Kinematic Coordination in Human Gait: Relation to Mechanical Energy Cost

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Bianchi, L., D. Angelini, G. P. Orani, and F. Lacquaniti. Kinematic coordination in human gait: relation to mechanical energy cost. J. Neurophysiol. 79: 2155–2170, 1998. Twenty-four subjects walked at different, freely chosen speeds (V) ranging from 0.4 to 2.6 m s⁻¹, while the motion and the ground reaction forces were recorded in three-dimensional space. We considered the time course of the changes of the angles of elevation of the trunk, pelvis, thigh, shank, and foot in the sagittal plane. These angles specify the orientation of each segment with respect to the vertical and to the direction of forward progression. The changes of the trunk and pelvis angles are of limited amplitude and reflect the dynamics of both right and left lower limbs. The changes of the thigh, shank, and foot elevation are ample, and they are coupled tightly among each other. When these angles are plotted one versus the others, they describe regular loops constrained on a plane. The plane of angular covariation rotates, slightly but systematically, along the long axis of the gait loop with increasing V. The rotation, quantified by the change of the direction cosine of the normal to the plane with the thigh axis (uₜ), is related to a progressive phase shift between the foot elevation and the shank elevation with increasing V. As a next step in the analysis, we computed the mass-specific mean absolute power (Pᵥ) to obtain a global estimate of the rate at which mechanical work is performed during the gait cycle. When plotted on logarithmic coordinates, Pᵥ increases linearly with V. The slope of this relationship varies considerably across subjects, spanning a threefold range. We found that, at any given V > 1 m s⁻¹, the value of the plane orientation (uₜ) is correlated with the corresponding value of the net mechanical power (Pᵥ). On the average, the progressive rotation of the plane with increasing V is associated with a reduction of the increment of Pᵥ that would occur if uₜ remained constant at the value characteristic of low V. The specific orientation of the plane at any given speed is not the same in all subjects, but there is an orderly shift of the plane orientation that correlates with the net power expended by each subject. In general, smaller values of uₜ tend to be associated with smaller values of Pᵥ and vice versa. We conclude that the parametric tuning of the plane of angular covariation is a reliable predictor of the mechanical energy expenditure of each subject and could be used by the nervous system for limiting the overall energy expenditure.

INTRODUCTION

The issue of the coordinative laws of gait has been explored from both a theoretical and an experimental standpoint. Modeling approaches, ranging from neuromodulation of coupled oscillators (Bay and Hemami 1987; Kopell 1995) to synergetics (Schöner et al 1990; Thelen and Smith 1994), group-theory (Collins and Stewart 1993), and topological dynamics (Das and McCollum 1988; McCollum et al 1995), have described gait in either continuous or discrete space and suggested that excess degrees of freedom (df) are constrained by the neural control. As a result, limb dynamics would be confined to an attractor space of lower dimensionality than that of the original parameter space.

Experimental studies have provided evidence for coordinative laws that lead to a reduction of df. In humans as in other mammals, the output of the central networks involved in the control of the rhythmic limb movements of locomotion gives rise to complex and variable patterns of activity in a large number of muscles (Basmaijian and De Luca 1985; Nilsson et al. 1985; Pedotti 1977; Winter 1991). However, when gait is considered at a more global level of analysis than that of the patterns of individual muscles, namely the level of whole body mechanics (kinematics, kinetics, energetics), the describing patterns appear remarkably simple and consistent (Borghese et al 1996; Mah et al. 1994; Shen and Poppele 1995; Willems et al 1995; Winter 1991). It is then likely that the neural control signals encode flexible muscle synergies (Horak and Macpherson 1996; McCollum et al. 1985) for intersegmental coordination leading to a reduction of df in the parameter space of gait mechanics (Borghese et al. 1996).

In this vein, Winter (1991) has shown the existence of a law of kinetic covariance that involves a tradeoff between the hip and knee torques, such that the variability of their sum is less than the variability of each joint torque taken separately. Borghese et al (1996) instead have described a law of kinematic coordination. The temporal changes of the elevation angles of lower limb segments with respect to the vertical and forward directions do not evolve independently of each other, but they covary along an attractor plane common to both the stance and swing phase. This law is closely reminiscent of that previously described for the maintenance of cat posture in response to perturbations of the support platform (Lacquaniti and Maioli 1994a,b). The existence of laws of intersegmental coordination, common to the control of posture and locomotion, presumably assures the maintenance of dynamic equilibrium during forward progression and the anticipatory adaptation to potentially destabilizing factors by means of coordinated kinematic synergies of the whole body.

The stereotypical aspects of the law of planar covariation of segment elevation were emphasized in the previous study of gait from our laboratory (Borghese et al. 1996). Here we
METHODS

Experimental setup and procedures

Kinematic data were obtained at 100 Hz by means of the ELITE system (Ferrigno et al. 1990). The overall spatial accuracy of the system was enhanced by using four television (TV) cameras placed 0.8 m above the floor, at 2.7 m from the walkway, with a distance of 6.5 m between the two outer cameras and 4 m between the two inner ones. The cameras mounted wide-angle (8.5 mm) lenses the optical axes of which intersected at the center of the field, resulting in a total length of the longitudinal field of 2.25 m. Before each recording session, the optical distortion was corrected, the three-dimensional (3-D) viewfield calibrated, and the procedures validated by running a standard accuracy test that involved shaking a 1-m rigid bar within the field for 5 s. The position of the bar end points was recorded by attaching hemispherical reflective markers (1.5-cm diam). The SD accuracy of the estimated length of the bar had to be <1.5 mm, else the entire calibration procedure was repeated.

The position of selected points on the right side of the subject was recorded by attaching the reflective markers (same as previously mentioned) to the skin overlying the following bony landmarks (Fig. 1): gleno-humeral joint (GH), anterior superior iliac spine (ASIS), posterior superior iliac spine (PSIS), greater trochanter (GT), a point midway between the lateral epicondyle of the femur and the fibula head (LE), lateral malleolus (LM), and fifth metatarsophalangeal joint on the lateral aspect of the foot (VM).

The ground reaction forces under both feet were recorded by means of two force platforms (0.6 × 0.4 m, Kistler 9281B), placed at the center of the walkway, spaced by 0.2 m between each other in both the longitudinal and the lateral direction.

Protocols

Experiments were approved by the ethics committee of S. Lucia Institute and conformed with the Declaration of Helsinki on the use of human subjects in research. Twenty-four normal volunteers (whose characteristics are reported in Table 1) participated after giving informed consent. Four of them (DA, DL, GO, and RD) were trained in several sport disciplines at a precompetitive level, having graduated from Istituto Superiori di Educazione Fisica, the Italian college of physical education. ABX was a long-distance runner in amateur competitions. None of them, however, was trained in competitive walking.

All subjects were instructed to walk barefoot, with the arms folded on the chest, tracing repetitive loops along an approximately rectangular path with the long side (~8 m) roughly parallel to the line of the ELITE TV cameras and intersecting the force platforms half-way. Subjects were asked to walk at different speeds, ranging from slow to fast. Because we were interested in natural, unconstrained locomotion, only general, qualitative instructions were provided and each subject was free to choose his/her own cadence and speed. Before data acquisition, subjects looped a few times to reach a steady pace in which the right foot stepped on the first platform. Because of the longitudinal spacing between the two platforms, the left foot often stepped onto the second platform, although this was not requested of the subjects. The lateral spacing between the platforms ensured that one foot only stepped on each of them. At the end of the recording session, 22 anthropometric
where the subscripts $p$ and $d$ denote the proximal and distal end points of the segment, respectively (Fig. 1). $\alpha_i$ corresponds to the absolute orientation of $i$ with respect to the vertical and to the walking direction and is positive in the forward direction. In addition to analyzing these raw data, we also expanded the time course of the elevation angles in a 10-harmonics Fourier series for each trial separately. The cutoff for this expansion corresponded to the highest low-pass cutoff frequency that was present in the data.

**Gait parameters.** Stance phase was defined as the interval during which the vertical reaction force exceeded 7% of body weight, gait cycle ($T$) as the time interval between the zero crossings of the rate of change of the elevation angle of the limb axis, step length ($S$) as the linear translation of $GT$ during $T$, and average forward speed $V = S/T$ (Borghese et al 1996).

**Intersegmental coordination.** The patterns of intersegmental coordination of each limb in the sagittal plane were described by the temporal covariances among the elevation angles of the thigh, shank, and foot segments. The statistical structure underlying the distribution of these geometrical configurations was investigated by computing the covariance matrix $A$ of the ensemble of time-varying angles ($\alpha_i$) over the gait cycle ($T$) after subtraction of their mean value ($\bar{\alpha}$). Note that the matrix $A$ was computed separately for each trial, whereas it was computed for sets of trials performed at different speeds in the previous study (Borghese et al. 1996).

The three eigenvectors $u_1$ to $u_3$ of $A$, rank-ordered on the basis of the corresponding eigenvalues, correspond to the orthogonal directions of maximum variance in the sample scatter. The first two eigenvectors $u_1$ to $u_2$ identify the best-fitting plane of angular covariation. The third eigenvector ($u_3$) is the normal to the plane and defines the plane orientation in the position-space of the elevation angles. For each eigenvector, the parameters $u_{x1}$, $u_{x2}$, and $u_{y}$ correspond to the direction cosines with the positive semi-axis of the thigh, shank, and foot angular coordinates, respectively.

**Body segment inertial parameters.** Mass ($m_i$), relative location of center of mass, and moment of inertia in the sagittal plane ($I_{si}$) of each body segment were derived using the anthropometric measurements taken on each subject (see previous text), and the geometrical models based on the gamma-scanner method of Zatsiorsky et al (1990)

$$m_i = K_i L_i C_i^2$$

$$I_i = K_i m_i L_i^2$$

$L_i$ is anthropometric lengths of segments converted to biomechanical lengths according to the corresponding correction factors (Zatsiorsky et al 1990). Segment masses $m_i$ are summed over all segments, and the calculated total body mass is compared with the measured mass ($m$); in the case of discrepancies, the appropriate coefficient of correction is introduced. $K_i$ and $K_{m}$ are constants tabularized in Zatsiorsky et al (1990).

**Instantaneous mechanical energy.** We used the rigid-links model in which mechanical power is supplied to or absorbed from each segment by intersegmental forces and moments and by environmental forces (Aleshinsky 1986; Eftman 1939; Robertson and Winter 1980; van Ingen Schenau and Cavanagh 1990; Winter et al. 1976). At each instant of time, the total mechanical energy $E_i$ of a given body segment $i$ was computed as the sum of the corresponding gravitational potential energy, translational kinetic energy, and rotational kinetic energy. Only the components in the sagittal plane were considered, as those in the frontal plane were found to be negligible.

$$E_i = 1/2(m_i v_i^2 + I_i \alpha_i^2) + m_i g h_i$$

$v_i$ and $\alpha_i$ are the linear and angular velocity, respectively, of the center of segment mass, and $h_i$ is its vertical position. Seven body

**Table 1. Subjects’ characteristics**

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</tbody>
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$m$, male; $f$, female.

measurements were taken on each subject following the procedures proposed by Zatsiorsky et al. (1990). These included the length ($L_i$) and circumference ($C_i$) of each body segment $i$ (head, upper arm, forearm, hand, upper, middle, and lower part of torso, thigh, shank, and foot), in addition to the mass ($m$) and stature of the subject.

**Data analysis**

Synchronized sampling of ground reaction forces and kinematic data was performed at rates of 500 and 100 Hz, respectively. Two-dimensional kinematic data were converted to 3-D coordinates and filtered with an optimal low-pass FIR filter with automatic bandwidth selection (for details, see Borghese et al. 1996). Normally subjects walked parallel to the ELITE reference system (x, y, and z axes correspond to forward, upward, and lateral directions, respectively). In a few trials, systematic deviations were corrected by rotating the $x$ and $z$ axes by the angle of drift computed between start and end of the gait cycle.

**Geometric variables.** The body was modeled as an interconnected chain of rigid segments. The orientation of a cranio-caudal axis of each segment was defined by the 3-D coordinates of the corresponding proximal and distal end points (Borghese et al 1996; Lacquaniti and Maïoli 1994a; Mah et al. 1994). A more robust estimate for the ilium (IL) was obtained by averaging the coordinates of ASIS and PSIS. The following segments were considered: 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. In addition, the main axis of the limb was defined as the GT-LM segment.

Gait kinematics was described in terms of the time changes of the orientation angles of each segment (Borghese et al. 1996; Mah et al. 1994; Shen and Popple 1995; Soechting and Ross 1984). The angle of elevation ($\alpha_i$) in the sagittal plane for a given segment $i$ is

$$\alpha_i = \arctan \left( \frac{x_i - x_p}{y_i - y_p} \right)$$

$\alpha_i$ and $\alpha$ are the linear and angular velocity, respectively, of the center of segment mass, and $h_i$ is its vertical position. Seven body
segments were included in the analysis: H.A.T. and thigh, shank, and foot of right and left limbs. H.A.T. is composed of head, folded arms, and trunk and is assumed to be one rigid link because the motion of the head and folded arms relative to the trunk is negligible. Motion of the left side of the body was estimated by time-shifting the data recorded from the right side by T/2, under the assumption of symmetrical gait (Winter 1979). Both the above assumptions were verified in pilot experiments where the motion of both body sides and of the head were monitored. H.A.T. segment was defined by GH-IL—spatial coordinates, averaged between the left and right side.

**Instantaneous mechanical power.** With insignificant environmental forces (except gravity), the instantaneous power for each body segment is given by (Robertson and Winter 1980; van Ingen Schenau and Cavanagh 1990)

\[ F_d \dot{d} + F_p \dot{p} + M_d \dot{d} + M_p \dot{p} = E_i, \]

where the joint forces \( F_d \) and \( F_p \) at the distal and proximal end points of the segment, respectively, are multiplied by the corresponding velocities of the points of application \( \dot{d} \) and \( \dot{p} \), respectively, and the moments at the distal \( M_d \) and proximal \( M_p \) joints by the angular velocity \( \dot{\theta}_i \) of the segment. \( E_i \) is the rate of change of the total mechanical energy of the body segment, and includes the effect of gravity.

The equations for the separate segments are added to obtain the instantaneous power \( P(t) \) of the whole body (Aleshinsky 1986; van Ingen Schenau and Cavanagh 1990). The forces applied to the two opposite (proximal and distal) aspects of a joint are equal and opposite, and the corresponding terms cancel out, whereas the sum of each pair of terms involving the moments yields the net joint power \( M_i \dot{\theta}_i \). This implies that the joint forces cannot generate power, they can only redistribute power among different segments (Robertson and Winter 1980). The resulting equation for the net mechanical power \( P(t) \) of the whole body is (Aleshinsky 1986; van Ingen Schenau and Cavanagh 1990)

\[ P(t) = \sum_{i=1}^{7} M_i \dot{\theta}_i = d \sum_{i=1}^{7} E_i / dt \]

Summation was carried out over the seven body segments considered above.

**Mean cycle power.** The net work done during each gait cycle \( T \) is obtained by integrating Eq. 5 over \( T \). However, in level walking without significant power dissipation to the ground, positive work tends to equal negative work within a cycle, and this time integral is close to zero (Aleshinsky 1986; van Ingen Schenau and Cavanagh 1990; Winter 1990). Thus to obtain a global estimate of the rate at which mechanical work is performed over one cycle, we computed the mean absolute power \( P_a \) over \( T \) (Caldwell and Forrester 1992; Winter 1979)

\[ P_a = \frac{1}{mT} \int_0^T |P(t)| dt \]

Mass-specific power values (W kg\(^{-1}\)) were obtained by dividing by the subject’s mass \( m \). The power index \( P_a \) derived above takes into account all possible transfers of potential and kinetic energies within and between segments, weighs equally the phases of energy increment and the phases of energy decrement (positive work tends to equal negative work in level walking, see preceding text), and does not consider explicitly the elastic (strain) energy stored in muscles, tendons, and ligaments.

For each trial we also computed a power index \( P_e \) that has been proposed by Williams and Cavanagh (1983) to take into account the energy recovery due to elastic storage and the different efficiency of the conversion of metabolic energy into mechanical energy for positive and negative work

\[ P_e = (1 - a)(1 - b)TPOS + c/d|TNEG| \]

where TPOS and TNEG are the total positive and negative power, respectively, over one gait cycle, \( a \) and \( b \) correspond to the fraction (63%) of positive power attributable to between segment energy transfer and to the fraction (35%) attributable to elastic storage of energy, respectively; \( c \) is the fraction (85%) of the total negative power that is the result of eccentric muscular contraction rather than passive resistance within the musculoskeletal system, and \( d \) is the relative metabolic efficiency of negative to positive muscular power (3 times). In Eq. 7, TPOS (TNEG) was computed by summing the positive (negative) increments of \( E \) over each body segment separately, and then summing over all body segments (Williams and Cavanagh 1983).

**Results**

Because walking speed was indicated by means of qualitative instructions, the range covered in different experiments overlapped but did not coincide exactly. Here we restrict the analysis to trials in the range of speeds 0.4–2.6 m s\(^{-1}\). In this range, several gait parameters exhibited the monotonic relationship with speed that one would expect (Borghese et al. 1996). Step length increased (on average, by 0.32 m per 1 m s\(^{-1}\) speed increment, \( r = 0.89, n = 24 \)), gait cycle duration decreased (by 0.68 s, \( r = 0.97 \)), and the duration of stance as percentage of gait cycle decreased (by 3.4%, \( r = 0.83 \)).

**Gait kinematics**

To understand the nature of segmental coordination, we examined the time course of the changes in the geometrical configuration of the body and lower limbs. In particular we concentrated on the angles of elevation in the sagittal plane, which define the absolute orientation of each segment with respect to the vertical and to the direction of forward progression. Figure 2 shows the time course of the angular changes of the trunk, pelvis, thigh, shank, and foot segment of the right limb in trials performed at slow (~1 m/s) or fast (~2 m/s) speed by two subjects.

The changes of the trunk and pelvis elevation are of limited amplitude and reflect the dynamics of both right and left lower limbs. Thus Fourier series expansion (see METHODS) reveals that the fundamental component of the changes in pelvis angle tends to parallel the corresponding changes in thigh angle of the same side, but higher-order harmonics reflect the (half-cycle) phase-shifted motion of the contralateral side. In contrast with the trunk and pelvis elevation, the changes of the elevation angles of the lower limb segments are ample. In early stance, the shank and foot start rotating backward before the thigh. In midstance, the thigh and shank rotate backward at about constant velocity, while the foot orientation remains approximately constant. In late stance, the thigh motion reverts to the forward direction, while the shank and foot rotate further in the backward direction. During the swing phase, all limb segments rotate forward, the thigh angle reaching a plateau before the end of the gait cycle, and the shank and foot angles reaching the maximum at the end of the cycle.

**Intersegmental coordination**

A priori the elevation angles of the limb segments define a set of independent generalized coordinates, equal in num-
FIG. 2. Time course of kinematic variables in subject DA (A and B) and LB (C and D). A and C are at slow speed (0.93 and 0.98 m s$^{-1}$, respectively), whereas B and D are at fast speed (2.06 and 2.00 m s$^{-1}$, respectively). Elevation angles of trunk (--), pelvis (····), thigh (····), shank (---), and foot (···) are positive in the forward direction. Mean value has been subtracted from each trace, and the time base has been scaled to the duration of the gait cycle. , time limits of the stance phase: RHC, right heel contact, LTO, left toe-off, LHC, left heel contact, RTO, right toe-off.

Changes of limb kinematics with speed

The synthetic plots of Fig. 3, obtained by pooling together the data obtained at all speeds, emphasize the basic stereotypy of the patterns of intersegmental covariations, but they hide subtle yet important trends with speed changes. These trends can be appreciated by comparing single trials performed at different speeds. Slow (0.7 m s$^{-1}$), moderate (1.3 m s$^{-1}$), and fast (2.2 m s$^{-1}$) gait performed by one subject are plotted in Fig. 4, left, middle, and right, respectively. The data of single trials, just as those pooled across speeds (see Fig. 3), are well fitted by a plane [the mean residual variance is 0.9 ± 0.4% (SD) over all trials and experiments, n = 477]. The orientation of the graphic coordinate frame is the same in all panels of Fig. 4, and it has been chosen to show the best-fitting plane of the slow trial in an orthogonal view.

It can be noticed that the best-fitting plane of the faster trials is rotated about the long axis of the gait loop with respect to the plane of the slow trial (by 10 and 24$^\circ$ in Fig. 4, middle and right, respectively). As we shall see later, the extent of plane rotation with speed is not the same in all subjects. The subject of Fig. 4 is among those exhibiting a greater extent of plane rotation.
The variability of $u_1$ is low, both across trials performed at a given speed as well as across trials performed at different speeds (Fig. 5, A–C). Thus the mean values of its parameters ($u_{1t}$, $u_{1s}$, and $u_{1f}$) vary by $<4^\circ$ across the speed range, and their SD is $\sim 2^\circ$ for all speed classes. The parameters $u_{1t}$ and $u_{1s}$ of the normal also are characterized by a low variability (Fig. 5, E and F). $u_{3t}$ is more variable instead (Fig. 5D): its SD ranges from $2^\circ$ at speeds between 1.7 and 1.9 m s$^{-1}$ up to $8^\circ$ at speeds between 0.7 and 0.8 m s$^{-1}$. Moreover, there is a systematic change of the mean value of $u_{3t}$ with increasing speed: this value decreases by $21^\circ$ from the slowest speed class to the fastest one. This analysis reinforces the previous observation that the main effect of a speed change involves the rotation of the plane of angular covariation along the long axis of the gait loop.

To visualize the orientation of the plane in the 3-D space of the elevation angles, we plotted the plane normal ($u_3$) for all trials in the speed range of 1–2 m s$^{-1}$ (Fig. 6). Each black point corresponds to the projection of the normal onto the unit sphere for an individual trial. The frame of reference of the sphere is given by the direction cosines with the semi-axis of the thigh ($u_{3t}$, blue arrow), shank ($u_{3s}$, yellow), and foot ($u_{3f}$, red). It can be noticed that the data cluster in a relatively narrow region, spanning $29^\circ$ in longitude and $12^\circ$ in latitude (taking the foot axis as the virtual north pole of the sphere). In agreement with the analysis presented in Fig. 5, western points (smaller values of $u_{3t}$) generally correspond to faster speeds than eastern points (larger values of $u_{3t}$).

Figure 7 zooms in on the Fig. 6. The data of a subset (10) of the subjects are plotted in different colors. At this level of magnification, the data of individual subjects are clearly distinguishable, indicating that each subject occupies a specific region in this 3-D space, despite considerable overlap among subjects. In other words, the specific orientation of the plane at any given speed may differ slightly among subjects. However, all subjects exhibit the same trend with increasing speed of gait: the plane normal shifts to the west and slightly north. This shift corresponds to the rotation of the plane of angular covariation along the long axis of the gait loop, rotation that we noted before (see Fig. 4). The significance of the changes of orientation of the plane will be taken up in subsequent sections.

**Fourier analysis of the elevation angles**

**Mean characteristics.** On the average ($n = 477$), the first two harmonics of the Fourier series expansion (see Methods), computed for each trial separately, account together for 95.2, 99.7, 98.7, and 99.5% of the experimental variance of the pelvis, thigh, shank, and foot angles, respectively. Thus we concentrate here on the amplitude and phase of these two harmonics, and neglect higher-order harmonics. The ratio between the amplitude of the first and second harmonic is $3.79 \pm 1.18$, $5.19 \pm 1.05$, $2.11 \pm 0.22$, and $1.75 \pm 0.28$ for the pelvis, thigh, shank, and foot angles, respectively. The first harmonic of the thigh angle leads that of the pelvis by $10.9 \pm 10.3^\circ$ and leads that of the shank by...
50.3 ± 7.2°. The first harmonic of the shank angle leads that of the foot by 10.9 ± 4.5°.

CHANGES WITH SPEED. On the average, the amplitude of both first and second harmonics of all limb elevation angles tends to increase with increasing speed ($P < 0.05$), except the amplitude of the second harmonic of the foot angle, which decreases with speed. A general increase of amplitude with speed is to be expected given the corresponding increase in the overall step length (see previous text). The ratio between the amplitude of the first and second harmonic is not significantly correlated with speed for any limb segment except for the foot the ratio of which increases with speed (by 0.54 per 1 m s$^{-1}$ speed increment).

The phase of the first harmonic of the thigh angle is not significantly correlated with speed, whereas there is a systematic phase advance of the second harmonic relative to the gait cycle with increasing speed. The phase of both the first and second harmonics of the shank and foot angles is advanced with increasing speed ($P < 0.001$), but more so the phase of the foot. As a consequence, there is a progressive phase shift of the foot angle relative to the shank angle with increasing speed. On the average, the phase difference between the first harmonics of the shank and foot decreases by 6.7° per 1 m s$^{-1}$ speed increment, whereas the phase difference between the corresponding second harmonics decreases by 10.7°.

The rotation of the plane described above is related precisely to this phase shift. Figure 8 shows the correlation between the phase lead of the first harmonic of the shank angle relative to that of the foot angle (ordinates) and the corresponding value of plane orientation ($u_3$, abscissas) across all trials ($n = 477$).

On the average, there is a 39° phase shift per unit change in $u_3$. A similar phase shift occurs between the second harmonics (47° mean change per $u_3$ unit change).

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**FIG. 5.** Mean changes of the plane parameters with speed. A–C: first eigenvector ($u_1$) is in the direction of maximum variance in the sample scatter, aligned with the long axis of the gait loops of Figs. 3 and 4. D–F: third eigenvector ($u_3$) is the normal to the plane. For each eigenvector, the parameters $u_t$, $u_s$, and $u_f$ correspond to the direction cosines with the positive semi-axis of the thigh, shank, and foot angular coordinates, respectively. Mean values (±SD) of the parameters have been obtained by grouping the trials performed by all subjects in different classes of average speed. Abscissas denote classes at speeds between that indicated and that of the next class. First class includes speeds in the range 0.4–0.7 m s$^{-1}$, and the last class speeds in the range 2.3–2.6 m s$^{-1}$.
Mean mechanical power

To obtain a global estimate of the rate at which mechanical work is performed during the gait cycle, we computed the mass-specific mean absolute power ($P_a$) for each trial (see METHODS). When plotted on logarithmic coordinates, $P_a$ increases linearly with $V$, in agreement with several previous data (Cavagna and Kaneko 1977; Taylor and Heglund 1982; Willems et al 1995). This relationship is robust in all subjects (on average, $R^2 = 0.94$, $n = 24$). However, the slope (indicating the rate of increment of $\ln P_a$ with $\ln V$) varies considerably across subjects (see Table 1, last column), spanning a threefold range from the most economical subject (GO) to the least economical one (SMX). Accordingly, $P_a$ values do not differ substantially across subjects for $V < 1$ m s$^{-1}$, but the values diverge rapidly for increasing $V$. Thus the ratio between the $P_a$ value of SMX and that of GO is 0.99 at $V = 1$ m s$^{-1}$, but it becomes 1.85 at $V = 1.4$ m s$^{-1}$ and 3.66 at $V = 2$ m s$^{-1}$. The subjects’ ranking does not appear to be very sensitive to the specific mean power index used. The values of $P_a$ (Eq. 7 in METHODS) computed for each trial are highly correlated ($r = 0.85$, $n = 477$) with the corresponding values of $P_u$, although they differ in magnitude (on average, $P_a$ is 54% of $P_u$). The subjects’ ranking appears also in reasonably good agreement with the level of training. Thus four (DA, GO, ABX, and RD) of the trained subjects (see METHODS) are in the first five positions, and the fifth trained subject (DL) is in the median position of the overall range.

Relationship between kinematics and mechanical power

As a next step in the analysis, we correlated the kinematics of gait with the corresponding changes in mechanical power. This was done by considering the general trend with speed first (this section) and then the individual trends exhibited by each subject (next section).

In multivariate regression, both the gait speed ($V$) and the orientation of the plane of angular covariation ($u_3$) explain highly significant ($P < 0.0000002$) proportions of the total variance of the mass-specific mean power ($P_a$). Figure 9 shows the specific form of the relationship of $P_a$ with $V$ and
Fig. 7. Magnified view of the spherical surface that includes all trials of 10 representative subjects in the same speed range as that of Fig. 6. Each subject is denoted by a different color (AA, green; ABX, orange; DA, yellow; GO, black; LA, cyan; LB, red; LP, purple; ME, beige; RD, white; and SMX, blue). Angular width and height of the spherical surface are 30° and 22.5°, respectively, at the center.

Fig. 8. Correlation between the phase lead of shank elevation relative to foot elevation (1st harmonics) and the orientation of the plane of angular covariation ($u_i$). Correlation coefficient is based on the least-squares linear regression on all trials from all subjects ($n = 477$).
FIG. 9. Relationship of the mass-specific mean power ($P_u$) with the gait speed ($V$) and with the orientation of the plane of angular covariation ($u_3t$). Iso-power contour lines are spaced by 0.25 W kg$^{-1}$ (color scale: left). Violet and blue lines correspond to $u_3t = 0.3$ and to $u_3t = 0.42 - 0.18 V$ (least-squares regression on all trials, $n = 477$), respectively. Values of $P_u$ at different $V$ are provided by the intersection of the iso-power contours with the blue oblique line in the case of plane rotation or with the violet horizontal line in the case of constant plane orientation.

Two trends that we previously described can be recognized in Fig. 9: the mean power increases and the plane of angular covariation rotates with increasing speed. In addition, however, the figure reveals a strong interaction between these parameters. The progressive rotation of the plane with increasing speed is associated with a reduction of the corresponding increment of the power that would occur if the plane orientation remained fixed at the value characteristic of low speeds. This can be appreciated by comparing the values of $P_u$ corresponding to the mean observed values of $u_3t$ at increasing speeds (the blue oblique line), with the theoretical values of $P_u$ that one would find if $u_3t$ remained constant at the value characteristic of low speeds (the violet horizontal line). The relative power-saving associated with the average plane rotation amounts to 13, 23, and 36% at $V = 1.5, 1.9,$ and 2.3 m s$^{-1}$, respectively.

Another important aspect of the relationship between mechanical power and kinematics is related to the scatter of the experimental values of $u_3t$ around the regression line in Fig. 9. At a given speed within the range of moderate to fast speeds, the output power is related to a large extent to the specific value of plane orientation: in general, the smaller is the value of $u_3t$, the smaller the corresponding value of $P_u$. For instance, the extremes of the range of $u_3t$ values are associated with a twofold change and a fourfold change of $P_u$ values at $V = 1.2$ and 2 m s$^{-1}$, respectively. At low speeds ($V < 1$ m s$^{-1}$) instead, $P_u$ is essentially independent of $u_3t$, as indicated by the fact that the corresponding iso-power contours are almost parallel to the $u_3t$ axis. As noted above, however, the intertrial variability of $P_u$ values is rather limited at those speeds.

**Individual trends**

The scatter of the data points around the regression line of Fig. 9 is largely due to the intersubject variability of the changes of $u_3t$ with speed. $u_3t$ is correlated negatively with $V$ in 23 of the 24 subjects (on average, $r = -0.78$), but the regression parameters vary widely among subjects. Figure 10 shows the orderly shift of the $u_3t - V$ relationship in three representative subjects. At comparable speeds, the $u_3t$ values of DA are smaller (the plane is more rotated) than those of LB, and LA’s values in turn are smaller than those of LA. Note that this trend is congruent with the ranking of these
The regression parameters of the $u_{3t} - V$ relationship vary across the subjects. The rotation of the plane, as assessed by the change in $u_{3t}$, ranges from 5 to 23° (9° mean value) per 1 m s$^{-1}$ speed increment across the sample of subjects. However, there is a statistically significant correlation between the slope (rate of change of $u_{3t}$) and the intercept ($u_{3t}$ value at $V = 0$ m s$^{-1}$): the greater the intercept, the more negative the slope of the regression (Fig. 11). As a consequence, those subjects in which the plane is less rotated ($u_{3t}$ is more positive) at low speeds avoid the region of high energy expenditure at higher speeds (see Fig. 9) by means of a faster rate of plane rotation with speed.

This mechanism of compensation is incomplete, however, so that the power output at $V > 1.2$ m s$^{-1}$ is correlated significantly ($P < 0.001$) with the orientation of the plane across subjects: smaller values of $u_{3t}$ tend to be associated with smaller values of $P_u$ and vice versa. Figure 12 shows the correlation between these two parameters at $V = 2$ m s$^{-1}$ (A similar regression exists for $V > 1.2$ m s$^{-1}$.) This trend can be noticed also from the 3-D scatterplot of Fig. 7.

**DISCUSSION**

We have described two kinematic laws of intersegmental coordination and their relationship with the mechanical energy expenditure. The first law states that, at any given gait speed, the changes of the elevation angles of the lower limb segments covary along a plane common to both the stance and swing phase. The second law states that the plane of angular covariation rotates with increasing speed of locomotion. For speeds $>1$ m s$^{-1}$, the plane orientation is correlated with the corresponding value of the net mechanical power.

**FIG. 10.** $u_{3t} - V$ relationship in subjects DA, LA, and LB. Least-squares regression lines are fitted to each data set.

**FIG. 11.** Correlation between the slope and the intercept of the $u_{3t} - V$ relationship. Each point corresponds to a different subject, and all points are fitted by means of a least-squares regression line.

**FIG. 12.** Correlation between log $P_u$ and $u_{3t}$ at $V = 2$ m s$^{-1}$. Each point corresponds to a different subject, and all points are fitted by means of a least-squares regression line.
Thus the progressive rotation of the plane with increasing speed is associated with a reduction of the corresponding increment of the power that would occur if the plane orientation remained fixed at the value characteristic of low speeds. Although the general mechanism is similar in all subjects, its specific implementation differs among subjects and so does the mechanical energy expenditure. In particular, the specific orientation of the plane at any given speed is not the same in all subjects, but there is an orderly shift of the plane orientation that correlates with the net power expended by each subject. In the following text, we take up each issue separately, and we discuss their possible functional significance and neural basis.

**Planar covariation of elevation angles**

Motion in the sagittal plane only was considered here, because it represents the major and most systematic component of normal gait (Borghese et al. 1996; Mah et al. 1994). Motion in the frontal plane generally is limited and contributes relatively little to the overall energy expenditure (a description of gait kinematics in the frontal plane can be found in Borghese et al. 1996; MacKinnon and Winter 1993; Mah et al. 1994). The changes of the elevation angles of the thigh, shank, and foot are coupled tightly among each other in contrast with the loose relationship existing among the corresponding joint angles (Borghese et al. 1996). When the elevation angles are plotted one versus the others, they describe regular loops constrained close to a plane (first kinematic law). The strength of the constraint is indicated by the high percentage (>99%) of the total experimental variance of the angular joint angles or segment orientation angles of the limbs that is explained by the planar regression. Trunk and pelvis motion in the sagittal plane is limited and reflects the dynamics of both right and left lower limbs because of the inertial and visco-elastic coupling between the trunk and the limbs (Alexandrov et al. 1994; Cappozzo et al. 1976; Thorstensson et al. 1984; Winter 1991). Thus the fundamental component of the changes in the pelvis angle tends to parallel the corresponding changes in the thigh angle of the same side, but the smaller, higher-order harmonics reflect the (half-cycle) phase-shifted motion of the contralateral side. The degree of interlimb synchronization is normally very high (MacKinnon and Winter 1993). Therefore it is not surprising that the planar constraint holds even when the angular motion at the pelvis is taken into account in addition to the motion of the lower limb segments, in other words when gait trajectories are examined in a 4-D—position-space instead of a 3-D—position-space (Borghese et al. 1996).

**Changes with speed**

When the normal to the plane of angular covariation is plotted in the 3-D space of the elevation angles, the data of all trials cluster in a relatively narrow region (see Fig. 6). Moreover, the scatter of data points, though limited, is not random but tends to be related with speed. Thus the plane orientation rotates along the long axis of the gait loop with increasing speed in 23 of 24 subjects (second kinematic law). The rotation of the plane is related to a progressive phase shift between the foot and shank elevation with increasing speed. Thus the greater is the speed, the less is the phase lead of the shank relative to the foot.

From a functional standpoint, this phase shift is an important outcome of the need to bring the foot through faster during the swing phase to place the heel for the subsequent stance phase earlier as gait speed increases. The swing of the foot depends on both active joint torques (corresponding to tibialis anterior activation) as well as passive inertial forces due to the acceleration of the shank and thigh. The weight of these components differs as a function of speed (Hollerbach and Flash 1982), and both components appear to be controlled actively by the central nervous system (Smith and Zernicke 1987; Winter 1983).

We have noted above that a key aspect of the second kinematic law is the control of the timing of the intersegmental coordination. Shen and Popple (1995) have argued previously for a control of the timing of the turning points of the elevation angles during cat locomotion (see also Halbertsma 1983). They found that the changes of the elevation angles of all hindlimb segments conform to a common waveform and differ only in the timing and amplitude. In addition, the relative time difference between the turning points of pairs of limb segments scales with the duration of the forward swing (related to gait speed). This result is closely reminiscent of the phase shift we have described for increasing speeds; the latter shift in turn is related to the rotation of the plane of angular covariation.

**Origin of constraints on limb segment angles**

A covariation of limb angles is by no means an exclusive finding of locomotion. Similar constraints involving either joint angles or segment orientation angles of the limbs are observed frequently in several different forms of motor behavior, encompassing wiping reflexes, postural responses, and arm pointing, and in different animal preparations, from the spinal frog to intact cats and humans (Alexandrov et al. 1994; Berkinblit et al. 1986; Flanders et al. 1992; Giszter et al. 1989; Kelly and Chapple 1990; Lacquaniti and Maioli 1994a; Soechting and Lacquaniti 1981).

Biomechanical and neural factors interact in the generation of such constraints. The contribution of passive visco-elastic coupling among limb segments has been demonstrated recently by Bosco et al. (1996). These authors investigated in the anesthetized cat the geometrical configurations of the hindlimbs associated with displacements of the foot in the sagittal plane and found that the values of the limb angles covary along a plane. They attributed this mechanical constraint to the springlike properties of biarticular muscles such as the hamstrings and gastrocnemius.

Studies on intact cats have shown that, when the base of support is pitched, the reactive changes of the limb angles also covary along a plane (Lacquaniti and Maioli 1994a,b). However, the spatial orientation of this plane is completely different (roughly orthogonal) from that found in the passive experiments of Bosco et al. (1996). Moreover, abnormal somesthesic stimuli applied to the trunk of intact cats result in a substantial tilt of the plane of angular covariation (Lacquaniti and Maioli 1994a). In sum, the bulk of these studies in both anesthetized and intact cats indicate that planar constraints may be determined by biomechanical factors, but that the plane parameters may be tuned by neural factors.
This interpretation probably also holds true for the present findings. Nonlinear interaction terms play a very significant role in driving the passive motion of a multijointed limb (Hollerbach and Flash 1982). However, a linear interjoint coupling may result from the visco-elastic properties of the biarticular muscles (e.g., the ilio-psosas, rectus femoris, hamstrings, and gastrocnemius) that are modulated actively during locomotion (Basmajian and De Luca 1985; Nilsson et al. 1985; Pedotti 1977; Winter 1991). Also, it has been shown that motion-dependent feedback can be effective in offsetting the effect of the interaction torques (Smith and Zernicke 1987). The idea that a planar law of coordinative control may result from a minimal active tuning of the passive inertial and visco-elastic coupling among limb segments is congruent with the idea that gait has evolved according to optimization criteria (Alexander 1989).

Neural substrates of the kinematic laws

The neural substrates involved in the generation and control of the described laws of intersegmental coordination cannot be identified at this stage. Nevertheless, tentative links can be established with data from animal preparations and simulation studies. In several animal species, locomotion is controlled by central pattern generating networks (CPGs) located in the spinal cord and under the continuous influence of several peripheral and supraspinal signals (cf. Grillner 1981; Pearson 1993; Rossignol 1996). Thus the lamprey swimming CPGs have been worked out in detail (Grillner et al. 1991). A chain of segmental oscillators generates the undulatory gait of this species. Each oscillator is a local subnetwork of neurons that produces rhythmic patterns of membrane potentials, giving rise to alternating sequences of activation in the various segmental muscles. The general pattern is a constant speed wave with phase-lags between adjacent oscillators. The system can be reduced to one in which all of the original physical variables are determined by the behavior of the phases of the set of oscillators (Kopell 1995). Speed increments correspond to phase changes. The anatomic organization of CPGs is not so clearly established in higher vertebrates, but the functional concept applies in a similar manner. Thus a network of coupled oscillators has been proposed for the control of multisegment motion in bipeds (Bay and Hemami 1987). Each oscillator controls the movement of a single segment. Changing the interoscillator coupling generates speed changes and gait transitions. In sum, despite the lack of sufficient data on the network organization, current views on CPGs are compatible with the idea that a law of intersegmental coordination, such as the planar law we have described, may emerge from the dynamic interaction of segmental oscillators between each other and with limb mechanics. Phase would be one natural control variable in this scheme (a collective variable in the terminology of synergetics) (see Schöner et al 1990). We noted above how phase changes correspond closely to the rotation of the plane of intersegmental coordination. Plane rotation could depend on tonic or phasic modulatory actions from supraspinal centers (such as the mesencephalic locomotor region, basal ganglia, cerebellum, or motor cortex).

A distinctive aspect of the kinematic laws considered so far for gait (in addition to the present data, see also Borghese et al. 1996; Mah et al. 1994; Shen and Poppele 1995) is that they apply to the absolute angles of elevation of each segment with respect to the direction of gravity and that of forward progression but do not apply to the anatomic angles of flexion-extension at the individual joints. Although the existence and location of neural structures that may encode these parameters still remains to be determined, there is growing evidence that whole-limb parameters involving multijointed coordination are represented in both premotor (Bizzi et al. 1991) and proprioceptive sensory areas of the spinal cord (Bosco et al. 1996) as well as somatosensory and motor cortices (Helms Tillery et al. 1996; Lacquaniti et al. 1995; Scott and Kalaska 1997). In particular, the activity of both ventral and dorsal spinocerebellar (DSCT) neurons is modulated rhythmically with the different phases of fictive locomotion (Arshavsky et al. 1983). These neurons send to the cerebellum an effenter copy from spinal locomotor networks and afferent information from the moving leg. The integrative role played by DSCT neurons in encoding whole-limb parameters has been uncovered recently by Bosco, Poppele, and co-workers in anesthetized cats (Bosco and Poppele 1993, 1996; Bosco et al. 1996). Thus these neurons encode linear combinations of the limb elevation angles during static changes in limb geometry, without necessarily reflecting the passive covariance of the joint angles summarized above (Bosco et al. 1996). Moreover, the directional tuning of these neurons changes in time in a highly specific manner in response to dynamic changes in limb posture (Bosco and Poppele 1996). These authors have proposed (Bosco and Poppele 1996) “that the DSCT responses to perturbations may reveal a utilization at the spinal level of a coordinate system that is similar to that deduced from the behavioral studies. Moreover, this coordinate representation of proprioceptive sensory information would have the proper form to provide the basis for segmental feedback that may be essential for the fine tuning of motor strategies to control limb geometry.” On the basis of data from intact cat locomotion, Smith and Zernicke (1987) also have suggested that motion-dependent feedback can be effective in monitoring changes in limb dynamics, and thus spinal pattern generators do not need to precompute compensatory muscle responses to interaction forces.

The planar law of angular covariation involves the absolute angles of elevation of each segment with respect to the direction of gravity. Vestibulospinal and reticulospinal tracts, which project extensively onto the spinal locomotor centers, encode postural responses of the limbs in a gravity-based, head-centered frame (Bolton et al. 1992; Boyle and Pompeiano 1981; Wilson 1991). The head normally is stabilized in space during normal posture and locomotion and provides an inertial platform for monitoring gravity direction (Pozzo et al. 1990).

Functional significance of the kinematic laws

Although the general characteristics of human locomotion appear fairly stereotyped across subjects, there exist nevertheless qualitative and quantitative features that make everyone’s style unmistakably recognizable, so that the individual posture and locomotion have been defined as the signature traced by the body (Thomas 1940). Indeed, we found both
stereotypical and idiosyncratic features in the individual expression of the kinematic laws of intersegmental coordination: the changes of elevation angles are constrained by a plane in all subjects, but the plane orientation may differ among subjects.

The determinants of gait are most likely multifactorial. The specific walking style adopted by an individual represents a complex Gestalt the significance of which encompasses both the mechanical requirements of gait (such as equilibrium, forward progression, speed, and energy) as well as the expressive and emotional aspects of life. Here we focused on one particular aspect, namely on the relationship between the individual patterns of kinematic coordination and the corresponding expenditure of the net mechanical energy. We found that, at moderate and fast speeds, some subjects expend much less energy than others. Intersubject variability in energy usage needs to be qualified, however. It could depend on intrinsic individual variance, based on gait characteristics that are determined epigenetically or evolve with training and fitness. This hypothesis is supported by the finding that most trained subjects of the present population ranked low in terms of energy usage. In addition, however, variability could arise due to the subjective interpretation of the task. Because endurance was not especially emphasized in our protocols (experiments usually lasted <30 min.), it is quite possible that some subjects did attempt to minimize energy expenditure, whereas others simply did not care to do so.

Irrespective of its basis, the experimental variance proved instrumental for revealing the correlation between kinematics and energy expenditure. We found a systematic correlation, at both a global level and an individual level, between the parameters of the planar law of angular covariation and the net power output. Globally, the progressive rotation of the plane with increasing speed is associated with a reduction of the corresponding increment of the net mechanical power that would occur if the plane orientation remained fixed at the value characteristic of low speeds. Moreover, the specific orientation of the plane at any given speed is not the same in all subjects, but there is an orderly shift from the energy-saving subjects to the less economical ones. There are some important details to be added to this general picture. The net mechanical power varies little at low speeds and increases curvilinearly with increasing speed. In parallel, the net power is essentially independent of the plane orientation at low speeds and becomes highly correlated with it above ~1.2 m s⁻¹. However, the specific value of the plane orientation at low speeds, which is variable across subjects, appears to determine the rate of the plane rotation that is necessary to save energy at higher speeds. Indeed, the region of high energy expenditure at high speeds is avoided by means of a faster rate of plane rotation in those subjects in which the plane is less tilted at low speeds. This mechanism of compensation is not perfect, however, so that the power output at intermediate and high speeds is correlated significantly with the orientation of the plane across subjects: the greater is the plane tilt, the smaller the net power expended.

The correlation between kinematics and energy expenditure leads us to suggest that the specific tuning of the law of planar covariation can be used by the nervous system also for limiting energy expenditure, for instance, to maximize endurance or simply to walk in a smooth and effortless manner. As for the possible mechanisms involved in saving energy, the following considerations are in order. The kinematic laws we have described involve the coordination of the motion of the limbs segments among each other, on the one hand, and with the motion of the trunk, on the other hand. Because the df of angular motion in the sagittal plane are reduced to two by the planar constraint, they match the corresponding df of linear motion (horizontal and vertical translation) of the center of body mass (which lies in the trunk, the heaviest body segment). In locomotion, therefore, the control of limb segments rotations is tantamount to a control of the position of the center of body mass, as is also the case for the postural sway of the body in response to perturbations of the support base (Lacquaniti and Maioli 1994a,b; Massion 1992). The control of the center of body mass is instrumental for conserving the mechanical energy of the body by converting the kinetic and the potential energy into each other during the gait cycle (Cavagna and Kaneko 1977; Cavagna and Margaria 1966; Winter 1979). In addition, the law of intersegmental coordination probably contributes to the other main mechanisms of energy conservation, namely to the energy transfer between the lower limbs and the trunk and to that between limb segments (Caldwell and Forrester 1992; Cappozzo et al. 1976; Martin and Cavanagh 1990; Mochon and McMahon 1980; Pandy and Zajac 1991; Prilutsky and Zatsiorsky 1994; Robertson and Winter 1980).

The idea that the dynamic coupling between segments can be exploited to save mechanical energy is congruent with previous reports on both locomotion (Williams and Cavanagh 1983), as well as other forms of motor behavior. Thus the role of dynamic coupling for limb coordination has been previously emphasized (Hasan 1991; Hollerbach and Flash 1982; Koshland et al. 1991; Smith and Zernicke 1987; Soechting and Lacquaniti 1981), and an improved utilization of interjoint dynamics has been reported during the practice of rapid arm movements (Schneider et al. 1989). It also has been shown that proprioception is important in controlling and optimizing the effect of interaction forces during multi-jointed movements (Hasan and Stuart 1988; Sainburg et al. 1993; Smith and Zernicke 1987).

A correlation between kinematics and energetics has been found previously in other forms of motor behavior. Thus Soechting et al. (1995) have shown that the specific geometric configuration of the arm in 3-D space at the end of pointing movements is selected among the many possible alternatives according to the criterion of the minimum mechanical work that must be done to transport the arm from the starting point to the end point. Also, Fung and Macpherson (1995) have shown that the preferred posture in cats tends to minimize the sum of squared joint torques, and thus the overall energy expenditure.

Although kinematics plays an important role in determining the power output during locomotion, kinetic parameters, such as the patterns of ground reaction forces and musculoskeletal forces, also are involved in energy control (Alexander 1989; Fung and Macpherson 1995; Pedotti et al. 1978). Pedotti et al. (1978) could reproduce the time course of muscle activity during human locomotion by minimizing a performance criterion related to the total muscular force summed over all limb joints. Also, Alexander (1980)
showed that minimization of positive work is associated with specific values of the duty factor and of the patterns of the ground reaction forces. Farley and Taylor (1991) argued that the transition between different gait modes in horses is triggered when the peak vertical force exceeds a critical value. It remains to be elucidated whether or not the kinematic control is independent of the kinetic control in locomotion (Jacobs and Macpherson 1996; Lacquaniti and Maioli 1994). For instance, Winter (1991) has shown the existence of a specific tradeoff between the hip and knee torques during gait. This implies a law of kinetic covariance, in addition to the kinematic covariance on which we have focused.

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