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RESEARCH ARTICLE

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# Development of a kinematic coordination pattern in toddler locomotion: planar covariation

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**Abstract** The purpose of this study is to analyze the coordination patterns of the elevation angles of lower limb segments following the onset of unsupported walking in children and to look for the existence of a planar covariation rule as previously described in adult human locomotion. The kinematic patterns of locomotion were recorded in 21 children (11–144 months of age) and 19 adults. In 4 children we monitored the very first unsupported steps. The extent to which the covariation of thigh, shank, and foot angles was constrained on a plane in 3D space was assessed by means of orthogonal regression and statistically quantified by means of principal component analysis. The orientation of the covariation plane of the children was compared with the mean value of the adults' plane. Trunk stability with respect to the vertical was assessed in both the frontal (roll) and sagittal (pitch) planes. The evolution with walking experience of the plane orientation and trunk oscillations demonstrated biexponential profiles with a relatively fast time constant (<6 months after the onset of unsupported locomotion) followed by a much slower progression toward adult values. The initial fast changes of these walking parameters did not parallel the slow, monotonic maturation of anthropometric parameters. The early emergence of the covariation plane orientation and its correlation with trunk vertical stability reflect the dynamic integration of postural equilibrium and forward propulsion in a gravity-centered frame. The results support the view that the planar covariation reflects a coordinated, centrally controlled behavior, in addition to biomechanical constraints. The refinement of the planar covariation while morphological variables drastically change as the child grows implies a continuous update of the neural command.

**Keywords** Toddlers · Children · Locomotion · Coordination · Kinematics

## Introduction

In order to organize normal locomotion, the human central nervous system must meet at least two requirements: (1) postural stability of the erect posture integrating the direction of gravity and (2) dynamic control of the body and limbs for forward progression. For the acquisition of the upright posture and walking, toddlers must find a compromise between these two aspects.

The ontogeny of postural control has been studied before independent sitting develops in children (Bertenthal and von Hofsten 1998; Bertenthal et al. 1997; Hadders-Algra et al. 1996a, b; Harbourne et al. 1993). Postural responses to optical flow stimulation can be recorded from the age of 5 months (Bertenthal et al. 1997). Direction-specific activation of the dorsal trunk muscles is present in 4- to 5-month-old infants, indicating an ability to use relevant afferent information for trunk stabilization with respect to gravity (Harbourne et al. 1993). However, at this age the patterns of response to postural challenge are extremely variable, involving different strategies that are progressively selected when approaching the age of 9–10 months (Hadders-Algra et al. 1996a, b). Moreover, prewalking children are able to stand up and maintain static equilibrium from about 10 months of age, even

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though they sway more than the adults (Zernicke et al. 1982).

The ontogeny of propulsive movements during supported stepping also has been studied thoroughly from the first days after birth up to the age of independent walking (Berger et al. 1984; Forssberg 1985, 1999; Forssberg and Wallberg, 1980; Lamb and Yang 2000; Thelen and Cooke 1987; Yang et al. 1998a, b). Infant stepping, either spontaneous or evoked on a treadmill, is modulated by speed changes and by external perturbations. It increases with training and can be elicited in different directions (forward, backward, sideways; see Lamb and Yang 2000). It differs markedly from more mature walking in that it shows synchronous flexion–extension at all limb joints, a high degree of co-contraction of antagonist muscles, and no heel strike at foot contact. Spinal and brain stem control has a dominant influence on infant stepping (Forssberg 1985; Yang et al. 1998a, b).

Segmental networks are thought to be integrated with supraspinal control as automatic stepping evolves into walking. In particular the transition to unsupported walking around the age of 1 year requires that the control of stepping is integrated with postural control. A number of studies have shown that when children start to walk without support, several features of locomotion are still immature, such as the step frequency and length, head and trunk stability, the amplitude of hip flexion, and the coordination of lower limb movements (Berger et al. 1984; Brenière and Bril 1998; Cioni et al. 1993; Clark and Phillips 1993; Forssberg 1985, 1999; Lasko-McCarthey et al. 1990; Ledebt et al. 1995; Leonard et al. 1991; Sutherland et al. 1980). Walking proficiency improves considerably during the first few months of unsupported locomotor experience; in particular, the step frequency and length increase, while the oscillations of the head and trunk decrease (see Forssberg 1999). However, detailed studies of the maturation of the patterns of kinematic coordination in unsupported locomotion and of the correlation between the limb kinematics and trunk stability are still lacking.

Our understanding of the emerging coordinative principles in toddlers may benefit from recent advances in the study of walking kinematics. Thus mathematical approaches, ranging from neuromodulation of coupled oscillators (Kopell 1995), to synergetics (Thelen and Smith 1996) 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 are constrained by neural control. As a result, limb dynamics would be confined to an attractor space of lower dimensionality than that of the original parameter space.

In adults, a series of experimental studies have provided detailed evidence for coordinative laws that lead to a reduction of kinematic degrees of freedom (Bianchi et al. 1998a, b; Borghese et al. 1996; Grasso et al. 1998, 1999, 2000; for a review, see Lacquaniti et al. 1999). The temporal waveform of the elevation angles of the lower limb segments (pelvis, thigh, shank, and foot) relative to the vertical is much more stereotypical across trials, speeds, and subjects than the corresponding waveform of either the joint angles (Borghese et al. 1996; Grasso et al. 1998) or the EMG patterns (Grasso et al. 1998, 2000). Moreover, the temporal changes of these elevation angles do not evolve independently of each other, but they are tightly coupled together (Borghese et al. 1996). When the elevation angles of the thigh, shank, and foot are plotted one versus the others, they describe a regular gait loop which lies close to a plane. The plane orientation and the shape of the loop reflect the phase relationship between the different segments and therefore the timing of intersegmental coordination (Bianchi et al. 1998b), on which postural stability with respect to gravity and dynamic equilibrium for forward progression depend. The plane orientation shifts in a predictable way with increasing speed of walking (Bianchi et al. 1998b) and with the walking posture adopted (Grasso et al. 2000). Moreover, it reliably correlates with the mechanical energy expenditure (Bianchi et al. 1998a, b).

The aim of the present study is to characterize the developmental emergence of the planar covariation in toddlers and children, and to correlate this with the development of postural stability as assessed in terms of trunk oscillations relative to the vertical. We hypothesize that the maturation of intersegmental coordination and that of postural stability of the trunk develop in parallel, given that the kinematic laws described in normal adults apply to the elevation angles relative to the gravity vector, and the postural control of trunk orientation also involves gravity information. We have examined a population of children spanning a wide range of ages (11–144 months). In a few toddlers we succeeded in recording the very first unsupported steps, that represent an early form of integration of propulsive and postural requirements. A preliminary communication of this work has appeared in abstract form (Bouillot et al. 1999).

## Materials and methods

### Subjects

Twenty-one healthy children (13 females and 8 males), 11–144 months of age and 19 healthy adults [9 females and 10 males, 25±4 (mean ± SD) years old] participated in this study. Informed consent was obtained from all the adults and from the parents for their children. The procedures were approved by the local ethics committee of the University Children Hospital Queen Fabiola and conformed with the Declaration of Helsinki. Special attention was given to recording the very first steps of some of the toddlers. Daily recording sessions were programmed around the parents' expectation of the very first day of walking until unsupported locomotion was recorded. When we succeeded in recording this event, the same infant was recorded again in order to follow the early maturation of the walking cycle pattern. This was done for 4 children, who started to walk at 11, 11, 13, and 14 months, respectively. The other 17 children spanned the range of 0.7–131 months of unsupported walking experience. The information about the age at which each child started independent locomotion was provided by the parents.

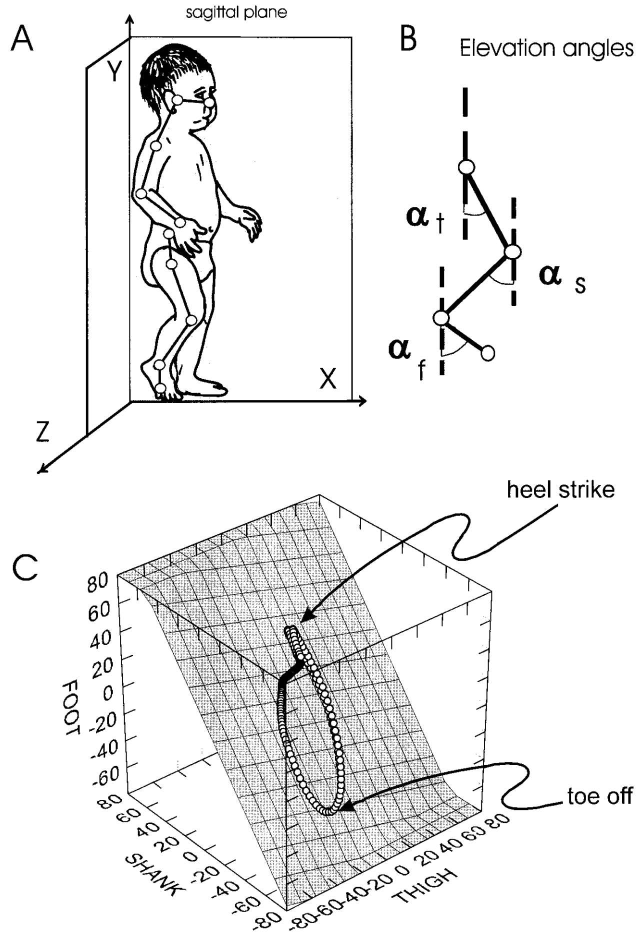

**Fig. 1A–C** Schematic illustration of the experimental setup. **A** Markers placed on the head, and right upper and lower limb, for monitoring by the optoelectronic system. The convention of the 3D coordinates is given by the *XYZ* axes. **B** Absolute angles of elevation of the thigh ($\alpha_t$), shank ($\alpha_s$), and foot ($\alpha_f$) with respect to the vertical indicated in the sagittal plane (XY). **C** 3D representation of the mature covariation of lower limb elevation angles during two consecutive gait cycles in a 12-year-old child, characterized by a quasi-elliptic loop progressing in the counterclockwise direction and lying on a plane (*grid*)

### Task and experimental set-up

For the recording of the very first steps, the toddlers were initially supported by the hand of one of their parents. Then, when the parent moved forward, letting go the child's hand, the child was encouraged to walk on the laboratory floor coated with a red band of linoleum (0.6 m wide and 8 m long). Toddlers were never supported during the actual recording of locomotion trials. For each subject, 10 to 15 trials were recorded in the same condition. Subjects were instructed to look straight forward and to walk as naturally as possible from one end of the ground band to the other end.

Kinematics of the locomotor movements were recorded and analyzed using the optoelectronic ELITE system (Ferrigno and Pedotti 1985). This system consists of two CCD cameras detecting retro-reflective markers using a sampling rate of 100 Hz. The cameras were placed on a line parallel to and 4 m away from the progression line of the subjects, 1 m above the floor, and 3 m apart. After calibration, two-dimensional data were corrected for optical distortion and converted to 3D coordinates according to Borghese et al. (1996). The position in space of ten passive markers, including nine links, was recorded. Spherical reflective markers (1.5 cm in diameter) were fastened on to the skin overlying the following bony landmarks (Fig. 1A): the nose at the horizontal extent of the lower border of the orbit, the meatus of the ear, the acromial process, the lateral condyle of the elbow, the styloid process of the wrist, the tubercle of the anterosuperior iliac crest, the greater trochanter, the lateral condyle of the knee, the lateral malleolus and the fifth metatarsal.

### Data analysis

After reconstruction of the stick diagrams representing successful locomotion of subjects, we focused our analysis on the orientation of the trunk and the lower limb segments with respect to the vertical. The following segments were analyzed: trunk (defined by the line connecting the acromion and the iliac spine markers), thigh (trochanter–knee), shank (knee–lateral malleolus), and foot (lateral malleolus–fifth metatarsal). The elevation angles of the thigh, shank, and foot in the sagittal plane are noted $\alpha_t$, $\alpha_s$, and $\alpha_f$, respectively (Fig. 1B).

The methods for analyzing the planar covariation of elevation angles were the same as those used by Borghese et al. (1996) in adult subjects. Briefly, the statistical structure underlying the distribution of the geometrical configurations associated with the observed changes of the elevation angles was described by principal component (PC) analysis. The PCs were computed by pooling together the samples of time-varying angles after subtraction of the mean value, and identified the best-fitting plane of angular covariation for each session (Borghese et al. 1996). The orientation of this plane in each child (Fig. 1C) was compared with the mean orientation of the corresponding plane of all the adults ($n$=19) by computing the angle $\theta$ between the respective plane normal vectors.

In order to evaluate the relationship between angle $\theta$ and trunk stability with respect to the vertical axis, we measured the peak-to-peak angular deviation of the trunk (defined by the line joining the iliac spine and the acromion markers) in both sagittal (pitch angle, $\pi$) and frontal (roll angle, $\rho$) planes.

Statistical analysis was performed using Statistica software (StatSoft).

## Results

Figure 2 shows the stick diagram of the very first three steps of an 11-month-old toddler (Fig. 2A) and two steps performed by the same toddler at 20 months (Fig. 2B). For the very first steps, locomotion patterns are variable across steps, and the trajectory of the joint markers, the step length, and the fluency show marked heterogeneity. The first step, for instance, is characterized by a more curved trajectory of the foot associated with higher elevation of the thigh, and a larger length of the step as compared with the following steps. The trunk presents a forward sway during the initial part of the swing phase followed by a backward sway initiated well before the onset of the stance phase. This latter movement of the trunk is accompanied by neck hyperextension culminating in the middle of the swing phase. Synergic arm swing is minimal. In contrast, at 20 months, step length, marker trajectories, and fluency are more reproducible across steps. During the swing phase, thigh elevation is smaller corresponding to a less marked hip flexion; hip extension occurs at the end of the stance phase. Trunk sway is minimal and synergic arm swing is present. Head orientation in the sagittal plane is much better stabilized than at 11 months.

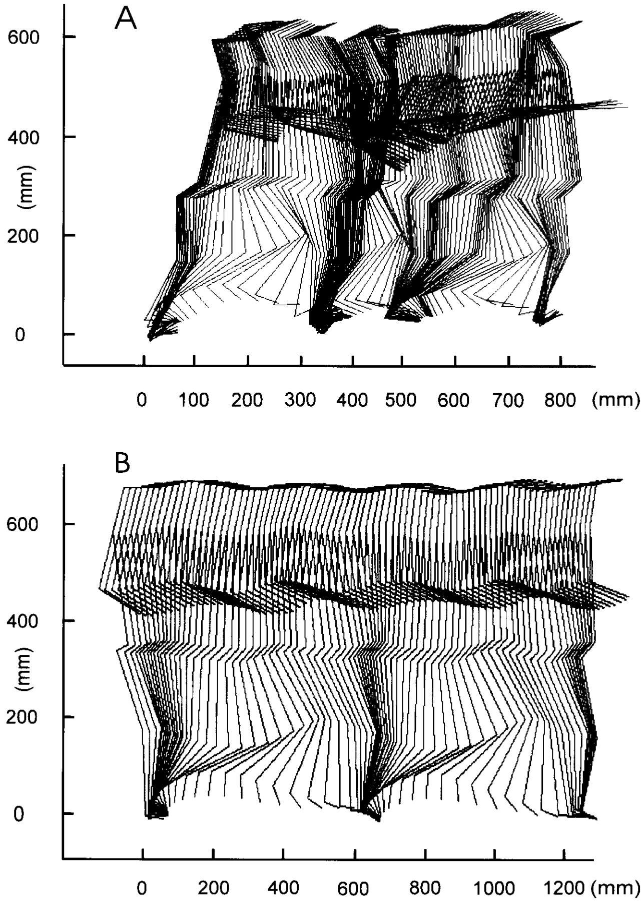

**Fig. 2A, B** Sagittal stick diagrams at two stages of early walking. **A** Very first three steps of an 11-month-old toddler. **B** Two steps of the same child aged 20 months

### Evolution of standard gait parameters

In order to verify that our population sample is representative of normal walking children, we measured walking speed and stride length as standard gait parameters (Cavagna et al. 1983; Ledebt et al. 1995; Sutherland et al. 1980). Exponential functions were fitted to the data either excluding or including the very first steps to verify whether these prefigure the evolution of the rest of the data. Velocity and stride length evolve along exponential curves with similar correlation coefficients (*r*) and time constants (t) whether the very first steps are excluded (*r*=0.89, t=18.7 months after the onset of unsupported locomotion; *r*=0.96, t=27.3 months, for velocity and stride length, respectively) or included (*r*=0.90, t=17.2 months; *r*=0.95, t=27.9 months, for velocity and stride length, respectively).

### Elevation angles of the lower limb segments

Figure 3 shows the time course of $\alpha_t$, $\alpha_s$, and $\alpha_f$ at different ages for one child and one adult. Two swing phases separated by a stance phase are illustrated for each represented age. The extent and profile of angular excursions show a clear difference between the very first steps (Fig. 3A, F) and 18 months later (Fig. 3D, I). In the illustrated case, for the very first steps, $\alpha_t$ presented a short high peak of forward motion followed by backward motion; it then remained quasi-constant near the vertical axis during the prolonged stance phase. The amplitude of thigh forward excursion was greatly decreased at 3 weeks of walking experience (Fig. 3B). Thereafter, the $\alpha_t$ excursion pattern gradually tended toward the adult one (Fig. 3E). The temporal evolution of $\alpha_s$ was characterized by an early backward peak due to flexion of the knee (Fig. 3A–C). This peak occurred just before the forward peak of $\alpha_t$ and it was followed by a higher forward peak culminating after $\alpha_t$ peaked. The following backward motion of $\alpha_s$ was gradual, contrasting with the backward movement of $\alpha_t$ which ended steeply. After 3 weeks of walking experience, the $\alpha_s$ forward peak was followed by a plateau of forward elevation (Fig. 3B, G). For the first steps, $\alpha_f$ presented numerous small peaks of elevation occurring throughout the step (Fig. 3F). This complex profile gradually evolved into the mature profile of backward and forward elevation followed by a plateau.

Figure 3K–N shows the evolution of the maximum excursion in the forward direction for $\alpha_t$, $\alpha_s$, and $\alpha_f$ for the same child represented in Fig. 3A–I. Three consecutive steps at four different ages of walking experience are compared with the mean adult pattern. In contrast with the adult pattern which shows a greater forward excursion of $\alpha_s$ and $\alpha_f$ relative to $\alpha_t$, the very first steps show a prevalence of $\alpha_t$ over $\alpha_s$ and $\alpha_f$ (Fig. 3K). After 3 weeks (Fig. 3L) or 6 weeks (Fig. 3M), the values of $\alpha_t$, $\alpha_s$, and $\alpha_f$ still differ greatly from the adult values. At 9 weeks the proximal to distal trend is reversed and a pattern more comparable to the adult one begins to be observed (Fig. 3N).

### Emergence of the planar covariation

In order to study the intersegmental coordination, we plotted the elevation angles $\alpha_t$, $\alpha_s$, and $\alpha_f$ one versus the others in 3D-position space. A mature pattern of coordination is characterized by a quasi-elliptic loop lying close to a plane (Bianchi et al. 1998b; Borghese et al. 1996; Lacquaniti et al. 1999). The pattern of a 12-year-old child is plotted in Fig. 1C. The walking cycle progresses in the counterclockwise direction, heel strike and toe-off roughly corresponding to the top and bottom of the loop, respectively. The ellipsoidal trajectory depends on the harmonic oscillations of the limb segments with fixed phase delays between each other (Fig. 3E–J). It has previously been shown that the first two harmonics of a Fourier series expansion account together for >99% of the experimental variance of the thigh, shank, and foot angles in normal adult locomotion (Bianchi et al. 1998b).

Figure 4 illustrates the evolution of the intersegmental coordination in one child, from her very first steps at the

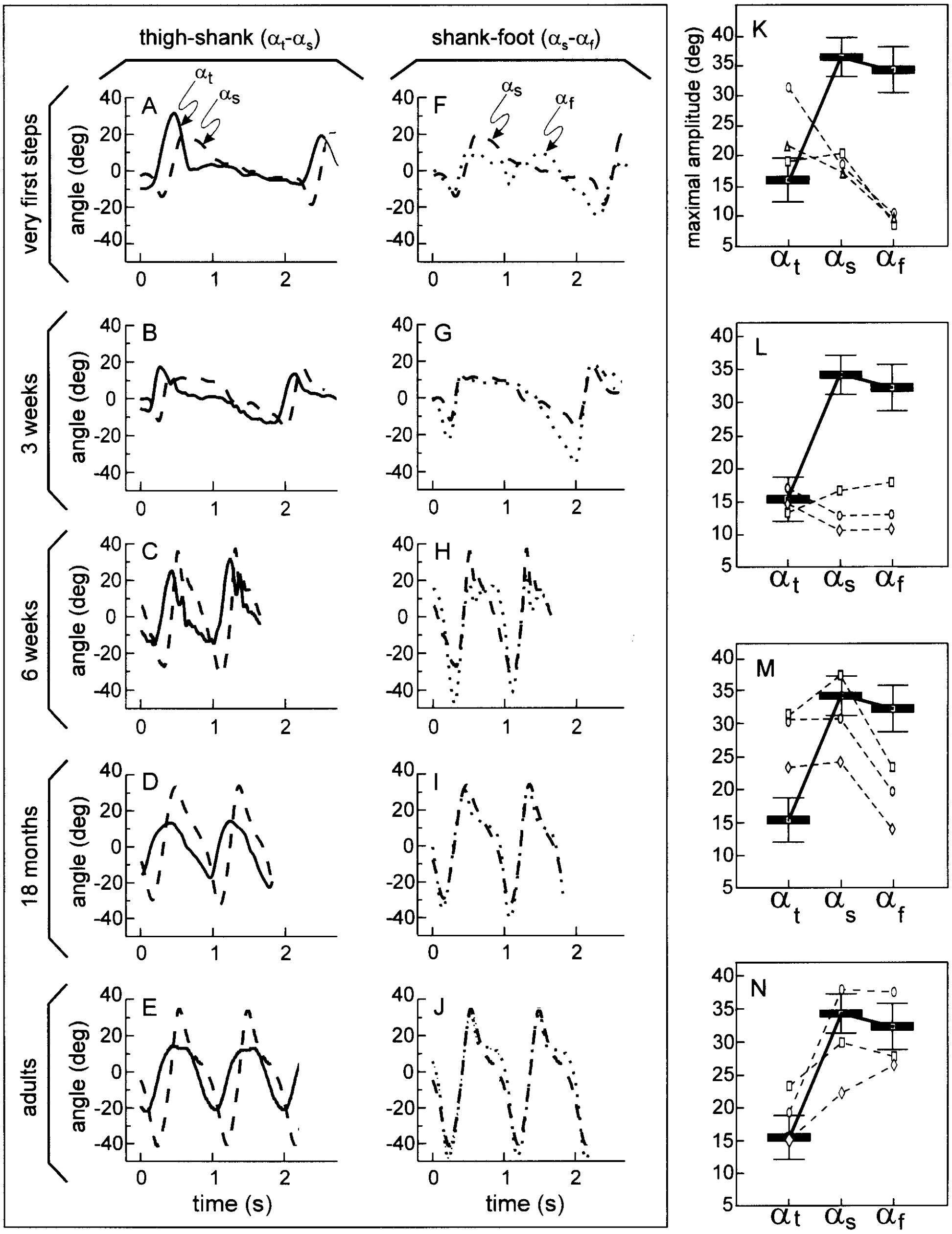

**Fig. 3A–N** Time course of the elevation angles of the lower limb segments. The elevation angles of the thigh (*continuous line*) and shank (*dashed line*), and shank and foot (*dotted line*) are plotted superimposed in the *left*, and *right column*, respectively. Mean values have been subtracted from each curve. Positive and negative angular values correspond to forward and backward elevation, respectively. Two successive swing phases separated by a stance phase performed by the same toddler during four maturation states are represented, namely the very first steps (**A, F**), 3 weeks (**B, G**), 6 weeks (**C, H**), and 18 months after the onset of walking (**D, I**). Data from a representative adult subject are plotted in the last row (**E, J**). The evolution of the maximal forward elevation angle of the thigh ($\alpha_t$), shank ($\alpha_s$), and foot ($\alpha_f$) of three representative trials performed by the same child are shown for the very first steps (**K**), 3 weeks (**L**), 6 weeks (**M**), and 9 weeks after the onset of walking (**N**). These diagrams are superimposed on the adult means (*white squares*), standard errors (*gray boxes*), and standard deviations

age of 14 months (Fig. 4A, B) to the age of 32 months (Fig. 4G, H). In spite of the production of successful walk, the temporal changes of the elevation angles were far from being sinusoidal during the very first steps (see also Fig. 3A, F). Accordingly, the gait loop in 3D space departed significantly from an elliptic shape (Fig. 4A), and the data were not well fitted by a plane (Fig. 4B). A planar covariation emerged early on during the following weeks of walking experience (Fig. 4C, D), and was stabilized afterwards. Note, however, that the changes in shape of the gait loop were much slower, with a progressive elongation of the loop along an axis roughly orthogonal to the thigh (Fig. 4E, G). This trend is related to the progressive reduction of the amplitude of thigh movement relative to that of shank and foot (see Fig. 3K–N).

The differential maturation of planarity and shape of the gait loop is concisely described by means of PC analysis (Fig. 5). In normal adults, PC1 and PC2 lie on the plane of angular covariation and describe the global form of the gait loop, whereas PC3 is orthogonal to the plane (Borghese et al. 1996). The percentage of variance accounted for by PC3 (PV3) is an index of planarity of the loop (0% corresponds to an ideal plane). In adults, PV3 is 0.9±0.3% (over all trials and subjects, $n$=324 trials). At the first steps of unsupported walking, PV3 of the toddlers was much higher (5–16%) than in the adults (Fig. 5C), confirming and extending the observation of a significant deviation from planarity reported for the child of Fig. 4B. However, PV3 dropped very rapidly toward the adult values, in agreement with the observation of

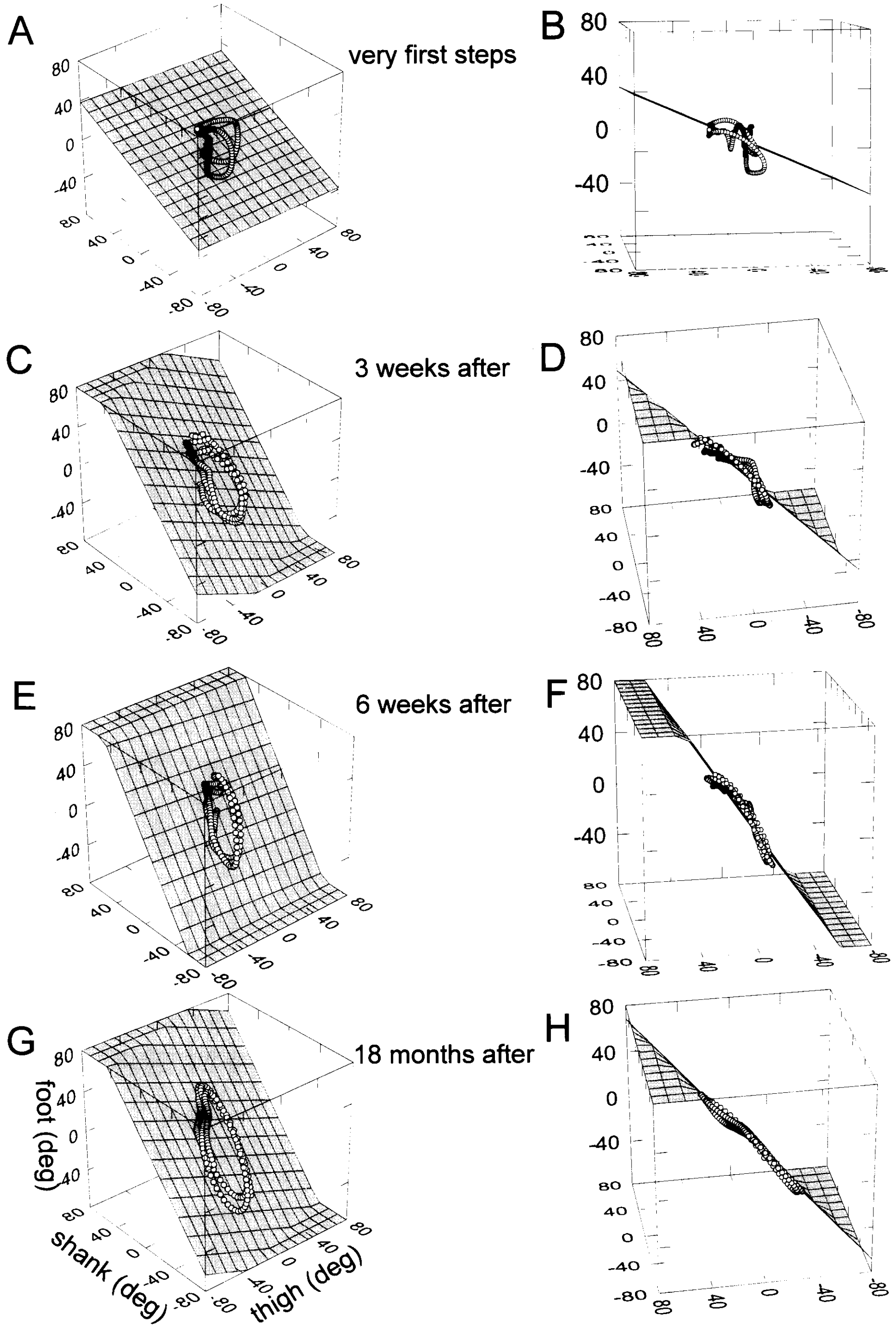

**Fig. 4A–H** Emergence of the planar covariation of the elevation angles of the thigh, shank, and foot. Covariation of thigh, shank, and foot elevation angles during two successive gait cycles performed by the same toddler at the onset of unsupported walking at the age of 14 months (**A, B**), 3 weeks after it (**C, D**), 6 weeks after it (**E, F**), and 18 months after it at the age of 32 months (**G, H**). Mean value of each angular coordinate has been subtracted. The data are represented with respect to the cubic frame of angular coordinates and the best fitting plane (*grids*) in two different perspectives (**A, C, E, G**) and (**B, D, F, H**). Gait cycle paths progress in time in the counterclockwise direction, heel strike and toe-off phases corresponding roughly to the top and bottom of the loops, respectively (see also Fig. 1C)

early emergence of a planar covariation (Fig. 4D, F, H). Development of planarity did not correlate with the extent of angular excursion at each limb segment. Thus no statistically significant correlation exists between PV3 and the amplitude of angular excursion on a trial by trial basis ($r$=0.2, 0.4, and 0.4 for $\alpha_t$, $\alpha_s$, and $\alpha_f$, respectively), nor is PV3 correlated with $\alpha_t/\alpha_f$, $\alpha_t/\alpha_s$, and $\alpha_s/\alpha_f$ ratios (r=0.33, 0.55, and 0.26, respectively).

PV1 and PV2 reflect the shape of the gait loop (Borghese et al. 1996). The greater the value of PV1 relative to PV2, the more eccentric (closer to a line segment) is the elliptic loop. The temporal evolution of PV1 and PV2 was much slower than that of PV3 (Fig. 5A, B), indicating that the shape of the gait loop approaches the mature pattern much more slowly than does planarity. Interestingly, even the oldest children of our sample (around the age of 12 years) had not yet reached the adult parameters.

### Maturation of plane orientation compared with that of anthropometric parameters

The orientation of the planar covariation represents another important parameter of the intersegmental coordi-

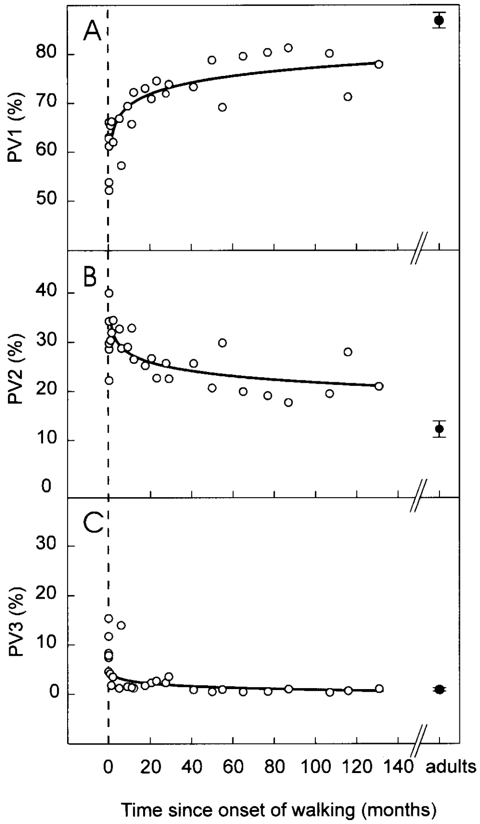

**Fig. 5A–C** Developmental trends of the percentage of variance (PV) accounted for by each principal component (PC). For each child the mean value of the percentage accounted for by each PC [PV1 for PC1 (**A**), PV2 for PC2 (**B**), and PV3 for PC3 (**C**)] is represented by a circle (○) as a function of the time since the onset of unsupported walking. The adult values are represented by their pooled mean (●) and standard deviation

nation, because it reflects the phase relationship between the different segments (Bianchi et al. 1998b). As seen in Fig. 5, the plane orientation in toddlers changed drastically over the first weeks of walking experience. These changes were quantified and compared with the changes in child morphology.

*Filled points* in Fig. 6 correspond to the angle (θ) between the best-fitting plane in each child and the mean adult plane. The overall time course of changes with age can be described by a biexponential function ($y=a^{-x/t_1}+b^{-x/t_2}$, where x is the time since onset of unsupported walking, $t_1$ is the fast time constant and $t_2$ is the slow one). In order to avoid an unrealistic fit due to the dispersion of data corresponding to the very firsts steps, data were fitted using the mean θ value at time 0 (mean θ=38.7°, range from 19.8° to 64.0°). The function fitted the experimental data reasonably well (*r*=0.89). The first time constant was fast ($t_1$=0.59 months after the onset of unsupported locomotion) and the orientation of the plane rapidly converged toward the adult values. Note that the values of angle θ were uncorrelated with $\alpha_t$, $\alpha_s$, and $\alpha_f$ maximal amplitudes on a trial by trial basis (*r*=0.01, 0.37, and 0.09, respectively).

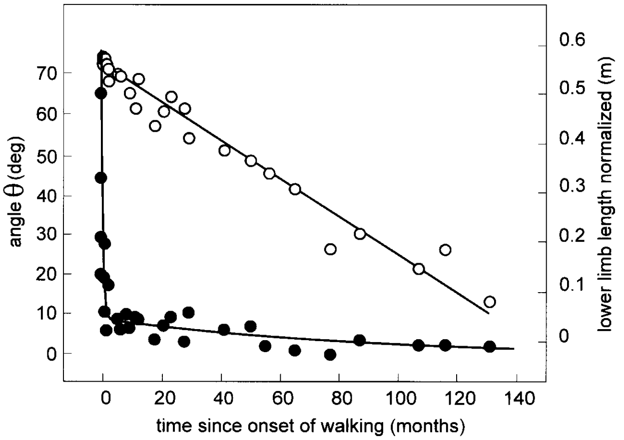

**Fig. 6** Comparison between the age changes in the covariation plane orientation and the corresponding changes in the lower limb length. For each subject and trial the angle θ between the subject's covariation plane and the mean adult plane (●) and the lower limb length normalized to the mean adult value (○) are represented as a function of time since the onset of unsupported walking. The adult components of the plane normal are: $u_3\alpha_t$=0.223±0.092, $u_3\alpha_s$=–0.772±0.026, and $u_3\alpha_f$=0.587±0.042. A biexponential function and a linear regression are fitted to the angle θ values and the lower limb length, respectively

We considered the age-related changes of two anthropometric parameters: the length of the lower limb (thigh plus shank length) normalized by the adult mean length (0.863±0.055 m, *unfilled points* in Fig. 6) and the ratio of the lower limb length over the child stature (ear to malleolus marker distance). The latter parameter was used to take into account the fact that the growth of children is not isomorphic, the growth of the lower limbs being relatively greater than that of the trunk (where the body center of mass lies) and head (Astrand and Rodahl 1986). In contrast with the biphasic time course of changes of plane orientation, with a first quick phase, the maturation of both the lower limb length and the limb length/stature ratio is monophasic and slow. The former anthropometric parameter changed linearly with age (Fig. 6), whereas the latter parameter changed exponentially (time constant of 32 months after the onset of unsupported locomotion).

## Correlation between trunk stability and planar covariation

Analysis of trunk oscillations showed rapid stabilization in both the frontal (ρ) and sagittal (π) planes (Fig. 7B). Initial peak-to-peak ρ and π oscillations were relatively high (14.0±7.2° and 13.6±5.8°, respectively; Fig. 7A). Subsequent evolution tended toward adult values (mean ρ and π=6.4±1.7° and 6.6±1.4°, respectively). As in the case of the evolution of angle θ, biexponential functions were calculated for ρ and π using the mean value of each angle at time 0. Despite the data scatter, the functions were reasonably well representative of the evolution of ρ and π changes (*r*=0.75 and 0.73, respectively). For both angles, the fast time constants ($t_1$=0.36 and 0.34 months

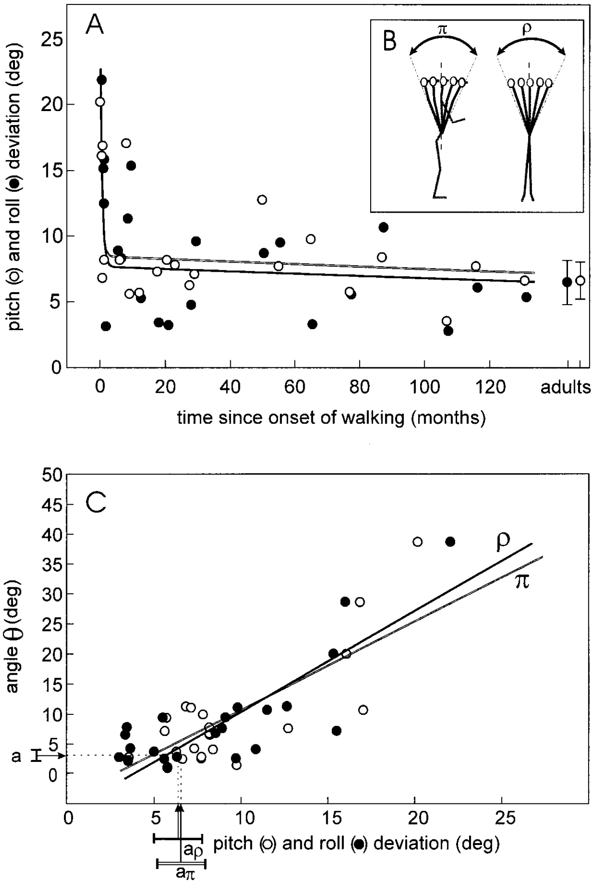

**Fig. 7A–C** Evolution of trunk stability. **A** Evolution of pitch and roll oscillations of the trunk. Age is from the onset of unsupported walking. **B** Schematic definition of pitch ($\pi$) and roll ($\rho$) peak-to-peak oscillation. **C** Relationship between angle θ and pitch (π) and roll (ρ) angles, with correlation coefficients (*r*) of 0.86 and 0.80 for θ-ρ and θ-π relationships, respectively. Adult means (*broken lines*) and standard deviations are indexed for θ (a), pitch ($a_\pi$) and roll ($a_\rho$) angles

after the onset of unsupported locomotion) were roughly comparable to that obtained for θ angle (0.59 months). A significant correlation ($r$=0.81) was found between ρ and π trends. Figure 7C shows the existence of a significant correlation between θ and π ($r$=0.80) and between θ and ρ ($r$=0.86).

## Discussion

The main point of the present study is that both the general pattern of the intersegmental coordination of the lower limb segments and the stabilization of the trunk with respect to the vertical are immature at the onset of unsupported walking in toddlers, but they develop in parallel very rapidly in the first few weeks of walking experience. By contrast, the maturation of the individual kinematic waveforms of each segment and their convergence toward waveforms that are more typical of adults is much slower, being acquired over a period of months to years.

In the following we discuss the results in the context of three main aspects: (1) mechanics of locomotion, (2) neural control, and (3) relationship between planar covariation and other concurrent coordination patterns during gait development.

### Mechanics of walking

When the elevation angles of the thigh, shank, and foot ($\alpha_t$, $\alpha_s$ and $\alpha_f$) are plotted one versus the others, they describe a regular loop constrained close to a plane in adults (Bianchi et al. 1998b; Borghese et al. 1996). This is not an inevitable mechanical consequence of a system of linked segments that are cross-coupled by passive inertial and visco-elastic forces. In fact, passive or active movements of the lower limbs that are unrelated to gait do not generate the plane of covariation in adults (Grasso et al., unpublished observations). Moreover, here we showed that some toddlers can successfully perform their very first steps even though the coordination pattern of the lower limb segments deviates very significantly from the standard planar loop observed in adults (see Fig. 5A, B). As it will be argued in a later section, the planar covariation represents a specific pattern of neural coordination of intersegmental kinematics (Lacquaniti et al. 1999).

The development of the planar covariation is functionally significant for the mechanics of walking. In healthy adults, the orientation of the covariation plane is directly related to the mechanical energy cost of walking (Bianchi et al. 1998a, b). Restoration of the covariation plane in treated patients with Parkinson's disease (Grasso et al. 1999) or hereditary spastic paraparesis (Dan et al. 2000a) also indicates that this parameter reflects the mechanical efficiency of walking. In toddlers, the planar covariation of the elevation angles of the lower limb segments is weak or absent at the very first unsupported steps, but is established over the first few weeks with an orientation in 3D segment space that is similar to the adult one. It should be noted that the parallel, progressive stabilization of the trunk also helps improve the mechanical efficiency of walking. Because of the body mass distribution, trunk stability plays a determining role in mechanical energy expenditure (Bianchi et al. 1998a). Thus it seems reasonable to hypothesize that children develop kinematic patterns that minimize energy expenditure as they approach adulthood. It is known that, to maintain a given speed, children generally perform a greater amount of work per unit mass per unit time with a greater weight-specific oxygen consumption than the adults (Astrand and Rodahl 1986; Cavagna et al. 1983).

### Relationship between the planar covariation and other coordination patterns during development

Maturation of stepping patterns has been shown to begin long before the child can walk (Forssberg 1985; Thelen

1985; Thelen and Cooke 1987; Yang et al. 1998a, b) and go on long thereafter (Berger et al. 1984; Brenière and Bril 1998; Cavagna et al. 1983; Cioni et al. 1993; Clark and Phillips 1993; Forssberg 1985, 1999; Lasko-McCarthey et al. 1990; Ledebt et al. 1995; Leonard et al. 1991; Sutherland et al. 1980). This is reflected by the gradual acquisition of gait parameters, some of them as early as fetal life (De Vries et al. 1984) and some as late as late childhood (Hirschfeld and Forssberg 1992). A basic problem in maturational studies is to define the limits of a mature pattern (Dietz 1992; Forssberg 1985; Hadders-Algra et al. 1996a). These limits depend on the considered parameters. For example, Bril and Brenière (Brenière and Bril 1998; Bril and Brenière 1992) have proposed two phases for walking maturation. The first phase, from 3 to 6 months after the onset of independent walking, is devoted to gait postural requirements, mainly dynamic equilibrium during forward propulsion, and the second one, lasting about 7 years, corresponds to further refinement of gait coordination.

The present results also support the existence of a two-phase process, as demonstrated by the biexponential time course of the kinematic parameters we focused upon. The first phase involves a relatively rapid emergence of the covariation plane and trunk stabilization. The second phase, expressed in our data by the slow time constants of the biexponential evolutions, represents fine tuning, which is developed more gradually than the first phase. Other authors consider that gait maturation is finalized by the age of 7–8 years, through fine tuning of kinematic parameters (Sutherland et al. 1980), muscle activation patterns (Berger et al. 1984; Okamoto and Kumamoto 1972; Woollacott and Jensen 1996), ground reaction forces (Gomez Pellico et al. 1995), head control and coordination (Assaiante and Amblard 1993), or anticipatory postural adjustments (Hirschfeld and Forssberg 1992; Ledebt et al. 1998). However, other gait parameters may require an even longer time to reach maturation.

The present data show that some toddlers can perform successfully their very first steps even though the intralimb coordination pattern of the lower leg deviates very significantly from the standard planar loop observed in adults. It should be noted that during these early steps the trunk is markedly unstable relative to the direction of gravity. After a few weeks, the same toddlers develop an adult-like coordination pattern in parallel with increasing trunk stability. This developmental parallelism reflects the relationship between the multilink intersegmental coordination of the lower limb during forward progression and the postural stability of the body with respect to gravity. In this framework, gravity can be viewed as a major referential determinant which can play an organizing role for the integration of different modes of coordination. Interestingly, it has been shown that otolith responses show marked changes during the period of the very first steps and immediately afterwards (Wiener-Vacher et al. 1996).

Both the planar covariation and the postural control of trunk orientation involve gravity information. Integration of the latter is reflected in the biphasic time course of changes in trunk pitch and roll oscillations with a fast time constant of a few weeks found by Ledebt et al. (1995) and confirmed in the present study. In normal adults and older children, the head and trunk tend to be stabilized with respect to the vertical during locomotion and other tasks (Dan et al. 2000b; Pozzo et al. 1990). Pitch and roll rotations of the trunk are minimal and reflect the control of dynamics of both lower limbs because of the inertial and visco-elastic coupling between trunk and limbs.

The maturation of the joint-angle covariance in toddlers should not only be considered as the progressive improvement of the kinematic control law, but it should also be viewed as an efficient solution to the problem of calibrating the sensorimotor space (Konczak and Dichgans 1997). In fact, the wide step-by-step variability exhibited by toddlers when they start unsupported locomotion permits the continuous exploration of a wide region of the cutaneous and proprioceptive sensory space. The multiplicity of different geometric configurations of the limb tends to generate a correspondingly wide range of different configurations in sensory space. This would allow the calibration of sensorimotor space by means of variable sensorimotor associations (Forssberg 1999; Sporns and Edelman 1993). The stable planar covariance of limb segment motion would be selected as the stable isomorphism between the internal model of the body scheme and the actual limb and body movement and its perception (Lacquaniti and Maioli 1994).

The gait loop path matures much more slowly than does the planar covariation. Thus the relative contributions of the first two PCs (that describe the shape of the gait loop) change progressively and have not yet reached adult values by 12 years of age. A similar situation has been described for the maturation of another kinematic law, the so-called 2/3 power law for hand-drawing in children (Sciaky et al. 1987). This law, which relates angular velocity to trajectory curvature, already exists in 3-year-old children but its strength (indicated by the correlation coefficient) increases monotonically through the age of 11 years. However, for simpler tasks such as reaching, mature kinematic patterns emerge after a few weeks of practice (Konczak and Dichgans 1997), following a time course similar to the planar law in walking in the present results.

The relatively rapid emergence of the planar covariation does not parallel the morphological maturation of the child. It also precedes the completion of the maturation of central pathways that are known to be involved in postural and locomotor control (Paus et al. 1999), which have been shown to parallel the evolution of body size (Eyre et al. 1991). The stability and refinement of the planar covariation while the morphological variables drastically change as the child grows, implicate a continuous update of the neural command to take into account these changing mechanical factors. The early independent gait, which significantly differs from later patterning, is presumably achieved through primary neuronal repertoires (in the sense of the "neural group selection" theory of Edelman 1989; Sporns and Edelman 1993) which do not take into account the single leg coordination priorities. In this context, further studies should still look into how multiple coordination patterns integrate.

Successful recordings of the very first independent steps, though in a limited sample of children, have provided an essential perspective. These recordings have shed a specific light on the emergence of the kinematic coordination pattern of the lower limb segments with respect to gravity. Our results show that the maturation of independent walking is more intense in the earliest period. It integrates a first form of dynamic control from which further refinement is more gradually accomplished in parallel to morphological and neuronal maturation. It must be noted that, although the time of performance of the first unaided steps is generally regarded as a milestone in motor development, it can correspond to widely variable maturation stages in different children. Multiple factors including morphological and/or neural development, motor practice, social and psychological environment, motivation, and stochastic aspects can influence the timing of this event. Irrespective of its exact timing, this motor event constitutes the first expression of a complex dynamic integration of feedforward and feedback mechanisms, including neural (for example, visual, vestibular, auditory, somesthetic) and non-neuronal processes [for example, mechanical "preflexes", as recently reviewed by Dickinson et al. (2000)], for independent bipedal locomotion. Specifically, as reinforced by our results, it constitutes the point of origin of further gait development. Rapid emergence of some aspects of coordination can be expected on grounds of the convergence of at least three driving processes which concur to improving motor behavior. The first one rests on environmental guiding of the toddler's walking performance, subserved by input from directional sensors (eyes, ears, etc.) and strengthened by motivational and other psychological and social factors. The second one concerns more specifically the equilibrium system related to the body configuration and posture control. The third one is comprised of phasic feedback mechanisms activating, modulating, and further developing central pattern generators (CPGs) and other neural networks, using reflexive (neural; Duysens et al. 2000) and preflexive (mechanical; Zehr and Stein 1999) factors.

## Neural control

According to the dynamic systems approach, stable locomotion can be viewed as a global entrainment of neural and musculoskeletal oscillations (Kopell 1995; Schoner et al. 1990; Thelen and Smith 1996). The system would settle in preferred activation patterns, that may or may not be hardwired. Development of locomotion would imply learning the global entrainment of the multilink chain of the body and limbs. Irrespective of the conceptual framework used to interpret the motor pattern, we remarked that the planar kinematic trajectory depends on the harmonic oscillations of the limb segments with fixed phase delays between each other (Bianchi et al. 1998b). Thus the planar covariation probably results from the coupling of neural oscillators between each other and with limb mechanical oscillators. Muscle contraction intervenes at variable times to re-excite the intrinsic oscillations of the system when energy is lost.

How the plane of angular covariation emerges during development and which neuronal networks participate in this process remain a matter of speculation. The following considerations are in order. According to current views, the network of burst generators (CPGs) are already in place at birth (Forssberg 1985; Lamb and Yang 2000). However, the phase coupling between the CPG units driving different limb segments may change during development, for instance because of the maturation of suprasegmental control of the locomotion pattern. This is consistent with the present results that indicate how the phase-coupling between different limb segments changes progressively with age.

It has been hypothesized that a stable and mature covariation plane can be achieved by tuning muscle activity patterns that appropriately modify the passive biomechanical coupling among limb segments (Bianchi et al. 1998b; Bosco et al. 1996; Lacquaniti and Maioli 1994; Lacquaniti et al. 1999). The control of posture and walking involves the precise regulation of the covariation of limb segments in such a way as to result in the desired position of the foot relative to the vertical. Because the degrees of freedom of angular motion of lower limb segments in the sagittal plane are reduced to two by the planar constraint, they match the corresponding degrees of freedom of motion of the foot. Any deviation of foot position from the desired path could be compensated by monitoring a mismatch between an endpoint-related signal and a segment angle-related signal, which could be used to reestablish the appropriate angular covariation (Bosco et al. 2000). Recent findings on the functional organization of both sensory systems, such as the dorsal spinocerebellar tract (Bosco and Poppele 1993; Bosco et al. 2000), and the primary motor cortex (Kakei et al. 1999; Scott and Kalaska 1997) indicate how this could be accomplished. At least two different subpopulations of neurons coexist at these levels. One set of neurons is tuned to the position and direction of movement of the endpoint (the hand or foot) independent of the limb geometrical configuration and of the pattern of muscle activity. The tuning function of another set of neurons instead is affected by the pattern of limb geometry and muscle activity. Bosco et al. (2000) have proposed how the spinocerebellar system could help regulating the joint-angle covariance. They argued that if each endpoint-related spinocerebellar cell was matched with a corresponding joint-angle cell that has a congruent endpoint-related activity, then as long as their activities remained congruent, it would indicate a consistent relationship between endpoint and joint-angle covariance. Instead, any mismatch in their respective discharges would signal a deviation from the desired joint-angle covariance. The cerebellum, that receives these inputs, could detect the mismatches of signals and could initiate appropriate control actions aimed at reestablishing the desired joint-angle covariance (Bosco et al. 2000). Therefore, one may speculate that the developmental changes of the joint-angle covariance plane also reflect the developmental changes of cerebellar control of gait and posture. This would also imply a role of cerebellar development for the control of intersegmental timing in lower limb kinematics.

## Conclusions

A synthetic view of our results indicates that the early emergence of a mature orientation of the covariation plane is correlated with increasing trunk stability, followed by progressive refinement of the gait loop. This approach may be used to quantify the developmental changes in gait in children. It has several advantages: it synthesizes the complex relationships that underlie the coordination of the lower limb, it provides explicit motor parameters which integrate upright posture and forward progression, it is a dynamic parameter and an invariant of adult gait, and it emerges at an early stage of development. We believe that this approach may be used also to reveal possible abnormalities in the emergence of this coordination pattern.

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