of motion reversals (from flexion to extension) differed at some joints. Therefore postural adaptation acts on the same variable, intersegmental kinematic phase, which has been shown previously to be centrally modified as a function of changes in walking speed (Bianchi et al. 1998b) or walking direction (Grasso et al. 1998). Intersegmental phase plays a role of global control variable similar to that previously advocated for the network of coupled oscillators involved in the generation of locomotion (see Grillner 1981; Pearson 1993; Rossignol 1996). According to the kinematic view we have exposed in the introduction, each unit oscillator would directly control a limb segment, alternately generating forward and backward oscillations of the segment. Intersegmental coordination would be achieved by coupling unit oscillators with a variable phase. Variable coupling could result, for instance, by changing the synaptic strength (or polarity) of the relative spinal connections. Supraspinal centers may drive or modulate functional sets of coordinating spinal interneurons to generate different walking modes. We shall take up the issue of the mechanisms of postural modulation of the coordinating network in a subsequent section.

**Planar covariation of elevation angles**

The changes in the elevation angles of the thigh, shank, and foot covaory along a plane common to both the stance and the swing phase. More than 98% of the data variance is explained by the planar regression in all postural conditions. However, the orientation of the plane differs across conditions: the plane is rotated about the long axis of the loop with bent postures as compared with the erect posture. The direction cosine of the

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**TABLE 4. Percent variance explained by the eigenvalues of the elevation angle covariance matrix**

<table>
<thead>
<tr>
<th></th>
<th>RE</th>
<th>KF</th>
<th>KT</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\lambda_1$</td>
<td>87.2 ± 2.8</td>
<td>90.0 ± 3.7</td>
<td>91.5 ± 2.3</td>
</tr>
<tr>
<td>$\lambda_2$</td>
<td>11.6 ± 2.7</td>
<td>8.4 ± 3.9</td>
<td>7.1 ± 2.3</td>
</tr>
<tr>
<td>$\lambda_3$</td>
<td>1.2 ± 0.4</td>
<td>1.6 ± 0.6</td>
<td>1.4 ± 0.5</td>
</tr>
</tbody>
</table>

Values are means ± SD.
FIG. 7. Direction cosine $u_3$ from the overall data set. This parameter represents the orientation of the normal to the best-fitting plane relative to the thigh axis. Its theoretical range goes from $-1$ to 1. Values in KF and KT are systematically higher than in RE. Initials refer to the 5 subjects.

FIG. 8. Compressed arrays of vertical ($A$) and longitudinal ($B$) ground reaction force profiles for the 3 experimental conditions in 1 subject as a function of walking speed ($y$ axis). Eleven trials at speeds ranging from 0.5 to 1.5 m s$^{-1}$ ($y$ axis) are included. Time scale of each profile was normalized over the gait cycle. $x$ axis represents percent of cycle length. Forces ($z$ axis) are expressed in Newton (N).
walking: the greater is the value of correlates with the mechanical energy expenditure during erect a gait cycle (Bianchi et al. 1998a). Here we found that the greater is the corresponding net mechanical power output over changes affects the intersegmental phase coupling. observation that the adaptation of locomotion to these postural (Bianchi et al. 1998b). Therefore the demonstration of changes the phase coupling between the limb segment elevation angles have shown previously that changes of sensitive to this type of rotation (see Bianchi et al. 1998b). We plane normal with the thigh axis (u_3t) is the parameter most sensitive to this type of rotation (see Bianchi et al. 1998b). We have shown previously that changes of u_3t reflect changes in the phase coupling between the limb segment elevation angles (Bianchi et al. 1998b). Therefore the demonstration of changes of u_3t in KF and KT relative to RE is consistent with the observation that the adaptation of locomotion to these postural changes affects the intersegmental phase coupling.

We have shown previously that the parameter u_3t generally correlates with the mechanical energy expenditure during erect walking: the greater is the value of u_3t, in any given trial, the greater is the corresponding net mechanical power output over a gait cycle (Bianchi et al. 1998a). Here we found that the values of u_3t for KF and KT are systematically greater than the corresponding values for RE. This result is consistent with the observation that the level of muscle activity (and therefore of overall energy expenditure) is systematically higher with bent posture than with erect posture (see next section).

Adaptation of limb kinetics to bent postures

The patterns of ground reaction forces and muscle activity change systematically as a function of walking posture. The time profile of the vertical reaction forces is multiphasic in erect posture but monophasic and of lower amplitude in bent postures (Li et al. 1996). In the latter case, in fact, the impact with the ground is attenuated, especially by the knee joint (McMahon et al. 1987). The monophasic profile is reminiscent of that measured during erect running. However, in bent walking the percent duration of stance is much longer than in running, so that McMahon et al. (1987) pointed out that knee-flexed locomotion is somewhat intermediate between walking and running. The peak amplitude of the longitudinal forces is greater in erect than in bent walking. In general, reaction forces are more variable in bent postures.

The level of muscle activity is systematically higher with bent posture than with erect posture. When the limb joints are flexed and displaced away from the main axis of the limb, the mechanical advantage of the muscles to support body weight during stance and to flex the limb during swing is reduced in comparison with that of the erect posture, and more muscle activity is needed to generate the appropriate joint torques. An increment of muscle activity also is required because the recovery of mechanical energy by means of the pendulum mechanism is less effective, and more muscular work needs to be done to move the center of body mass and to swing the limbs.

In erect walking, in fact, the center of body mass oscillates above the supporting limb like an inverted pendulum, thereby limiting energy expenditure by means of an exchange of the forward kinetic energy with the gravitational potential energy (Cavagna et al. 1977). By contrast, in bent postures the center of body mass tends to be displaced downward and forward, and its oscillations are reduced because the legs cannot fully extend (see Fig. 1). Thus the exchange of kinetic and potential energy is more limited. Indeed, human knee- and hip-flexed walking has been found to produce in-phase fluctuations in potential and kinetic energies (Li et al. 1996) rather than the out-of-phase fluctuations typical of erect locomotion.

Not only the amplitude but also the pattern of activation of individual muscles, as well as the time sequence of muscle synergies, vary substantially as a function of body posture. This was shown by considering the cross-correlation functions of pairs of EMG ensemble averages. In particular we observed considerable shifts in either the maximum or the minimum of several cross-correlation functions, indicating the transition from an agonistic activity in a given postural condition to a quasi-antagonistic activity in the same pair of muscles in a different postural condition (see Figs. 10 and 11). Trank et al. (1996) also found that muscle patterns for cats walking knee-flexed display some changes with respect to normal walking. The burst duration for three primary knee, ankle, and digit flexor muscles are longer and EMG amplitude has often a higher amplitude according to the increased range and duration of flexion during the swing phase. Furthermore
two muscles that show mainly swing-related activity in normal walking (digit extensors) have distinct stance-related bursts in crouched walking, similar to what we found for BF. Similar changes in the functional role of specific muscles with respect to normal walking also have been described for down-slope (Smith et al. 1998) and up-slope walking (Carlson-Kuhta et al. 1998). The extensive investigation of different forms of locomotion in cats (normal forward, backward, crouched, up slope,

![Cross-correlograms between pairs of EMG data](image)

**FIG. 10.** Cross-correlograms between pairs of EMG data from 1 subject. Correlation values are plotted as a function of time delay (expressed as percent of the gait cycle). A positive value of cross-correlation at a positive time delay indicates that the activation of the column muscle leads that of the row muscle, whereas a positive cross-correlation at a negative delay indicates a time lag of the column muscle relative to the row muscle.

![Abscissas correspond to lead](image)

**FIG. 11.** Abscissas correspond to the lead (positive values) or lag (negative values) of the maximum (left) or the minimum (right) of the cross-correlation functions (CCF) in RE condition for the indicated muscle pairs. Ordinates correspond to the values for KF (unfilled symbols) or KT (filled symbols). Data points on the diagonal line indicate no change between conditions, and the shaded area depicts the ±10% cycle duration band. Time delays are expressed as percent of the gait cycle.
and down slope) (reviewed in Zernicke and Smith 1996) has made clear that the coupling between muscle groups is an important functional variable and may be modified centrally depending on the behavioral context. Even robust stance-sustaining synergies, which rely on the excitatory coupling between hip and knee extensor units, may be switched off in particular cases (i.e., in down-slope walking). To explain these transitions to different synergies without dropping the schema of an array of joint-related CPG units (Grillner 1981), Zernicke and Smith (1996; see also Prochazka 1996) proposed that the rule for setting interunit connections may be issued by supraspinal control following conditional statements related to the behavioral goal.

Our view is that, in response to the kinematic reference signals, the appropriate muscle synergies are determined in a flexible manner to fit the current mechanical constraints. Indeed, the relationship between muscle activity and whole body mechanics seems too variable and complex to allow a direct control of the latter without an intermediate kinematic representation. Neurophysiological data indicate that intermediate kinematic representations may be found in both premotor (Bizzi et al. 1991) and proprioceptive sensory areas of the spinal cord (Bosc et al. 1996) as well as in somatosensory and motor cortices (Helms Tillery et al. 1996; Lacquaniti et al. 1995; Scott and Kalaska 1997).

**Integrated control of gait and posture**

Postural adaptation conserves the general kinematic waveforms with an appropriately tuned intersegmental phase and allocates specific patterns of muscle activity as a function of the required kinematic coordination. Integrated control of gait and posture is made possible because these two motor functions share some common organizational principles (Lacquaniti et al. 1997; Massion 1992). First, the frame of reference for the kinematic coordination for both postural responses and locomotion seems to be anchored to the vertical. Second, a control of the position of the center of body mass for static or locomotion is also mediated through the output patterns generated in the segmental CPGs (see also Armstrong 1988; Hasan and Stuart 1988).

A specific role in setting the spatial framework for the control of the postural geometry of the trunk and the coordination of lower limb segments is provided by the basal ganglia (Garcia-Rill 1986). A recent study addressed this issue in patients with Parkinson’s disease (Grasso et al. 1999). Patients could be switched on by means of either a D1-D2 receptor agonistic drug (apomorphine) or by globus pallidum internum (GPI) electrical stimulation. It was found that the inclination of the trunk with respect to the vertical, the waveforms of the elevation angles, and the planar law of angular co-variation change all in parallel in the transition from the OFF to the ON condition.

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