Erratum

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In the on-line version of this paper, an error appears in equation 6 (p. 3800). The correct version of the equation is as follows:

$$R_{\alpha\beta}(\Delta) = \frac{\int \alpha(t) \cdot \beta(t+\Delta)\mathrm{d}t}{\sqrt{\int \alpha^2(t)\mathrm{d}t \cdot \int \beta^2(t)\mathrm{d}t}} \ , \qquad (6)$$

In addition, in the on-line version, the first sentence of the second paragraph of the subsection 'Relation with speed' in the Results (p. 3805) should read:

Fig. 5A shows the *R vs Fr* function for our toddlers at the first unsupported steps, 1–5 months later, for children older than 2 years of age, and for adults.

The print version of the article is correct.

We apologise to authors and readers for any inconvenience these errors may have caused.

Development of pendulum mechanism and kinematic coordination from the first unsupported steps in toddlers

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Summary

The inverted pendulum model in which the centre of mass of the body vaults over the stance leg in an arc represents a basic mechanism of bipedal walking. Is the pendulum mechanism innate, or is it learnt through walking experience? We studied eight toddlers (about 1 year old) at their first unsupported steps, 18 older children (1.3–13 years old), and ten adults. Two infants were also tested repeatedly over a period of 4 months before the onset of independent walking. Pendulum mechanism was quantified from the kinematics of the greater trochanter, correlation between kinetic and gravitational potential energy of the centre of body mass obtained from the force plate recordings, and percentage of recovery of mechanical energy. In toddlers, these parameters deviated significantly ($P<10^{-5}$) from those of older children and adults, indicating that the pendulum mechanism is not implemented at the onset of unsupported locomotion. Normalising the speed with the Froude number showed that the percentage of recovery of mechanical energy in children older than 2 years was roughly similar to that of the adults (less than 5% difference), in agreement with previous results. By contrast, the percentage of recovery in toddlers was much lower (by about 50%). Pendulum-like behaviour and fixed coupling of the angular motion of the lower limb segments rapidly co-evolved toward mature values within a few months of independent walking experience. Independent walking experience acts as a functional trigger of the developmental changes, as shown by the observation that gait parameters remained unchanged until the age of the first unsupported steps, and then rapidly matured after that age. The findings suggest that the pendulum mechanism is not an inevitable mechanical consequence of a system of linked segments, but requires active neural control and an appropriate pattern of inter-segmental coordination.

Key words: locomotion, gravity, pendulum, child.

Introduction

Spatiotemporal dynamics of normal walking in human adults is governed by general principles, including mechanisms of propulsion, stability, kinematic coordination and mechanical energy exchange (Alexander, 1989; Capaday, 2002; Dietz, 2002; Lacquaniti et al., 1999; Poppele and Bosco, 2003; Saibene and Minetti, 2003; Vaughan, 2003; Winter, 1991). One basic mechanism of walking is represented by the inverted pendulum model in which the centre of mass (COM) of the body vaults over the stance leg in an arc (Cavagna et al., 1963, 1976). Kinetic energy in the first half of the stance phase is transformed into gravitational potential energy, which is partially recovered as the COM falls forward and downward in the second half of the stance phase. Recovery of mechanical energy by the pendulum mechanism depends on speed, amounting to a maximum of about 65% around the natural preferred speed (Cavagna et al., 1976).

The principle of dynamic similarity states that geometrically similar bodies that rely on pendulum-like mechanics of movement have similar gait dynamics at the same Froude number, i.e. all lengths, times and forces scale by the same factors (Alexander, 1989). The Froude number (Fr) is given by $Fr=V^2g^{-1}L^{-1}$, where V is the average speed of locomotion, g the acceleration of gravity, and L the leg length. Fr is directly proportional to the ratio between the kinetic energy and the gravitational potential energy needed during movement. Dynamic similarity implies that the recovery of mechanical energy in subjects of short height, such as children (Cavagna et al., 1983; Schepens et al., 2004), Pygmies (Minetti et al., 1994) and dwarfs (Minetti et al., 2000), is not different from that of normal sized adults at the same Fr. No overt violations of the pendulum mechanism have been reported so far for legged walking on land. It has been demonstrated not only in

humans, but also in a wide variety of animals that differ in body size, shape, mass, leg number, posture or skeleton type, including monkeys, kangaroos, dogs, birds, lizards, frogs, crabs and cockroaches (Ahn et al., 2004; Alexander, 1989; Dickinson et al., 2000; Farley and Ko, 1997; Goslow et al., 1981; Heglund et al., 1982).

The pendulum mechanism might arise from the coupling of neural oscillators with mechanical oscillators, muscle contraction intervening sparsely to re-excite the intrinsic oscillations of the system when energy is lost. But is the pendulum mechanism an innate property of the interaction between the motor patterns and the physical properties of the environment? Or is it acquired with walking experience in the developing child? Previous studies have demonstrated conclusively that the mechanics of walking of children 2–12 years old, in particular the pendular recovery of energy at each step, is very similar to that of the adults when the walking speed is normalised with the Froude number (Bastien et al., 2003; Cavagna et al., 1983; Schepens et al., 2004), though in younger children (from 2 weeks to 6 months after the onset of independent walking) the mechanical energy exchange occurs to a lesser degree (Hallemans et al., 2004). However, to the best of our knowledge, the pendulum mechanism has not been investigated in toddlers who are just beginning independent, unsupported locomotion, roughly around 1 year of age. At that time, toddlers are faced with the novel task of transporting their body in the upright position against full gravitational load. If the pendulum mechanism were an innate property, one would expect to discover it at the onset of unsupported locomotion.

Here we studied walking mechanics in toddlers at their first unsupported steps and in older children (overall age range, 1–13 years). We report that the pendulum mechanism is not implemented by newly walking toddlers, but it develops over the first few months of independent locomotion along with the inter-segmental kinematic coordination. Thus we argue that the pendulum mechanism is not innate, but is learnt through walking experience.

Materials and methods

Subjects

Twenty-six healthy children (13 females and 13 males), 11–153 months of age, and 10 healthy adults [5 females and 5 males, 28±7 (mean ± S.D.) years old] participated in this study. Informed consent was obtained from all the adults and from the parents of the children. The procedures were approved by the ethics committee of the Santa Lucia Institute and of the University Children Hospital Queen Fabiola, and conformed with the Declaration of Helsinki. The specific laboratory setting and the experimental procedures were adapted to the children so as to result in absent or minimal risk, equal or lower to that of walking at home. Both a parent and an experimenter were always beside the younger children to prevent them from falling. We recorded the very first unsupported steps of eight toddlers (five females and three males), who started to walk at 11, 11, 12.5, 13, 14, 14.5, 14.5 and 15 months, respectively.

Daily recording sessions were programmed around the parents' expectation of the very first day of independent walking, until unsupported locomotion was recorded. When we succeeded in recording this event, the same child was recorded again in order to follow the early maturation of the walking cycle pattern. Supported steps of two of these toddlers (1 male and 1 female) were also recorded between 1.5 and 4 months before the onset of unsupported walking. The other 18 children spanned the range of 0.5–141 months of unsupported walking experience. Information about the age at which each child started independent locomotion was provided by the parents.

Walking conditions

For the recording of the very first steps, one parent initially held the child by hand. Then, the parent started to move forward, leaving the child's hand and encouraging her/him to walk unsupported on the floor. For each subject, about ten trials were recorded under similar conditions. Children generally performed 2–3 steps on the force platform in each trial. They were encouraged to look straightforward and to walk as naturally as possible. Short trials (up to 3 min, depending on endurance and tolerance) were recorded with rest breaks in between. The mean walking speed in toddlers was 1.4±0.7 km h^{-1} (mean ± S.D.). Adult subjects were asked to walk at a natural, freely chosen speed (on average it was 3.8±0.4 km h^{-1}), and in additional trials at faster speeds (7.3±0.8 km h^{-1}) and lower speeds (2.4±0.8 km h^{-1}).

Two infants were recorded between 1.5 and 4 months before the onset of unsupported walking while they walked firmly supported by the hand of one of their parents.

Data recording

Kinematics of locomotion (Fig. 1A) was recorded at 100 Hz by means of either the ELITE (BTS, Milan, Italy) or the VICON (Oxford, UK) motion analysis systems. The position of selected points was recorded by attaching passive infrared reflective markers (diameter 1.5 cm or 1.4 cm, for the ELITE and the VICON, respectively) to the skin overlying the following bony landmarks on the right side of the body (Fig. 1A): gleno-humeral joint (GH), the tubercle of the anterosuperior iliac crest (IL), greater trochanter (GT), lateral femur epicondyle (LE), lateral malleolus (LM), and fifth metatarso-phalangeal joint (VM). In half of the children we measured kinematics bilaterally (with the VICON system).

In children and at low speeds in adults, the ground reaction forces (GRFs; F_x, F_y and F_z) under both feet (Fig. 1C) were recorded at 1000 Hz by a force platform (0.9 m×0.6 m; Kistler 9287B, Zurich, Switzerland). At natural, higher speeds in adults, the GRFs under each foot were recorded separately by means of two force platforms (0.6 m×0.4 m; Kistler 9281B), placed at the centre of the walkway, spaced by 0.2 m between each other in both the longitudinal and the lateral directions. Because of the longitudinal spacing between the two platforms, the left foot could step onto the first platform and the right foot could step onto the second platform. The lateral spacing between the platforms ensured that one foot only stepped on
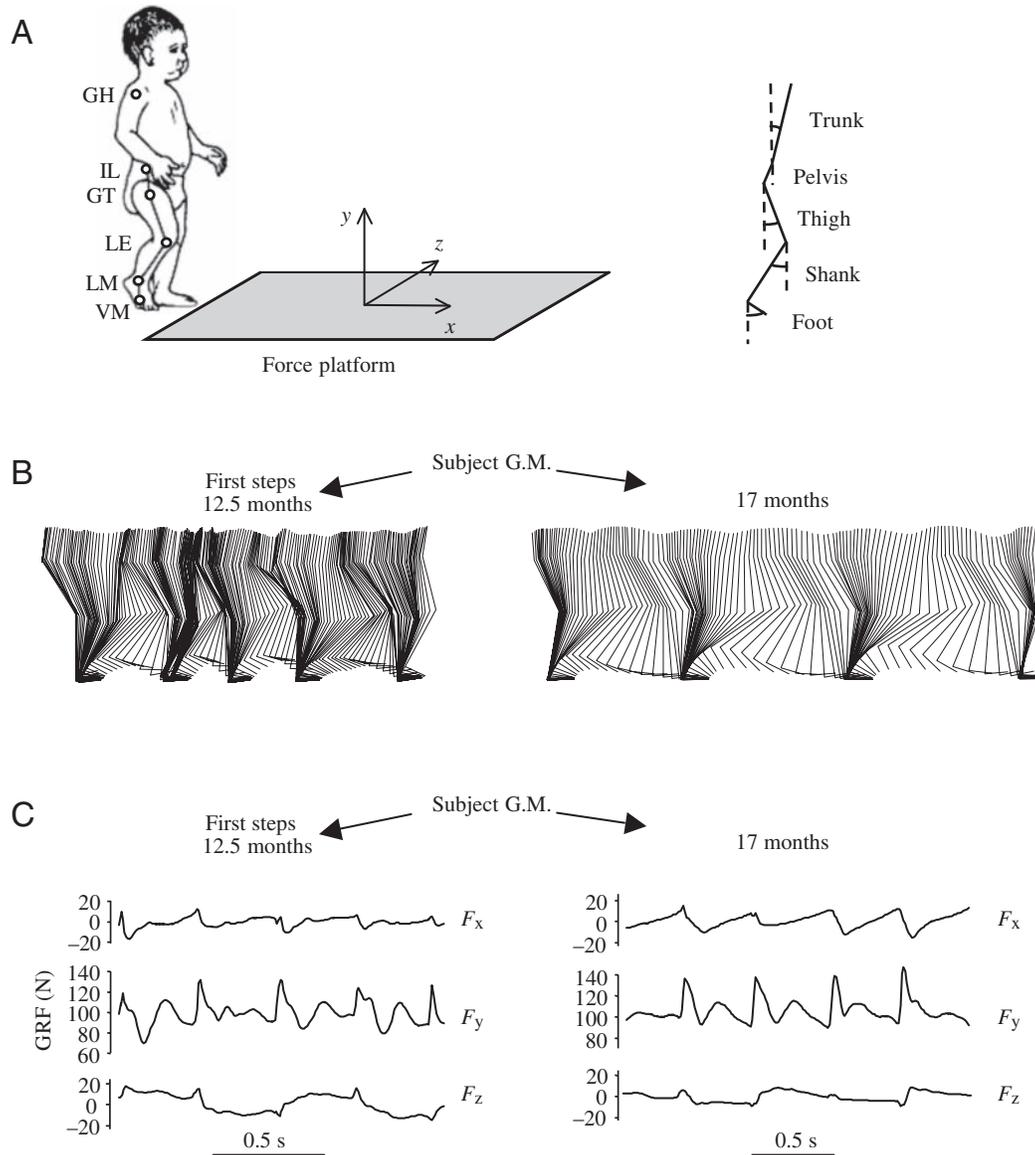
Fig. 1. Kinematic and kinetic recordings. (A) Experimental setup. Kinematic data were measured by monitoring markers on the gleno-humeral joint (GH), ilium (IL), greater trochanter (GT), lateral femur epicondyle (LE), lateral malleolus (LM), and fifth metatarso-phalangeal joint (VM). Trunk, pelvis, thigh, shank and foot are the limb segments identified by these markers. Elevation angles were computed relative to the vertical. Ground reaction forces were measured by force platforms along x,y,z axes. (B) Sagittal stick diagrams and (C) force platform measurements at two stages of early walking in the same child (subject G.M.): at 12.5 months (first independent steps), and at 17 months.

each of them. Sampling of kinematic and kinetic data was synchronized.

At the end of the recording session, anthropometric measurements were taken on each subject. These included the mass (m) and stature of the subject, the length and circumference of the main segments of the body (17 segments, according to the procedure of Schneider and Zernicke 1992).

Data analysis

Systematic deviations of gait trajectory relative to the x-direction of the recording system were corrected by rotating the x, z axes by the angle of drift computed between start and end of the trajectory. In the following, we will denote the variables in the forward direction with the subscript f, in the lateral direction with the subscript l and in the vertical direction with the subscript v. The body was modelled 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 (Fig. 1A). The main limb axis was defined as GT–LM. The elevation angle of each segment (including the limb axis) corresponds to the angle between the segment projected on the sagittal plane and the vertical (positive in the forward direction, i.e. when the distal marker falls anterior to the proximal one). In addition to the absolute

elevation angles, the relative angles of flexion–extension between two adjacent limb segments were also computed. The abduction angle corresponds to the angle between the segment projected on the frontal plane and the vertical (positive in the lateral direction). Walking speed was measured by computing the mean velocity of the horizontal IL marker movement. The length of the lower limb (L) was measured as thigh (GT–LE) plus shank (LE–LM) length.

Gait cycle duration was defined as the time interval T between two successive maxima of the elevation angle of the main limb axis of the same limb, and stance phase as the time interval between the maximum and minimum values of the same angle (Borghese et al., 1996). Thus, a gait cycle (stride) referred to a cyclic movement of one leg, and equalled two steps. When subjects stepped on the force platforms, these kinematic criteria were verified by comparison with foot strike and lift-off measured from the changes of the vertical force around a fixed threshold. In general, the difference between the time events measured from kinematics and the same events measured from kinetics was less than 3%. However, the kinematic criterion sometimes produced a significant error in the identification of stance onset in toddlers, due to an unusual forward foot overshoot at the end of swing (since the trajectory of the foot differed from that of adults: sometimes the toe reached its maximal height in front of the body and then the foot just hit the ground; see Forssberg, 1985). In such cases, foot contact was determined using a relative amplitude criterion for the vertical displacement of the VM marker (when it elevated by 7% of the limb length from the floor). In all experiments data from each gait cycle were time interpolated to fit a normalized 200-points time base.

Inter-segmental coordination

The inter-segmental coordination was evaluated in position space as previously described (Borghese et al., 1996; Bianchi et al., 1998a). In adults, the temporal changes of the elevation angles at the thigh, shank and foot covary during walking. When these angles are plotted one *vs* the others in a 3-D graph, they describe a path that can be fitted (in the least-square sense) by a plane over each gait cycle. Here, we studied the development of the gait loop and its associated plane in children. To this end, we computed the covariance matrix of the ensemble of time-varying elevation angles (after subtraction of their mean value) over each gait cycle. The three eigenvectors $\mathbf{u_1}$–$\mathbf{u_3}$, 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 $\mathbf{u_1}$, $\mathbf{u_2}$, lie on the best-fitting plane of angular covariation. The third eigenvector ($\mathbf{u_3}$) is the normal to the plane and defines the plane orientation. For each eigenvector, the parameters u_{it}, u_{is} and u_{if} correspond to the direction cosines with the positive semi-axis of the thigh, shank and foot angular coordinates, respectively. The orientation of the covariation plane in each child was compared both across all steps and with the mean orientation of the corresponding plane of all the adults.

Kinetic and potential energies of the COM in the sagittal plane

To compare our data with those previously obtained in children by Cavagna et al. (1983) and Schepens et al. (2004), we used a similar method to compute the changes of the instantaneous kinetic and potential energies of the COM from the force platform data. The vertical (F_v) and forward (F_f) components of the ground reaction forces (Fig. 1C) were used to calculate the vertical (a_v) and forward (a_f) acceleration of the COM, respectively:

$$F_f = ma_f \tag{1}$$

and

$$F_v - P = ma_v , \tag{2}$$

where m is the body mass and P is the body weight ($m\mathbf{g}$).

Equations 1 and 2 were integrated digitally in order to obtain the changes in the vertical (V_v) and forward (V_f) velocity of the COM:

$$V_f = \frac{1}{m} \cdot \int F_f \, dt + c \tag{3}$$

$$V_v = \frac{1}{m} \cdot \int (F_v - P) dt + c , \tag{4}$$

where c is a constant.

The integration constants were found by calculating the mean speed of the IL marker over the analysed stride on the assumption that this parameter is equal to the mean speed of the COM; this is reasonable since the location of the ilium marker is close to the COM and the displacements of the COM within the body are small. The mean vertical velocity (integration constant) was taken equal to zero on the assumption that upward and downwards vertical displacements are equal.

Equation 4 was integrated to obtain the vertical displacement of the COM (h):

$$h = \int V_v dt + c . \tag{5}$$

The integration constant is arbitrary and was taken equal to 0. The instantaneous potential energy (E_p) was calculated as $E_p = mgh$. The instantaneous kinetic energy (E_k) of the COM was calculated as $E_k = \frac{1}{2}mV_f^2 + \frac{1}{2}mV_v^2$. Environmental forces other than gravity (such as air resistance) can be neglected in low speed locomotion (Cavagna and Kaneko, 1977), and were not considered here. The cross-correlation function ($R_{\alpha\beta}$) between E_k and E_p waveforms was computed to quantify their phase shift ϕ by means of the following formula:

$$R_{\alpha\beta}(\Delta) = \frac{\int x(t) \cdot y(t + \Delta) dt}{\sqrt{\int \alpha^2(t) dt \cdot \int \beta^2(t) dt}} , \tag{6}$$

where α and β are the two waveforms (after subtraction of the respective means) and Δ is the time lag between the two signals. The numerator corresponds to the power of the common signal in α and β, and it is scaled to the product of total signal power (i.e. the autocovariance at 0 lag, the

denominator) so that the cross-correlation ranges from –1 to 1. A peak detection algorithm was used to determine the lowest (negative) correlation peak and its corresponding time lag ϕ. By convention, positive ϕ values indicate a lead of E_k waveform relative to E_p waveform, whereas negative values indicate a lag. Phase shift ϕ was expressed in percent of gait cycle.

Positive external work and recovery of mechanical energy

The total mechanical energy of the COM (E_{ext}) was the sum of E_k and E_p waveforms over a stride. The positive external work (W_{ext}) was the sum of the increments in E_{ext} over a stride (Cavagna et al., 1976). Similarly W_v and W_f were the positive vertical and forward works, respectively, obtained by the summation, over a stride, of all the increases in vertical ($mgh+\frac{1}{2}mV_v^2$) and forward ($\frac{1}{2}mV_f^2$) energies of the COM. To minimise errors due to noise, the increments in mechanical energy were considered to represent positive work actually done only if the time between two successive maxima was greater than 20 ms. For older children and adults, the records of E_k and E_p do not extend to the whole cycle. Therefore, we replaced a missing initial double support phase at the beginning of stance using the data from the double-support phase at the end of stance under the assumption of a symmetrical gait in older children and adults.

To estimate the ability to save mechanical energy, we used the percentage of recovery R (Cavagna et al., 1976):

$$R = \left(\frac{W_v + W_f - W_{ext}}{W_v + W_f} \right) \times 100 . \qquad (7)$$

Energy analysis in the frontal plane

The classical analysis of the inverted pendulum only involves sagittal components of body motion (Cavagna et al., 1976, 1983; Saibene and Minetti, 2003). In normal adults, it has been shown that the lateral component of kinetic energy of the COM is essentially negligible compared with the sagittal components (Tesio et al., 1998). In toddlers, however, the contribution of the lateral component might be higher due to postural instability in the frontal plane. Therefore, in addition to the measurements in the sagittal plane, we also computed the changes in total mechanical energy of COM including lateral E_k (Tesio et al., 1998), $E_p+\frac{1}{2}mV_f^2+\frac{1}{2}mV_v^2+\frac{1}{2}mV_l^2$, where V_l is the instantaneous velocity in the lateral direction. The mean lateral velocity (integration constant) was taken equal to zero on the assumption that left and right lateral displacements are equal. This is reasonable since systematic deviations of gait trajectory relative to the x-direction of the recording system and ground reaction forces (x and z) were corrected by rotating the x,z axes by the angle of drift computed between start and end of the trajectory. The percentage of recovery of total mechanical energy of COM (R_1) was computed as:

$$R_1 = \left(\frac{W_v + W_f + W_l - W_{ext}}{W_v + W_f + W_l} \right) \times 100 , \qquad (8)$$

where W_l (positive lateral work) was obtained by summing (over a stride) all the increases of lateral mechanical energy ($\frac{1}{2}mV_l^2$).

Positive internal work due to segment movements relative to COM

Here the methods were similar to those used by Willems et al. (1995). Mass (m_i), position of the centre of mass ($\mathbf{r_i}$), and moment of inertia (I_i) in the sagittal plane of each body segment i were derived using measured kinematics, anthropometric data taken on each subject (see above), and regression equations proposed by Schneider and Zernicke (1992) for infants less than 2 years, Jensen (1986) for older children, and Zatsiorsky et al. (1990) for adults. Seven body segments were included in the analysis of internal work: HAT (head, arms and trunk), thigh, shank and foot of right and left lower limbs. We computed the angular velocity (ω_i) of each segment and the translational velocity ($\mathbf{v_i}$) of its centre of mass relative to COM. COM position was derived as:

$$\text{COM} = \frac{\sum\limits_i^n m_i \cdot \vec{\mathbf{r_i}}}{\sum\limits_i^n m_i} . \qquad (9)$$

The kinetic energy of each segment ($E_{k,i}$) due to its translation relative to COM and its rotation was then computed as the sum of its translational and rotational energy: $E_{k,i}=\frac{1}{2}m_i\mathbf{v_i}^2+\frac{1}{2}I_i\omega_i^2$. The kinetic energy *vs* time curves of the segments in each limb were summed. The internal work due to the movements of the limbs and HAT was then calculated by adding the increments in their kinetic energy waveforms. As before, the increments in kinetic energy were considered to represent positive work actually done only if the time between two successive maxima was greater than 20 ms. Net internal work (W_{int}) was finally estimated as the sum of internal work for each limb and for the HAT. This procedure allowed energy transfers between segments of the same limb, but disallowed any energy transfers between different limbs and trunk (Schepens et al., 2004; Willems et al., 1995).

We could not measure the internal work made by one leg against the other during double contact (Bastien et al., 2003), because infants stepped on one platform only. However, this work contributes less than 10% of total power spent during walking both in adults and children (Schepens et al., 2004). Also, the internal mechanical work done for stretching the series elastic components of the muscles during isometric contractions, to overcome antagonistic co-contractions, viscosity and friction, cannot be directly measured.

Age-related changes

The time course of changes of kinematic and kinetic parameters as a function of age was fitted by an exponential function: $y=-a\cdot e^{-t/\tau}+b$, where y was the specific parameter under investigation, t was the time since onset of unsupported walking, τ was the time constant, and a, b, two constants. To avoid an unrealistic fit due to the dispersion of data

corresponding to the very firsts steps in toddlers, data were fitted using the mean value at $t=0$.

Statistics

Statistical analysis (Student's unpaired t-tests and analysis of variance, ANOVA) was used when appropriate. Reported results are considered significant for $P<0.05$. Statistics on correlation coefficients was performed on the normally distributed, Z-transformed values. Spherical statistics on directional data (Mardia, 1972) were used to characterize the mean orientation of the normal to the covariation plane (see above) and its variability across steps. To assess the variability, we calculated the angular standard deviation (called spherical angular dispersion) of the normal to the plane.

Results

Hip kinematics

In walking adults, the hip vaults over the stance leg as an inverted pendulum (Fig. 2A). Both hips are simultaneously lifted during mid-stance of the load-bearing leg, twice in each gait cycle. As a result, we found two peaks in the temporal profile of vertical hip position (GT_y and IL_y) over each gait cycle, in coincidence with mid-stance of the right and left leg, respectively (Fig. 2B, rightmost panel). The amplitude of these two peaks was similar, indicating comparable bilateral lift of the hip. Fourier series expansion of GT_y revealed a clear dominance of the second harmonic (Fig. 2C). The percent of GT_y variance explained was $13\pm7\%$ (mean ± S.D., $N=10$) and $80\pm7\%$ for the first and second harmonic, respectively. In
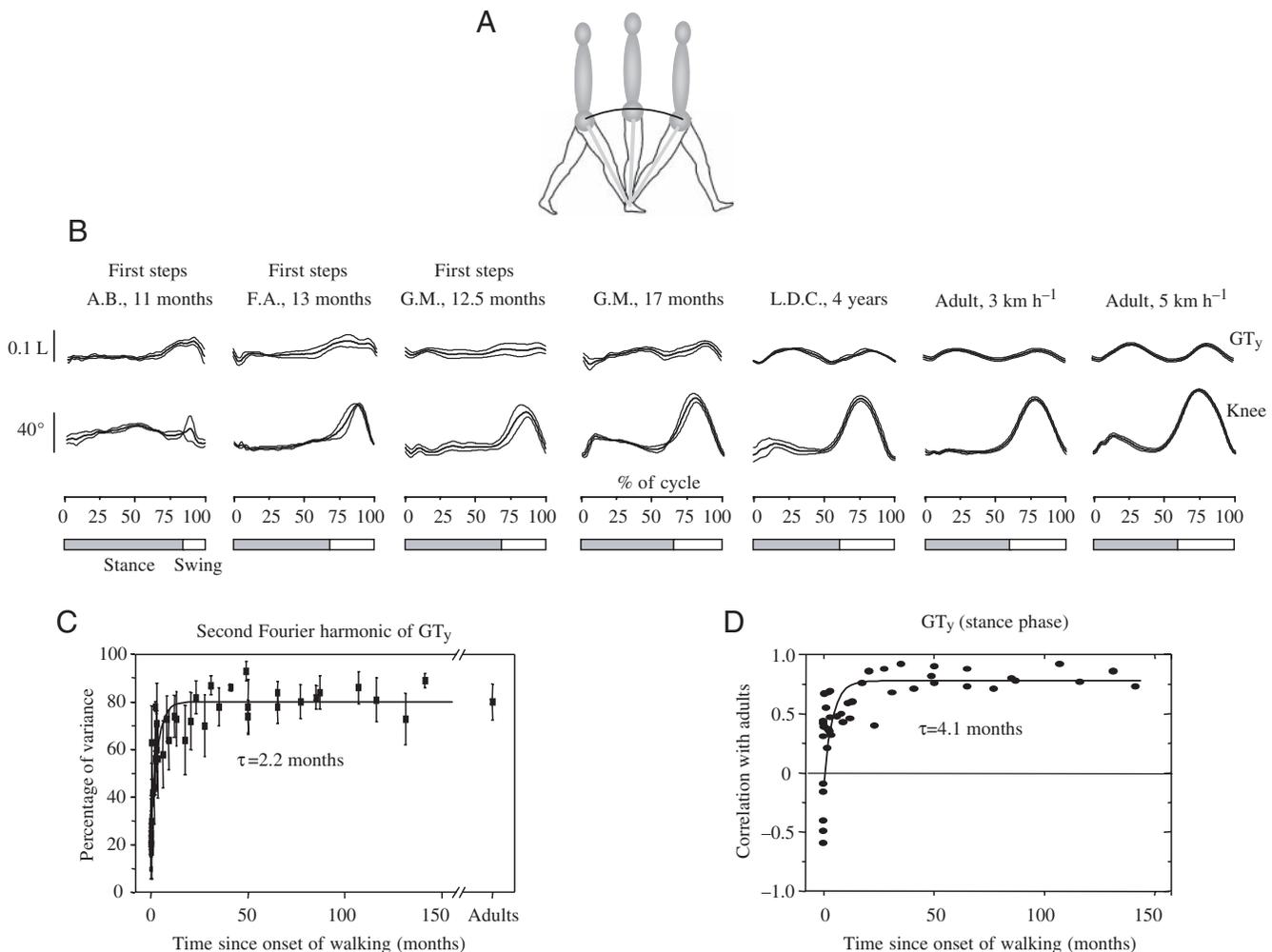

Fig. 2. Kinematics of the pendulum mechanism. (A) Schematic representation of the inverted pendulum: the hip vaults over the stance limb. (B) Ensemble averages (± S.D., $N=5$ steps) of vertical hip displacement (GT_y) and knee joint angle in children of different age, and in a representative adult walking at two different speeds (right panels). Data are plotted vs the normalised gait cycle. Each record begins with the right foot strike. GT_y is expressed in relative units (normalised by the limb length L). (C) Percent of variance (± S.D.) of GT_y data explained by the second Fourier harmonic is plotted as a function of the time after the onset of independent walking. The values for the adult group were obtained by computing the mean (± S.D.) from the pooled data obtained for walking at natural, freely chosen speed (on average, 3.8 ± 0.4 km h^{-1}). (D) Correlation coefficient between GT_y data in children and the corresponding ensemble average in adults during stance. For both C and D, the time course of changes with age was fitted by an exponential function ($r=0.93$ and 0.87 in C and D, respectively). τ, the corresponding time constant.

theory, the leg could be kept rigid in the inverted pendulum by locking the knee joint during stance (Fig. 2A). We found that the changes of knee joint angle were small at low speeds, but became appreciable at higher speeds (>3 km h^{-1}, Fig. 2B). The peak-to-peak GT$_y$ amplitude also increased monotonically with speed, being 0.023±0.003L (mean ± S.D., N=10) at 1 km h^{-1}, 0.033±0.005L at 3 km h^{-1}, 0.050±0.007L at 5 km h^{-1}, and 0.068±0.014L at 7 km h^{-1}.

In toddlers at the onset of unsupported locomotion, GT$_y$ oscillations were more variable from step to step than in adults. Their mean profile systematically differed from that of the adults (Fig. 2B, leftmost panels). Thus, the first peak in GT$_y$ of the adults (corresponding to the stance phase of the ipsilateral leg) was absent in toddlers even though the knee joint was often locked during stance (Fig. 2B, subjects F.A. and G.M.). Instead, the GT$_y$ peak corresponding to the second peak of the adults was generally present in toddlers and reflected a lift of the hip joint during swing relative to the contralateral hip joint of the load-bearing leg. This observation was confirmed during bilateral kinematic recordings and it also applied to the IL markers; therefore, it cannot depend on a misplacement of the GT marker relative to the centre of joint rotation. In toddlers, the percent of GT$_y$ variance explained was 56±9% (mean ± S.D., N=8) and 22±4% for the first and second harmonic, respectively, indicating a dominance of the first harmonic, in contrast with the dominance of the second harmonic in adults. The hip of the swinging limb was raised by a few centimetres above the hip of the contralateral load-bearing limb. Bilateral coordination of the two hip joints in toddlers, therefore, differs markedly from that of walking adults, and instead is reminiscent of that observed for stepping in place in adults. A few months after the onset of unsupported locomotion, the first peak of GT$_y$ at mid-stance became recognizable and was fully developed in older children (see central panels in Fig. 2B).

Age-related changes of kinematic parameters related to the pendulum mechanism are presented in Fig. 2C,D for the whole population of subjects. Both the power of the second harmonic of GT$_y$ (Fig. 2C) and the correlation coefficient between GT$_y$ in children and GT$_y$ in adults (Fig. 2D) were low at the onset of unsupported walking and increased rapidly afterwards. Changes with age were fitted by an exponential function (see Materials and methods). The time constant was fast both for the changes of the second harmonic (τ=2.2 months) and for the correlation with the ensemble average in adults (τ=4.1 months).

Mechanical energy

The pendulum mechanism has both kinematic and kinetic consequences for walking (Alexander, 1989; Cavagna et al., 1976). We computed the changes of mechanical energy of COM from force platform recordings (see Materials and methods). In adults (Fig. 3B,C, rightmost panel), kinetic energy (E_k) tends to fluctuate out of phase with gravitational potential energy (E_p) and with vertical hip displacements. Between touch-down and mid-stance, the forward velocity of the COM decreases as the trunk arcs upwards over the stance foot. In this phase, E_k is converted to E_p. During the second half of the stance phase, the COM moves downwards as the forward velocity of the COM increases. In this phase, E_p is converted back into E_k. Energy exchange by the inverted pendulum mechanism reduces the mechanical work required from the
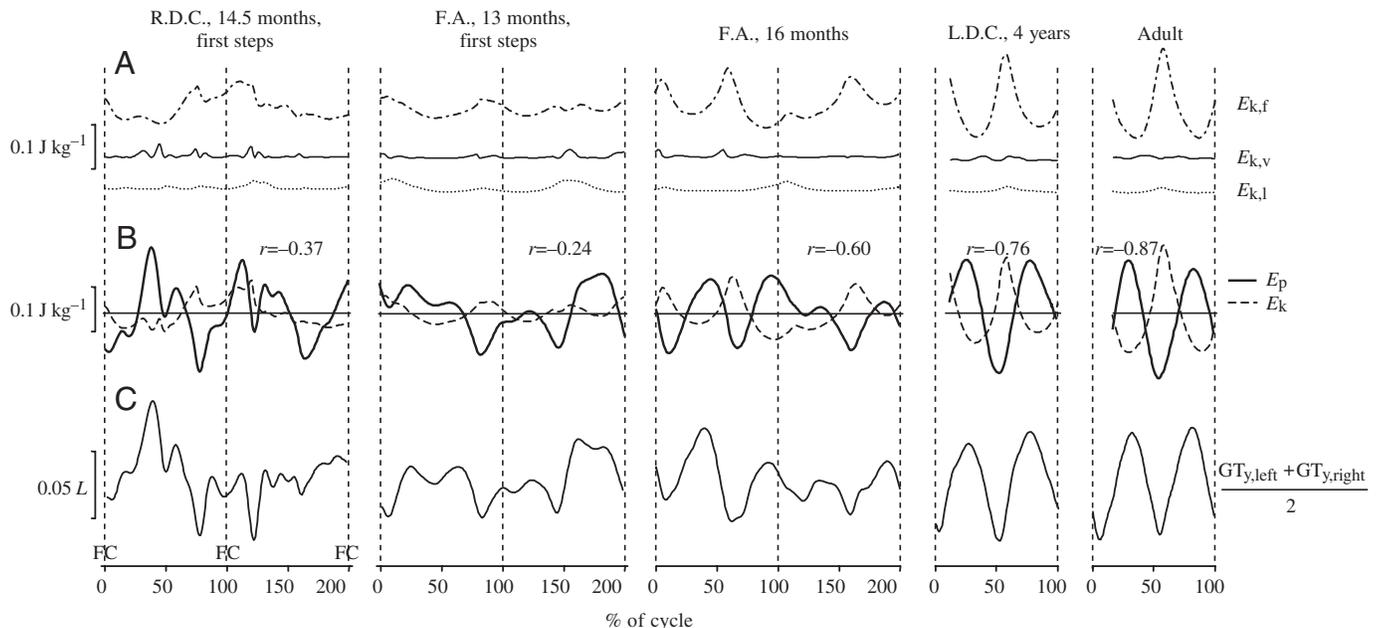

Fig. 3. Changes of vertical hip displacement (GT$_{y,left}$+GT$_{y,right}$)/2 (C), gravitational potential energy (E_p) (B) and kinetic energy (E_k) (A,B) of COM during walking in children of different age, and in a representative adult. The upper three traces show the forward ($E_{k,f}$), vertical ($E_{k,v}$) and lateral ($E_{k,l}$) kinetic energies of COM. E_k (B) refers to the kinetic energy in the sagittal plane (sum of $E_{k,f}$ and $E_{k,v}$) that we used to characterize the classic pendulum behaviour in the sagittal plane. Dotted vertical lines correspond to foot contact (FC) of one leg. For older children and adults, the recordings of E_k and E_p do not extend to the whole cycle. Correlation coefficient between E_p and E_k is indicated for each trial.

muscular system by an amount that depends on walking speed (Cavagna et al., 1976). Positive work is necessary to push forward the COM during early and late stance, to complete the vertical lift during mid-stance, and to swing the limbs forward.

At the onset of unsupported locomotion, all toddlers failed to demonstrate a prominent energy transfer (Fig. 3B, leftmost panels). In general, the changes of E_p and E_k were very irregular, with a variable phase relation between each other. Peak-to-peak changes of E_k were often smaller than the corresponding changes of E_p (in part due to a low walking speed). A few weeks following the onset of unsupported locomotion, children started to display a clear pendulum-like exchange of E_p and E_k in each step (central panels in Fig. 3B).

To quantify this energy exchange over each step, we computed the correlation coefficient r between E_k and E_p waveforms, their phase shift ϕ, the percentage of energy recovery R (Equation 7), and the external work W_{ext} performed per unit distance and unit mass (Fig. 4A–D). In an ideal pendulum, E_k changes are exactly equal and opposite to E_p changes: thus $r=-1$, $\phi=0\%$, $R=100\%$ and $W_{ext}=0$. In our sample of adults walking at natural speed (3.8 ± 0.4 km h^{-1}), we found: $r=-0.85\pm0.05$, $\phi=1.0\pm1.7\%$, $R=64\pm4\%$ and $W_{ext}=0.32\pm0.04$ J kg^{-1} m^{-1}. In toddlers at the onset of unsupported locomotion (1.4 ± 0.7 km h^{-1}), instead, we found: $r=-0.39\pm0.15$, $\phi=-2.2\pm8.5\%$, $R=28\pm7\%$, and $W_{ext}=0.97\pm0.20$ J kg^{-1} m^{-1}. The mean values of these parameters in toddlers were significantly ($P<10^{-5}$, Student's unpaired t-test) different from those in adults, except for ϕ values. ϕ values exhibited a very large step-by-step variability

in toddlers: the mean S.D. of ϕ values computed over all steps in each toddler was $27.5\pm6.2\%$, whereas it was $1.8\pm0.9\%$ in adults. Percentage of energy recovery R computed from Equation 7 only includes the components in the sagittal plane. We also computed R_1 from Equation 8, including lateral components. The relative amplitude of changes in the kinetic energy in the lateral direction (Fig. 3A) was somewhat higher in the toddlers ($31\pm10\%$ of total kinetic energy oscillations) than in the adults ($6\pm3\%$), likely due to a higher instability in the lateral direction and/or a wider step width (Assaiante et al., 1993; Bril and Brenière, 1993). The values of the energy recovery R_1 were $65\pm4\%$, and $36\pm4\%$ in adults and toddlers, respectively. Also the internal work W_{int} performed per unit distance and unit mass was significantly ($P<10^{-5}$) higher in toddlers (0.74 ± 0.09 J kg^{-1} m^{-1}) than in adults (0.27 ± 0.06 J kg^{-1} m^{-1}) walking at natural speed (1.4 ± 0.7 km h^{-1} in toddlers, 3.8 ± 0.4 km h^{-1} in adults).

Age-related changes of parameters related to energy exchange are presented in Fig. 4A–D for the whole population of subjects. They were fitted by exponential functions with fast time constants (2.3–5.1 months, Fig. 4A,C,D), closely comparable to those computed for the changes of kinematic parameters (Fig. 2B,C). The changes of W_{int} (J kg^{-1} m^{-1}) also were well fitted by an exponential (Fig. 4E, time constant of 2.8 months).

Relation with speed

In principle, the low recovery of mechanical energy of COM in toddlers could be due to their low height and low gait speed. It is known that at a given speed the net mass-specific mechanical work of locomotion is greater the smaller the
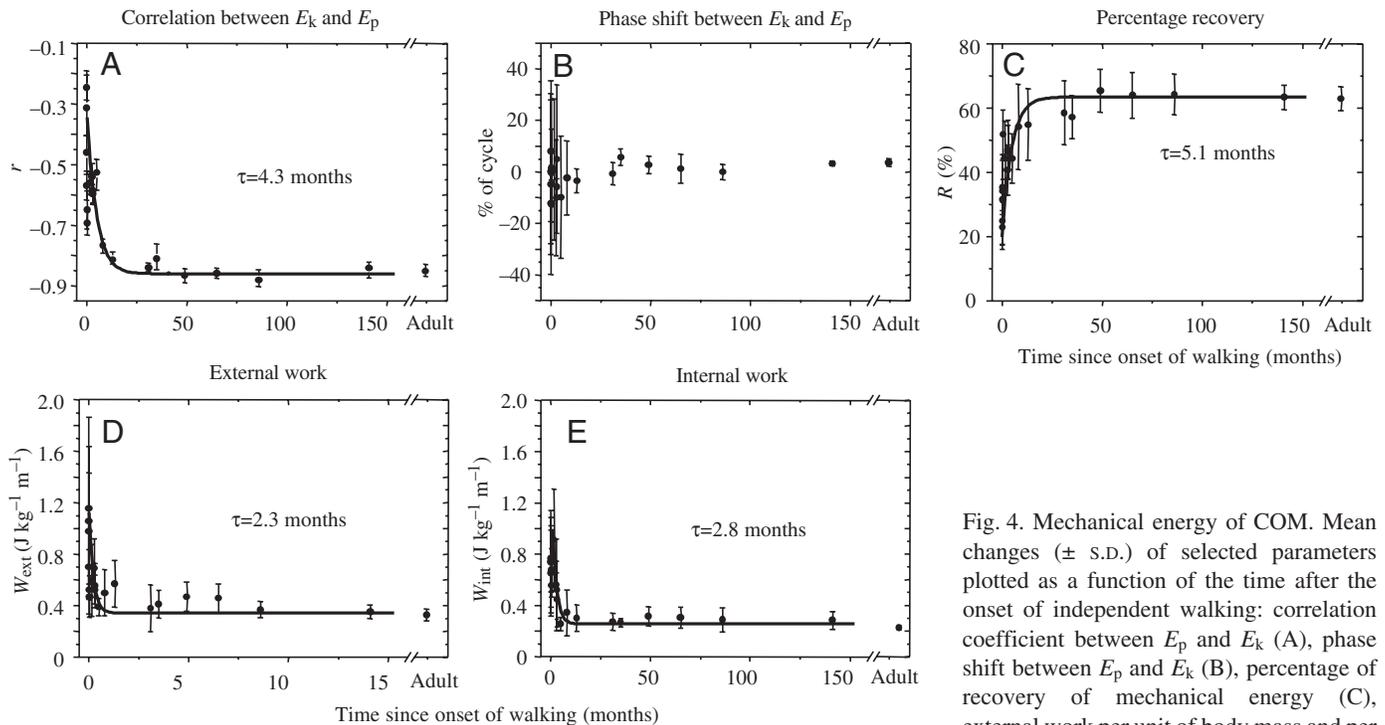

Fig. 4. Mechanical energy of COM. Mean changes ($\pm$ S.D.) of selected parameters plotted as a function of the time after the onset of independent walking: correlation coefficient between E_p and E_k (A), phase shift between E_p and E_k (B), percentage of recovery of mechanical energy (C), external work per unit of body mass and per unit distance (W_{ext}; D) and internal work per unit of body mass and per unit distance (W_{int}; E). The time course of changes with age was fitted by an exponential function ($r=0.93$, 0.89, 0.87 and 0.92 for A, C, D and E, respectively). Data refer to walking at natural speed.

height of the subject, and the slower the speed of locomotion (Alexander, 1989; Cavagna et al., 1983; Saibene and Minetti, 2003). The Froude number (*Fr*) is a dimension-less parameter suitable for the comparison of locomotion in subjects of different size walking at different speed (Alexander, 1989). Subjects with a dynamically similar locomotion are expected to output comparable values of mechanical power when walking with the same *Fr*. Thus, children between 2 and 12 years of age (Cavagna et al., 1983; Schepens et al., 2004), adult Pygmies (Minetti et al., 1994) and dwarfs (Minetti et al., 2000) have the same percentage of recovery *R* (Equation 7) of mechanical energy as normal-sized adults when they walk at the same *Fr* value. Typically, *R* peaks at ≈65% at *Fr* ≈0.3, and falls off at lower and higher *Fr* values (see fig. 10 in Saibene and Minetti, 2003).

Fig. 5A shows the *R vs Fr* function for our toddlers at the first unsupported steps, 1–5 months later, for children older than 2 years of age, and for adults (the data of children after the onset of independent locomotion, younger than 2 years of age are not shown). Adults walked at speeds that covered a wide range of *Fr* values, yielding an *R vs Fr* function comparable to published data (Saibene and Minetti, 2003). In general, the data points of older children roughly overlapped those of the adults, in agreement with previous results (Cavagna et al., 1983; Schepens et al., 2004). However, on average *R* values of children were slightly but significantly lower than those of the adults. Over the 0.07–0.42 range of *Fr* values, *R* was 62±7% in children and 65±4% in adults. Two-factor ANOVA on *R* values over that range of *Fr* values (discretised in 5 intervals) revealed a significant effect of subject group (children versus adults, *P*<0.03), but no significant effect of *Fr* value (*P*=0.14) or interaction (*P*=0.31).

Toddlers at the first unsupported steps never walked faster than *Fr*=0.14. Their data points fell systematically below those of both older children and adults for comparable values of *Fr*.

Over the 0.07–0.14 range of *Fr* values, *R* was 35±8% in toddlers and 61±9% in older children (*P*<10⁻⁷). As for the comparison with the adults, we performed a two-factor ANOVA on *R* values of toddlers and adults for the 0.04–0.14 range of *Fr* values (discretized in 5 intervals), and found a significant effect of both *Fr* value (*P*<10⁻⁷) and subject group (toddler *vs* adult, *P*<10⁻⁷), as well as a significant interaction (*P*<0.0005) consistent with the lower slope of the *R vs Fr* function in toddlers than in adults (Fig. 5A).

As another index of energy exchange, we considered the values of the correlation coefficient *r* between E_k and E_p (see previous section) plotted *vs Fr* values (Fig. 5B). Once again, the data points of older children roughly overlapped those of the adults, whereas the data of toddlers were systematically different. Two-factor ANOVA on *r* values for the 0.04–0.14 range of *Fr* values showed a significant effect of subject group (toddler *vs* adults, *P*<10⁻⁶), but no significant effect of *Fr* value (*P*=0.89) or interaction (*P*=0.45).

It might be questioned how the equivalent speeds should be computed. Thus, the toddlers are not geometrically similar to the adults. The COM is located higher in the toddlers (approximately at the level of the sternum) than in the adults (approximately at the level of the ilium). Therefore, we verified whether the *R* values and the correlation coefficients between E_k and E_p would differ significantly in the toddlers and the adults after normalisation of the walking speed to the distance from supporting foot to COM rather than to the limb length. This procedure shifts the results for the toddlers and the adults towards lower *Fr* numbers. However, even following this normalization, the *R* values and the correlation coefficients *r* between E_k and E_p were significantly lower in the toddlers (*R*=28±7%, *r*=–0.39±0.15) than in the adults (*R*=54±10%, *r*=–0.81±0.17) over the 0.02–0.10 range of newly defined *Fr* values. In general in the paper we used the limb length normalisation since it is commonly accepted in the literature.
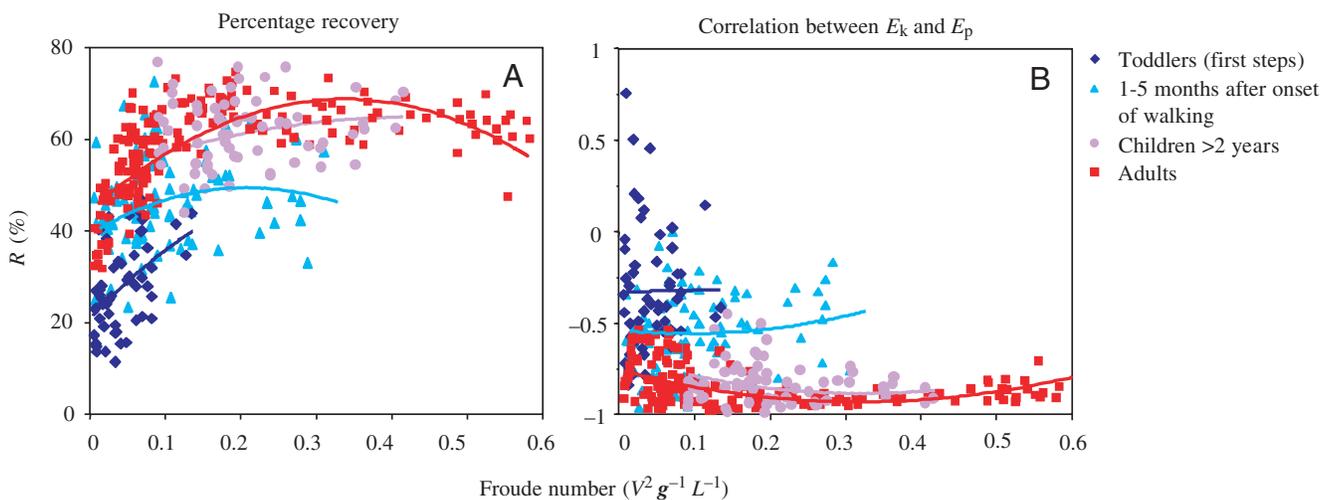

Fig. 5. Normalisation by the Froude number. Percentage of recovery of mechanical energy (A) and correlation coefficients between E_p and E_k (B) for toddlers at the first unsupported steps (blue), 1–5 months later (cyan), children older than 2 years of age (violet) and adults (red). Data points for individual steps are plotted as a function of Froude number ($Fr=V^2 \boldsymbol{g}^{-1}L^{-1}$, where *V* is the average speed of locomotion, $\boldsymbol{g}$ the acceleration of gravity, and *L* the lower limb length). Continuous lines represent second-order-polynomial fittings.

Both the normalised speed (Froude number), the correlation coefficient between E_k and E_p and energy recovery increased with age, but 1–5 months after the onset of independent walking they were still lower than these values in adults or in older children (Fig. 5). The recovery of mechanical energy for this age group (1–5 months after the onset of independent walking) was similar to that reported by Hallemans et al. (2004).

Inter-segmental coordination

The position of the COM in space and therefore the pendulum mechanism depend on the combined rotation of all lower limb segments. During walking, the thigh, shank and foot swing back and forth (Fig. 6A), and in so doing they carry the trunk along and shift the COM. In adults, the temporal changes of the elevation angles of lower limb segments co-vary along a plane, describing a characteristic loop over each stride (Fig. 6B). The gait loop and its associated plane depend on the amplitude and phase of the coupled harmonic oscillations of each limb segment (Bianchi et al., 1998a).

In toddlers, the gait loop departed significantly from planarity and the mature pattern. Planarity was quantified by the percentage of variance accounted for by the third eigenvector (PV_3) of the data covariance matrix (Fig. 6C): the closer PV_3 is to 0, the smaller the deviation from planarity. PV_3 was significantly higher in toddlers ($4.3\pm3.5\%$) than in adults ($0.8\pm0.3\%$, $P<0.001$ Student's unpaired t-test), in agreement with our previous findings (Cheron et al., 2001a,b). Also, because the amplitude of thigh movement was relatively higher with respect to that of shank and foot movements in toddlers, the gait loop was less elongated than in adults, as shown by the smaller contribution of the first eigenvector (PV_1). In toddlers, $PV_1=73.2\pm7.0\%$ and $PV_2=22.5\pm6.8\%$; in adults, $PV_1=85.9\pm1.5\%$ and $PV_2=13.3\pm1.5\%$. There were no systematic deviations in the orientation of the plane: the mean normal to the plane in toddlers was similar to that of the adults, but the individual values of plane orientation varied widely among toddlers (Fig. 6D). Moreover, the step-by-step variability of plane orientation (estimated as the angular dispersion of the plane normal) was considerably higher in
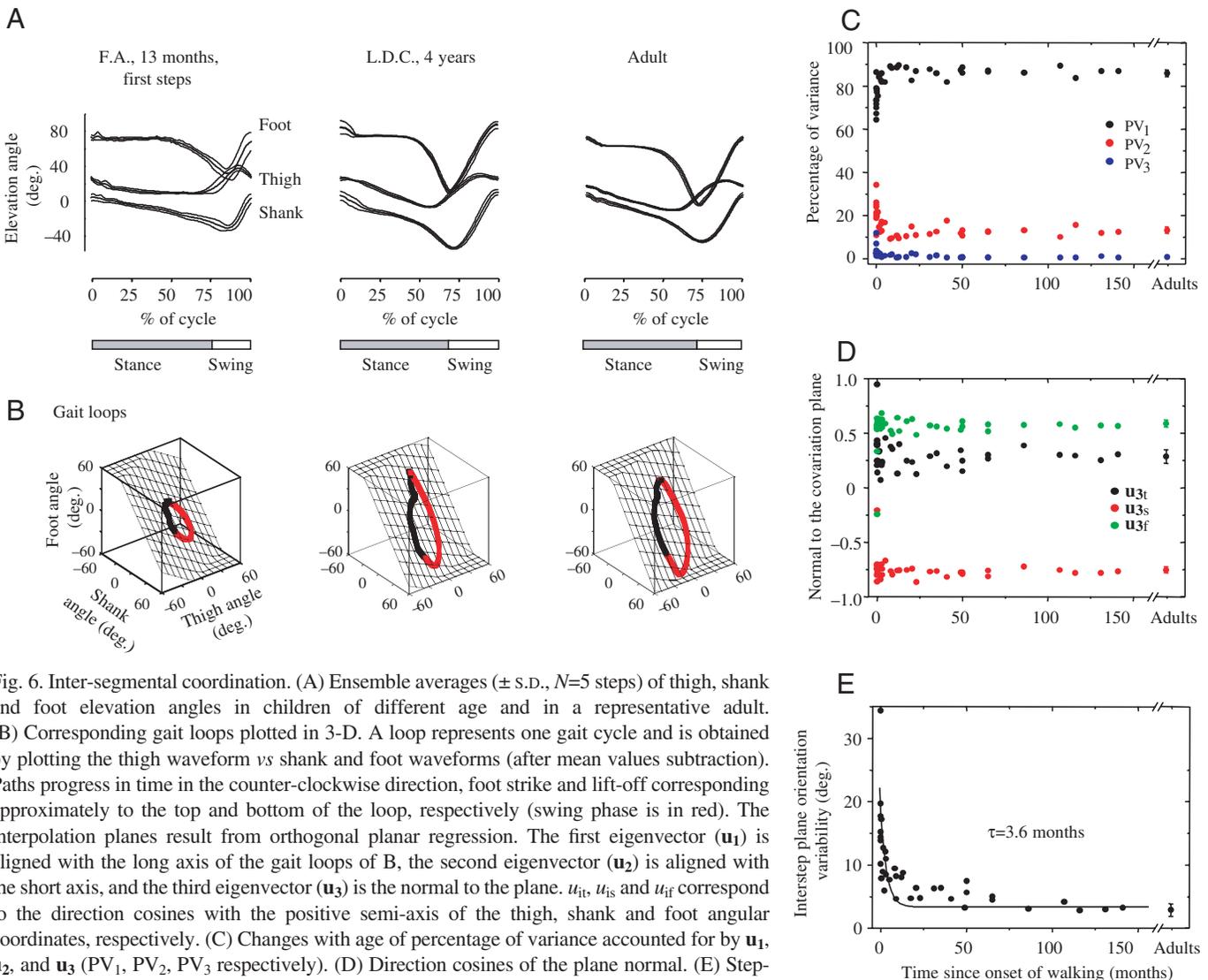
Fig. 6. Inter-segmental coordination. (A) Ensemble averages ($\pm$ S.D., N=5 steps) of thigh, shank and foot elevation angles in children of different age and in a representative adult. (B) Corresponding gait loops plotted in 3-D. A loop represents one gait cycle and is obtained by plotting the thigh waveform vs shank and foot waveforms (after mean values subtraction). Paths progress in time in the counter-clockwise direction, foot strike and lift-off corresponding approximately to the top and bottom of the loop, respectively (swing phase is in red). The interpolation planes result from orthogonal planar regression. The first eigenvector ($\mathbf{u_1}$) is aligned with the long axis of the gait loops of B, the second eigenvector ($\mathbf{u_2}$) is aligned with the short axis, and the third eigenvector ($\mathbf{u_3}$) is the normal to the plane. u_{it}, u_{is} and u_{if} correspond to the direction cosines with the positive semi-axis of the thigh, shank and foot angular coordinates, respectively. (C) Changes with age of percentage of variance accounted for by $\mathbf{u_1}$, $\mathbf{u_2}$, and $\mathbf{u_3}$ (PV_1, PV_2, PV_3 respectively). (D) Direction cosines of the plane normal. (E) Step-by-step variability of the plane normal (exponential fitting, r=0.91).

toddlers (18.0±8.1°) than in adults (2.9±1.0°, Fig. 6E), reflecting a high degree of instability in the phase relationship between the angular motion of different limb segments. When the data are compared across children at different ages, one notices that plane orientation stabilized rapidly after the onset unsupported locomotion. The time constant of the exponential function was 3.6 months.

An efficient pendulum mechanism also depends on inter-limb bilateral coordination in the direction of forward progression. When bilateral kinematic recording was available (see Materials and methods), we measured the phase shift between the maximum of the elevation angle of the main axis of left limb and the corresponding value of the right limb, expressed in percent of the gait cycle. Inter-limb phase should be 50% for symmetrical gait involving perfect inter-limb coordination. The measured phase was not significantly different from the ideal value either in toddlers (48.7±2.1%) or in adults (50.2±1.5%). However, toddlers exhibited a large step-by-step variability: the mean S.D. of phase values computed over all steps in each toddler was 6.7±3.9%, whereas it was 1.0±0.4% in adults (*P*<0.0005).

Toddlers also exhibited a greater amount of oscillations in the lateral direction (in the plane perpendicular to the direction of progression). The peak-to-peak amplitude of the adduction/abduction angle of the main axis of each limb over each stride was 14.9±3.5° in toddlers, as compared with 5.3±1.3° in adults (*P*<10^{-5}).

Behaviour before the onset of unsupported locomotion

Progressive changes of gait kinematics and kinetics as a function of child age presumably depend on the neural maturation of central pathways that are important for postural and locomotor control. In addition, however, walking experience under unsupported conditions might act as a functional trigger of gait maturation. These two developmental factors lead to predictable differences in the time course of changes of gait parameters. If anatomical maturation were the only dominant factor, one would expect monotonic changes of gait parameters beginning before and continuing through the age of the first unsupported steps. If, instead, walking experience under unsupported conditions acts as a functional trigger, one would expect that gait parameters remain more or less unchanged until the age of the first unsupported steps, and then rapidly mature after that age.

Evidence for the latter behaviour was observed in two infants who were tested repeatedly over a period between 4 months before and 13 months after the onset of independent walking (Fig. 7). The infants walked firmly supported by the hand of one of their parents before they could walk independently. In adults, hand support does not change gait parameters significantly, as shown in treadmill experiments where the subjects put their arms on the rollbars (Ivanenko et al., 2002). In infants, it could rather improve postural stability and gait kinematics. However, in all recording sessions performed before the onset of unsupported locomotion, both the pendulum-related pattern of vertical hip displacement and the pattern of inter-segmental coordination did not differ significantly from those recorded at the onset of unsupported locomotion. The percentage of variance accounted for by the second Fourier harmonic of the vertical GT displacement (denoting the double-peaked profile of pendular oscillations of COM, see Fig. 2B) exhibited inter-step variability but did not change systematically as a function of age up to the time of onset of unsupported locomotion, when it started to increase rapidly over the first few months of independent walking experience (compare Fig. 7A with Fig. 2C). A similar trend was exhibited by the step-by-step variability of plane orientation (compare Fig. 7B with Fig. 6E), and by the index of planarity (PV$_3$, not shown).

Discussion

In the present study we compared several kinematic and kinetic parameters related to the pendulum mechanism in children of different age and in adults. The results obtained for children 2–13 years old are in agreement with several previous studies (Bastien et al., 2003; Cavagna et al., 1983; Schepens et al., 2004). The pendular recovery of mechanical energy at each
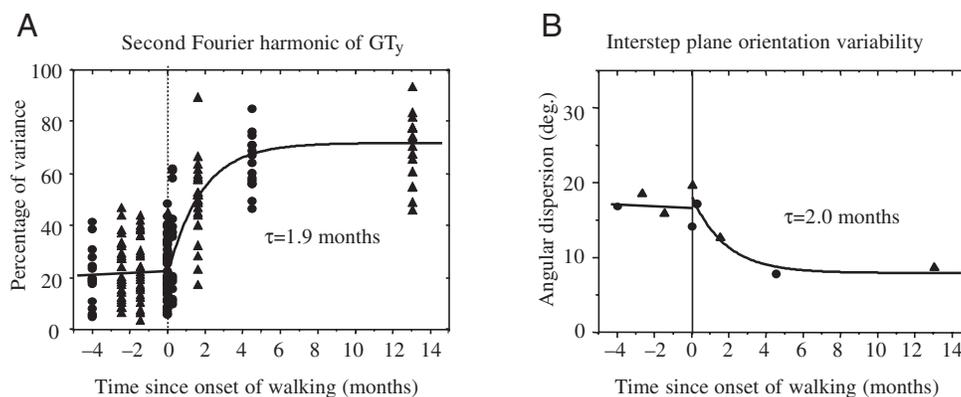

Fig. 7. Behaviour before and after the onset of independent walking. Percent of variance of GT$_y$ data explained by the second Fourier harmonic (A) and step-by-step variability of the plane normal (B) are plotted for experimental sessions performed at different times before and after the first unsupported steps. Triangles, subject R.D.C. data; circles, subject G.M. data.

step is roughly similar to that of the adults when the walking speed is normalised with the Froude number.

We report for the first time that toddlers at the onset of unsupported locomotion do not implement the pendulum mechanism. Thus the vertical oscillations of the hip lack the sinusoidal pattern at twice the frequency of the gait cycle that is observed in mature gait (Winter, 1991). A partial energy exchange may occur during some portions of the gait cycle (probably as a consequence of physics; see also Hallemans et al., 2004); however, the 'classic' inverted pendulum behaviour of a stance limb is lacking at the transition to independent walking (Figs 2, 3A) and develops within a few months of unsupported walking experience. Also, the changes of gravitational potential energy and forward kinetic energy of COM are very irregular, with a variable phase relation between each other. Normalising the speed with the Froude number showed that the percentage of recovery of mechanical energy in toddlers is systematically lower than in older children and adults (independent of whether normalisation was performed to the limb length or to the distance between foot and COM). The percentage of energy recovery was somewhat higher in toddlers when the lateral component was included, probably due to a greater amount of oscillations in the lateral direction and/or a wider step width; nonetheless, it remained significantly lower than in adults. Lack of pendulum may reflect a basic immaturity of the inter-segmental kinematic coordination.

Determinants of the pendulum mechanism

The finding that toddlers can organize spontaneous walking without using the pendulum mechanism demonstrates that it is not an inevitable mechanical consequence of a system of linked segments, cross-coupled by passive inertial and visco–elastic forces. Instead it must result from active neural control. What are the determinants of the pendulum mechanism? The simplest model of the inverted-pendulum for adult walking consists of a rigid rotation of the COM around a fixed contact point *via* a stiff supporting limb. This model has been shown to be incorrect (Lee and Farley, 1998). During stance, the contact point between foot and ground translates forward, and the supporting limb is compressed especially at higher speeds (Lee and Farley, 1998; Winter, 1991). The trajectory of the COM in space and the pendulum behaviour also depend on other kinematic parameters, such as the stance–limb touchdown angle (Lee and Farley, 1998).

The deceiving simplicity of the pendulum behaviour hides the inherent complexity of its neural control (Lacquaniti et al., 1999). The problem is that the COM has no anatomical or functional autonomy. It is a virtual point lying somewhere close to the ilium, but this location changes as a function of body posture, load carrying, and non-proportional growth of different body segments in childhood. There is no sensory apparatus that monitors COM position directly, and computing exactly how much work needs to be done for its motion may not be an easy task for the nervous system. However, neglecting possible deformations of the trunk, COM position depends on the combined rotation of body and limb segments.

Thus if the nervous system encodes a controlled pattern of covariation between segment rotations, the motion of COM would be specified implicitly. Such a kinematic covariance between limb and body segment rotations has been found in adult locomotion. The temporal changes of the elevation angles in the sagittal plane co-vary along a characteristic gait loop constrained on a plane (Borghese et al., 1996; Lacquaniti et al., 1999). (In a similar vein, a kinetic covariance has been demonstrated between limb joint torques; Winter, 1991). The specific shape and orientation of the planar gait loop accurately reflect COM trajectory and its modifications as a function of body posture (Grasso et al., 2000). In addition, the planar orientation changes systematically with increasing walking speeds (Bianchi et al., 1998a), and accurately predicts the net mechanical power output at each speed by both trained and untrained subjects (Bianchi et al., 1998b). Finally, the planar gait loops of left and right lower limbs are coupled (Courtine and Schieppati, 2004), as predicted by the 'ballistic walking' model proposed by Mochon and McMahon (1980), in which the swing limb behaves like a compound pendulum, coupled with inverted pendulum of the stance limb.

In toddlers at the first unsupported steps, pendulum-like behaviour of the COM, stable planar covariance of the angular motion of the lower limb segments, and bilateral coordination in both sagittal and frontal directions are not in place. A lack of the pendulum behaviour was also found in chicks (Muir et al., 1996): young chicks do not innately use their leg as a rigid strut during the first 2 weeks of life and need to acquire the ability to walk in an energy efficient manner. In toddlers, both the pendulum-like behaviour of the COM and the fixed planar covariance come into play soon after the onset of independent walking, and co-evolve toward mature values within a few months. Development of the pendulum and of the planar covariance have both energetic and stability consequences, since one of the benefits of pendular rhythmic movements is cycle-to-cycle stability and reproducibility (Goodman et al., 2000). The percentage of recovery of mechanical energy increases significantly with walking experience, in parallel with a decrease of the step-by-step variability of kinematic and kinetic parameters.

Role of walking experience in learning the pendulum mechanism

Walking mechanics depends on the interaction between feedforward motor patterns and neural feedback, on the one hand, and the physical properties of the body and the environment, on the other hand (Dickinson et al., 2000). The present findings and previous results in infants indicate that this interaction requires an active tuning of the motor commands through learning. Basic features of locomotor control are present several months before a child can walk independently (Forssberg, 1985). Thus, infants 1–12 months old can step (either spontaneously or on a treadmill) at a speed modulated by peripheral inputs, in different directions (forward, backward, sideways), and with bilateral coordinated behaviour in response to external perturbations (Lamb and Yang, 2000;

Pang and Yang, 2001; Yang et al., 1998). There is strong evidence that the spinal network of central pattern generators (CPGs) is already in place at birth, and is rapidly integrated with proprioceptive feedback to generate appropriate rhythmic patterns for locomotion (Forssberg, 1985; Yang et al., 1998). On the other hand, when children start to walk without support, several other features of locomotion are still immature, such as the stride fluency, head and trunk stability, amplitude of hip flexion and coordination of lower limb movements (Assaiante et al., 1993; Berger et al., 1984; Brenière and Bril, 1998; Bril and Brenière, 1993; Cheron et al., 2001a,b; Forssberg, 1985; Sutherland et al., 1980). Spinal and brainstem networks are thought to be integrated with supra-segmental control as automatic stepping evolves into walking. In particular, the transition to unsupported walking requires that the control of stepping is integrated with postural control. In human locomotion, this integration depends on motor cortical control much more heavily than it does in other mammals (Capaday, 2002; Dietz, 2002), and descending cortico-spinal tracts are not mature at the age of 1 year (Paus et al., 1999). It is conceivable that, while the spinal CPG units driving different limb segments are operational at birth, the phase coupling between different units may need to be tuned by descending supra-spinal signal during development.

Progressive changes of gait kinematics and kinetics as a function of child age depend on the neural maturation of central pathways that are important for postural and locomotor control, as result from myelination of descending tracts (Paus et al., 1999) and from improved cognitive capacity to generate different associations and to access memory rapidly, which may in turn permit the necessary integrative capacity for balance and coordination to occur (Zelazo, 1983). In addition, however, walking experience under unsupported conditions acts as a functional trigger of gait maturation. By repeatedly testing two infants over a period between 4 months before and 13 months after the onset of independent walking, we showed that gait parameters remained unchanged until independent walking, and then rapidly matured after that age. The role of walking experience is stressed by two other observations. (1) Infants undergoing daily stepping exercise exhibit an earlier onset of independent walk than untrained infants (Zelazo et al., 1972). (2) In normal untrained children, the rapid developmental changes are clearly recognized when plotted relative to the time after the onset of independent walking, but they are blurred when plotted relative to the time after birth, because of the variability of the age of independent walk (Sundermier et al., 2001; Yaguramaki and Kimura, 2002).

List of symbols

a_f	forward acceleration of the COM
a_v	vertical acceleration of the COM
COM	centre of mass of the body
CPG	central pattern generator
E_{ext}	total mechanical energy of the COM
E_k	kinetic energy of the COM
$E_{k,i}$	kinetic energy of the i-th segment
E_p	potential energy of the COM
F_f	longitudinal (forward) GRF
Fr	Froude number
F_v	vertical GRF
g	gravitational acceleration
GH	gleno-humaral joint
GRF	ground reaction force
GT	greater trochanter
h	vertical displacement of the COM
HAT	head-arms-trunk segment
I_i	moment of inertia of the i-th segment
IL	tubercle of the anterosuperior iliac crest
L	leg length (thigh+shank)
LE	lateral femur epicondyle
LM	lateral malleolus
m	body mass
m_i	mass of the i-th segment
P	body weight
PV_1, PV_2, PV_3	percentage of variance accounted for by the third eigenvector of the covariance matrix
r	correlation coefficient
$\mathbf{r_i}$	position of the centre of mass of the i-th segment
R	percentage recovery of mechanical energy in the sagittal plane through a pendular mechanism
R_1	percentage recovery of total mechanical energy through a pendular mechanism including the lateral component
$R_{\alpha\beta}$	cross correlation function
$\mathbf{u_1}, \mathbf{u_2}, \mathbf{u_3}$	three eigenvectors of the covariance matrix
u_{it}, u_{is}, u_{if}	direction cosines for each eigenvector with the positive semi-axis of the thigh, shank and foot angular coordinates, respectively
V	walking speed
V_f	forward velocity of the COM
v_i	translational velocity of the centre of mass of the i-th segment relative to the COM
V_l	velocity of the COM in the lateral direction
VM	fifth metatarso-phalangeal joint
V_v	vertical velocity of the COM
W_{ext}	external work
W_f	positive forward work
W_{int}	internal work required to accelerate the body segments relative to the COM
W_l	positive lateral work
W_v	positive vertical work
ϕ	phase shift between E_p and E_k
τ	time constant of an exponential fitting
Δ	time lag between the two signals
ω_i	angular velocity of the i-th segment

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