Control of Foot Trajectory in Walking Toddlers: Adaptation to Load Changes

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INTRODUCTION

What is the role of body weight for the control of locomotion? Foot–support interactions and load-regulating mechanisms play a crucial role in shaping patterned motor output during stepping (Duyssens et al. 2000). Transient loading of the limb enhances the activity of antigravity muscles during stance and delays the onset of the next flexion (Duyssens and Pearson 1980). Furthermore, the safe trajectory of the foot with minimal toe clearance at midswing is a precise endpoint control task that is under multisegmental motor control in both the stance and swing limbs (Bernstein 1967; Winter 1992). In adults, minimal contact forces are sufficient for accurate foot trajectory control because the required variation of the parameters that describe shape and variability of the foot path is very limited despite drastic changes in limb kinetics with body unloading (Ivanenko et al. 2002). These findings argue against a simple controller that commands a fixed change of limb positions when body weight is an inherent constraint, and accordingly, load-regulating mechanisms play an important role in terrestrial locomotion. How do toddlers deal with the effects of their full body weight when faced with the task of independent upright locomotion for the first time? Here we studied the effect of load variation on walking in 12 toddlers during their first unsupported steps, 15 older children (1.3–5 yr), and 10 adults.

To simulate various levels of body weight, an experimenter held the trunk of the subject with both hands and supplied an approximately constant vertical force during stepping on a force platform. During unsupported stepping, the shape of the foot path in toddlers (typically single-peak toe trajectory) was different from that of adults and older children (double-peak trajectory). In contrast to adults and older children, who showed only limited changes in kinematic coordination, the “reduced-gravity” condition considerably affected the shape of the foot path in toddlers: they tended to make a high lift and forward foot overshoot at the end of swing. In addition, stepping at high levels of body unloading was characterized by a significant change in the initial direction of foot motion during early swing. Intermediate walkers (1.5–5 mo after walking onset) showed only partial improvement in foot trajectory characteristics. The results suggest that, at the onset of walking, changes in vertical body loads are not compensated accurately by the kinematic controllers; compensation necessitates a few months of independent walking experience.

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appeared in the literature. Few previous studies have dealt with adaptation to limb loading (Schmuckler 1993; Thelen et al. 1984) and unexpected unloading (e.g., removal of the extra weight strapped around the lower limb, Lam et al. 2003b) to the additional body mass (Adolph and Avolio 2000), or with spontaneous leg movements in different postures (supine, angled and vertical), i.e., in different gravitational contexts in infants (Jensen et al. 1994). Such studies have reported mainly local or transient modifications in muscle activity, joint rotations, or step length characteristics.

In our previous work (Ivanenko et al. 2005), we used trunk support as a means toward reducing the effects of postural instability in walking toddlers and found no significant changes in lower limb kinematics. In that study, we reported only the effect of postural instability, and to this end, we supplied limited vertical force (typically <20% of the body weight). However, trunk stabilization (postural stability) and trunk unloading (weight bearing) may have separate consequences on stepping. Here, we report stepping with and without trunk support in toddlers who were just beginning to walk independently, and the amount of body weight support was varied from trial to trial to cover a wide range of values (0–90% of full body weight). Gait improvements during the first 1–3 mo showed a very high rate of change, which is followed by a less steep curve of maturation (Adolph et al. 2003; Hallemans et al. 2005, 2006; Holt et al. 2006; Ivanenko et al. 2007; Sutherland et al. 1988). We hypothesized that appropriate adaptation to body weight changes may also occur within the first several months after the onset of independent walking. To this end, we also compared toddlers’ gait with walking in older children and in adults at different levels of BWS. To analyze kinematic patterns, we used methods developed earlier for adult gait (Bianchi et al. 1998; Borghese et al. 1996; Ivanenko et al. 2002).

METHODS

Subjects

We recorded surface locomotion in 12 toddlers (6 males, 6 females, 11–15 mo of age), 6 intermediate walkers (4 males, 2 females, 1.5–5 mo after the walking onset), 9 children 2–5 yr old (7 males, 2 females, 9–50 mo after the walking onset), and 10 healthy adults (5 females and 5 males, 31 ± 7 (SD) yr; Table 1). We used the same developmental groups (Table 1) as in our previous paper (Ivanenko et al. 2004). Five of our toddlers were recorded a second time 0.1–2 yr after the first recording session (3 of our toddlers were the same as in our previous paper about the effect of posture stabilization, Ivanenko et al. 2005; but now we report their locomotor response to a full range of BWS levels). Informed consent was obtained from all the adults and from the parents of the children. The experimental procedures were approved by the ethics committee of the Santa Lucia Institute and conformed with the Declaration of Helsinki. The laboratory setting and experimental procedures were adapted to the children such that the minimal risks were equal or lower to that of walking at home. Both a parent and an experimenter remained astride the younger children to prevent them from hurting themselves during falls. For the toddlers, daily recording sessions were programmed around the parents’ expectation of the very first day of independent walking, until unsupported locomotion was recorded.

Walking conditions

WALKING WITHOUT SUPPORT. For the recording of the very first steps, one parent initially held the toddler by hand. Then, the parent started to move forward, leaving the toddler’s hand and encouraging her or him to walk unsupported on the floor. For each subject, about 10 trials were recorded under similar conditions. Short trials (≤3 min, depending on endurance and tolerance) were recorded with rest breaks in between. Only sequences of steps executed naturally by the toddler (e.g., no stop between steps) and while looking forward were retained to avoid initiation and braking phases and head movements caused by looking in other directions. Older children and adults were monitored while they walked at natural, freely chosen speeds. Typically, we analyzed two to five consecutive step cycles in each trial, for toddlers, older children, and adults.

WALKING AT DIFFERENT LEVELS OF BODY WEIGHT SUPPORT. In the toddlers we studied the effect of changing the load on the lower limb kinematics. To this end, after recording gait under standard conditions, some trials were recorded while an experimenter (or a parent) held the trunk of the child under his/her arms with both hands and supplied an approximately constant vertical force during stepping attempts (Fig. 1, A and B). The amount of the external BWS was varied from trial to trial to cover a wide range of values. The same procedure of body unloading was performed in older children during overground walking.

In adults, the experiments with different BWS levels (0, 35, 50, 75, and 95% of body weight) were carried out on a treadmill at 3 km/h. BWS was obtained by suspending the subjects in a parachute harness (Reha, BONMED) connected to a pneumatic device that applied a controlled upward force at the waist (WARD system, Gazzani et al. 2000). As a result, each supporting limb experienced a simulated reduction of gravity proportional to the applied force, while the swinging limb experienced 1g. The overall constant error in the applied force and dynamic force fluctuations monitored by a load cell
Bilateral kinematics of locomotion was recorded at a digitizing rate of 100 Hz by means of the VICON-612 motion analysis system (Oxford, UK). The positions of selected points on the body were recorded by attaching passive infrared reflective markers (diameter, 1.4 cm) to the skin overlying the following bony landmarks on both sides of the body: gleno-humeral joint (GH), the tubercle of the femur (F), the iliac crest (IL), greater trochanter (GT), lateral femur epicondyle (LE), lateral malleolus (LM), and fifth metatarso-phalangeal joint (VM). Particular care was taken to place the VM marker in the same position (on the lateral aspect of the 5th metatarso-phalangeal joint) in all subjects. Individual deviations of the VM marker position relative to the actual fifth metatarso-phalangeal joint (because the diameter of the marker was 1.4 cm and it was attached to the skin on a short 1-cm height stem) were measured before the recordings and corrected afterward with software.

The ground reaction forces under both feet (Fig. 1B) were recorded at 1,000 Hz by a force platform (0.9 × 0.6 m; Kistler 9287B, Zurich, Switzerland). Toddlers generally performed two to three steps on the force platform in each trial.

### Data analysis

Deviations of gait trajectory relative to the x-direction of the recording system were corrected by rotating the xz axis by the angle of drift computed between start and end of the trajectory. The body was modeled as an interconnected chain of rigid segments: GH-IL for the trunk, IL-GT for the pelvis, GT-LE for the thigh, LE-LM for the shank, and LM-VM for the foot. The main limb axis was defined as GT-LM. The elevation angle of each segment 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).

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.

In adults, gait cycle duration was defined as the time interval 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 equaled two steps. When children 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 kinetics was <3%. However, the kinematic criterion sometimes produced a significant error in the identification of stance onset in toddlers if there was an unusual forward foot overshoot at the end of swing (cf. Forssberg 1985). In such cases, foot contact was determined using a relative amplitude criterion for the vertical displacement of the VM marker (when it was elevated to 7% of the limb length from the floor).

The amount of the external body weight support in children and adults during overground walking was estimated as the percent reduction of the mean vertical force on the platform (Fig. 1B).

To verify whether the trunk angle in the sagittal plane varied with weight support, we measured the mean angle of the long axis of the trunk with respect to the vertical axis. The long axis of the trunk was defined by connecting the midpoint of the two (left and right) IL markers with the midpoint of the two GH markers.

### Intersegmental coordination

Intersegmental coordination was evaluated in position space as previously described (Bianchi et al. 1998; Borghese et al. 1996). In adults, the temporal changes of the elevation angles at the thigh, shank, and foot covary during walking. When these angles are plotted in three dimensions (3D), they describe a path that can be least-squares fitted to a plane over each gait cycle. In adults, changing BWS results in limited changes of the kinematic coordination (Ivanenko et al. 2002). Here, we studied this issue of intersegmental coordination (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 \( u_1 \), \( u_2 \), and \( u_3 \), rank ordered on the basis of the corresponding eigenvalues, correspond to the orthogonal directions of maximum variance in the sample scatter. For each eigenvector, the parameters \( u_{x_1} \), \( u_{y_1} \), and \( u_{z_1} \) correspond to the direction cosines with the positive semi-axis of the thigh, shank, and foot angular coordinates, respectively. The first two eigenvectors \( u_1 \) and \( u_2 \) lie on the best-fitting plane of angular covariation. The third eigenvector (\( u_3 \)) is the normal to the plane and thus defines the plane orientation. To quantify the rotation of the plane with BWS, we analyzed the \( u_3 \) parameter (the direction cosine of the normal to the plane with the axis of thigh elevation), which was found to vary systematically with BWS in toddlers (see RESULTS).
Foot trajectory

The shape of the endpoint path was compared by computing the vertical excursion of the VM marker (during swing) and correlating it with the corresponding ensemble average in adults (using Pearson correlation coefficient). VM trajectories were time-normalized over the swing phase duration. They were analyzed both in space and relative to the instantaneous hip (GT marker) position. To show the dynamics of foot motion during swing, we also calculated the instantaneous pitch angle of the VM velocity vector in the sagittal plane. In each gait cycle, the foot moves back and forth relative to the body. To emphasize the differences in the initial direction of foot motion during early swing across subjects, we computed the mean pitch angle of VM motion during the first 30% of swing (beginning from the moment when the VM marker reversed direction from backward to forward).

Foot trajectory variability

Foot-trajectory spatial variability in the sagittal plane was quantified in terms of spatial density and normalized tolerance area of VM, computed over the swing phase (Ivanenko et al. 2002, 2005). These indices describe the integrated variability of foot path, including variability in both the vertical and horizontal directions. To compare subjects of different heights, VM trajectories (relative to the instantaneous position of GT) were first scaled by the limb length (in proportion to the mean limb length of adults) and resampled in the space domain by means of linear interpolation of the x,y time series (1.5 mm steps) over all gait cycles. All steps (typically 7–15) from different trials under the same walking conditions were pooled together for this analysis.

Spatial density was calculated as the number of points falling in 1 × 1 cm² cells of the spatial grid divided by the number of step cycles. Normalized tolerance area was derived as follows. The mean length of foot trajectory over the swing phase across all steps was calculated from the corresponding path integral. For every interval corresponding to 10% of the maximal horizontal excursion, we computed the 2D 95% tolerance ellipsis of the points within the interval. The typical number of points in each interval ranged from 500 to 1,200 (depending on the number of gait cycles). The areas of all tolerance ellipses were summed and normalized by the mean length of foot trajectory. This normalized area provides an estimate of the mean area covered by the points along 1 cm of path. A greater tolerance area indicates greater variability.

Age-related changes

The time-course of changes of kinematic and kinetic parameters as a function of age was fitted by an exponential function, \( y = ae^{-\tau t} + b \), where \( y \) is the specific parameter under study, \( \tau \) is the time since onset of unsupported walking, \( \tau \) is the time constant, and \( a \) and \( b \) are two weighting constants.

Statistics

Statistical analyses (Student’s t-test) were used when appropriate. Reported results were considered significant for \( P < 0.05 \). Statistics on correlation coefficients was performed on the normally distributed, Z-transformed values. The algebra of angles (circular variables) is somewhat different from the rules governing other (linear) quantities. Circular statistics (Watson’s \( U^2 \) test) were used to compare the initial directions of foot motion during swing across subjects. Spherical statistics on directional data (Batschelet 1981) 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 directly, we calculated the angular SD (called spherical angular dispersion) of the normal to the plane.

RESULTS

General characteristics of foot trajectory in children

During unsupported walking, foot trajectory characteristics differed systematically in toddlers compared with those in adults and older children. The dominant template of foot motion is shown in Fig. 2A (left). All toddlers typically moved the leg in such a way that the foot lift (VM̂) had only one maximum at midswing. This behavior was entirely in contrast to that observed in the typical adult gait, which was characterized by prominent foot lift in early swing, a minimum foot clearance during midswing, and another separate toe lift in the end of swing. As a result, the correlation coefficient between the time series of the VM during swing in toddlers and the corresponding ensemble average in adults was typically negative (~0.51 ± 0.19). The spatial variability of the endpoint (foot) path in the sagittal plane was considerably greater than in the adults (see also Ivanenko et al. 2005): the normalized tolerance area (scaled to the mean limb length of adults) was...
20.5 ± 6.5 cm²/cm in toddlers and 3.8 ± 1.9 cm²/cm in adults (P < 0.0001, Student’s unpaired t-test).

Age-related changes of the kinematic parameters related to the foot trajectory control are presented in Fig. 2, B and C, for the whole group of subjects during overground walking at a natural speed. Both the correlation coefficient between VMᶜ in children and VMᶜ in adults (Fig.2B) and the foot path variability (normalized VM tolerance area; Fig.2C) changed rapidly over the first few months of independent walking experience. Changes with age were fitted by an exponential function (see METHODS). The time constant was fast both for the correlation with the ensemble average in adults (τ = 2.5 mo) and for the changes of the VM spatial variability across steps (τ = 1.9 mo).

Stepping at different BWS levels

To study the effect of BWS, an experimenter or a parent firmly held the trunk of the child with both hands providing an approximately constant vertical force while the child stepped. Supporters were instructed to avoid influencing the toddlers’ forward motion. However, we were unable to completely control for the possibility that some aspects of stepping were influenced by external forces generated by the supporter on the toddler’s forward motion. Nevertheless, during supported stepping, the mean walking speed and stride length (1.6 ± 0.5 km/h and 0.44 ± 0.08 m at 40–90% BWS) were similar to those during unsupported stepping (1.5 ± 0.4 km/h and 0.35 ± 0.06 m; P > 0.05, paired t-test). The position of the arms was also similar because the upper extremities in newly walking toddlers are typically held away from the body (Sutherland et al. 1980). The mean walking speed in nine older children (2–5 yr), supported in the same way as the toddlers, also did not change significantly (3.0 ± 0.5 km/h at 0 BWS and 3.1 ± 0.4 km/h at 40–90% BWS).

The walking speed freely chosen by toddlers was in general lower than in adults or in older children when expressed in dynamically equivalent terms—using the Froude number (Fr = V²/gL, where V is the average speed of locomotion, g is the acceleration of gravity, and L is the limb length). The Froude number is a dimension-less parameter suitable for the comparison of locomotion in subjects of different size walking at different speeds, under the assumption of the gravity-related pendulum mechanism of movement (Cavagna et al. 1983). Fr was 0.07 ± 0.04 in our toddlers (across all conditions) versus 0.18 ± 0.05 in older children and 0.19 ± 0.04 in adults during overground walking. The mean walking speed in toddlers (~1.5 km/h) corresponds to ~2.5 km/h in adults when normalized using the Froude number (i.e., to the square root of L). Therefore, although the general characteristics of foot motion in adults do not depend significantly on the walking speed (Ivanenko et al. 2002), for the sake of comparison, we recorded treadmill locomotion with BWS in adults at a comparable equivalent speed (3 km/h).

It is worth noting that the general characteristics of the foot path in adults did not differ significantly during overground walking and walking on the treadmill at 0 BWS except that the foot path variability was slightly larger during overground walking: VM tolerance area was 3.8 ± 1.9 cm²/cm during overground walking and 2.7 ± 1.1 cm²/cm during treadmill walking at 3 km/h. This difference was likely caused by some variability in the walking speed (and consequently in the stride length) across overground trials.

Effect of BWS on intersegmental coordination

Figure 3A plots averaged thigh, shank, and foot elevation angles and corresponding gait loops in toddlers, older children (2–5 yr), and adults at two levels of BWS. In adults and older children, temporal changes of the elevation angles of lower limb segments covaried along a plane, describing a characteristic loop over each stride. Paths progress in time in the counter-clockwise direction, lift-off and touch-down corresponding approximately to the top and bottom of the loop, respectively (Fig. 3A). Planarity was quantified by the percentage of variance accounted for by the third eigenvector (PV₃) of the data covariance matrix: the closer PV₃ is to 0, the smaller the deviation from planarity. Planar covariation was obeyed at all tested BWS levels (on average, PV₃ was 1.0 ± 0.2%), although the 3D gait loop became slightly narrower with increasing BWS (e.g., at 95% BWS, in 4 of the 10 adults PV₂ was <3%), consistent with our previous study; (Ivanenko et al. 2002; PV₁ increase and PV₂ decrease; Fig. 3B, right). The first two eigenvectors u₁ and u₂ of the covariance matrix lie on the best-fitting plane of angular covariance, whereas the third eigenvector (u₃) is the normal to the plane and is characterized by the direction cosines plotted in Fig. 3B (bottom panels).

The gait loop and its associated plane depend both on the amplitude and phase of the limb segment oscillations. The plots of Fig. 3A show the basic stereotypy of the patterns of intersegmental covariations obtained at different BWS levels, but they hide subtle yet important trends with BWS changes. In all subjects, the plane of angular covariation rotated with increasing BWS (U₃ monotonic decrease; Fig. 3B).

In toddlers, at 0 BWS, the gait loop departed significantly from planarity and the mature pattern. Although the plane (PV₁ ≥ PV₂ ≥ PV₃) resembled that of the adults, PV₃ was significantly higher in toddlers (3.1 ± 0.8%) than in adults (0.9 ± 0.2%, P < 0.001 Student’s unpaired t-test), in agreement with previous findings (Cheron et al. 2001b; Ivanenko et al. 2004). Moreover, the step-by-step variability of plane orientation (estimated as the angular dispersion of the plane normal) was considerably higher in toddlers (15.8 ± 7.3°) than in adults (2.9 ± 1.0°). In addition, because the amplitude of thigh movements was relatively higher with respect to that of shank and foot movements in toddlers (Fig. 3A), the gait loop was less elongated than in adults, as shown by the larger contribution of the second eigenvector (PV₂), although with increasing BWS, the gait loop in toddlers (Fig. 3A) tended to be more elongated (PV₂ decreased; Fig. 3B, left).

Effect of BWS on foot trajectory

BWS did not influence appreciably the shape of the endpoint path in adults (Fig. 4) in agreement with our previous study (Ivanenko et al. 2002). At 95% BWS (nearly complete unloading), adult subjects were still able to step on the treadmill, typically with only forefoot loading during stance (no heel contact). However, the correlation coefficient between the time series of the VMᶜ during swing at 0 and 95% BWS was still very high (0.94 ± 0.03). The path and its variability were relatively conserved from 0 to 95% BWS. Finally, the addi-
tional kinematic data from smaller-weight adults (n = 5, Table 1) during overground walking with manual unloading were not significantly different from those obtained during walking on a treadmill when suspending the subjects in a parachute harness connected to a pneumatic device that applied a controlled upward force. The correlation coefficient between the time series of the VM, during treadmill and overground walking was very high (0.97 ± 0.02 at 0 BWS and 0.95 ± 0.03 at 40–90% BWS), and the maximal foot lift during swing and the relative position of the main peak were also similar at all BWS levels, independent of the unloading procedure (Fig. 4, bottom).

In contrast, the reduced “gravity” considerably affected the shape of the foot path in toddlers: all toddlers tended to make an unusual high foot lift and forward foot overshoot (a kicking-like movement) at the end of swing at high levels of body unloading (Fig. 4A, right). For instance, at 0 BWS, the mean peak position of the VM was at midswing, whereas at 40–90% BWS, it was significantly shifted forward (Fig. 4B; P < 0.001, paired t-test). This behavior (forward foot overshoot) persisted over all consecutive steps performed at high BWS levels in one trial (typically 2–5 steps). It is worth noting that the same unloading procedure that was used in toddlers did not change significantly the shape of the foot path in older children (Fig. 4).

Variability inherent in the toddlers’ stepping pattern may have limited our ability to draw definitive conclusions about...
the exact dependence of the foot trajectory on the BWS level (Fig. 4). To estimate the level at which changes in the forward foot overshoot become significant, we compared the relative peak position (Fig. 4B) obtained at 0 BWS and under weight supported conditions within each 20% interval of BWS: we moved the BWS window every 10% (10–30%, then 20–40%, etc.) until the difference with the 0 BWS condition became significant (using t-test). Such procedure revealed significant changes with respect to the unsupported walking condition beginning from the 30% BWS values.

Figure 5A shows the average template of the foot trajectory and the dynamics of the pitch (α) angle in toddlers, older children (2–5 yr), and adults. In the time domain (Fig. 5B), at all levels of BWS, the vertical excursion of the foot in toddlers tended to have only one maximum at midswing, and the correlation coefficient between the time-series of the VMx during swing in toddlers and the corresponding ensemble average in adults remained negative at 40–90% BWS (−0.72 ± 0.10). However, there were significant changes in the hip angle during swing initiation at high levels of BWS (Fig. 5C): the hip tended to be slightly extended (by ~7°) in toddlers, whereas it was similar in older children and adults during body unloading. The knee angle tended to be somewhat flexed during stance-to-swing transition in toddlers at high levels of BWS (Fig. 5C).

The amplitude of the vertical hip (GTy) oscillations throughout the gait cycle did not change significantly with BWS (2.8 ± 0.6 cm at 0 BWS and 3.2 ± 0.8 cm at 40–90% BWS,
making it unlikely that the increased trunk oscillations could govern larger foot movements in space. In addition, the mean trunk orientation in toddlers tended to tilt forward during body unloading (BWS > 40%; by 3.1 ± 5.6°, \( P < 0.05 \), one-tailed t-test), although in older children (2–5 yr) the amount of forward tilt was similar (6.1 ± 4.8°). We also analyzed the foot path relative to the instantaneous hip position. Again, the distinctive forward foot overshoot was present in toddlers at high levels of BWS (Fig. 6A), and stepping at these levels was characterized by an apparent change in the initial VM direction during early swing. The VM tolerance area also remained high (19.8 ± 3.7 cm²/cm with 40–90% body support and 20.5 ± 6.5 cm²/cm without). In toddlers, the pitch angle of this directional vector (mean ± circular SD, relative to the horizontal) was 32 ± 9° at 0 BWS and 0 ± 4° at 40–90% BWS, whereas in older children it was 0 ± 7 and –5 ± 6° and in adults it was 4 ± 6 and –1 ± 6°, respectively. At 0 BWS, this angle (32 ± 9°) was significantly different from that of adults and older children (\( P < 0.001 \), Watson’s \( U^2 \) test), indicating a high initial foot elevation during swing in toddlers, whereas at high levels of BWS, the difference was minor (Fig. 6B).

Figure 7 shows the effect of BWS on the shape of the foot path in all groups of subjects (Table 1). Older children (2–5 yr) displayed quite mature foot trajectory characteristics, whereas intermediate walkers (1.5–5 mo after the onset of walking)
showed only partial improvement, supporting the conclusion that a few months of walking experience is the minimum practice duration for the beginning of an effective (adult-like) foot trajectory control.

**DISCUSSION**

Our study supports the common notion that toddlers are able to adapt to environmental changes and they can step at different levels of BWS. The intersegmental coordination (rotation of the covariance plane; Fig. 3B) showed similar monotonic changes with BWS in all subjects, suggesting similar amplitude and phase regulation of segment motion with body unloading. We also confirmed our previous findings (Ivanenko et al. 2005) that trunk stabilization (low BWS levels) did not affect significantly limb motion. Our main finding in this study, however, was that, in contrast to adults and older children, foot trajectory characteristics in toddlers showed systematic changes with limb unloading. This difference was exemplified by the higher foot lift, forward foot overshoot (Figs. 4 and 5A).

**Fig. 6.** Foot trajectories relative to instantaneous hip position (swing phase). A: example of 1 toddler, the same child recorded 3 yr later, and 1 representative adult. Top to bottom: stick diagrams of 1 cycle relative to instantaneous hip position and VM spatial density plots. Initial direction of VM path (1st 30% of swing) is indicated by an arrow. Spatial density of VM path was integrated over swing phase (across 10–15 steps) performed at different BWS. Density of each cell was depicted graphically by means of a color scale (empty cells were excluded): the lower the density (toward blue in color-cued scale), the greater the variability. Plots are anisotropic, vertical scale being expanded relative to horizontal scale. B: mean initial directions of VM path for toddlers, older children, and adults for stepping at 0 and high levels of BWS.

**Fig. 7.** Effect of BWS on the shape of foot path (swing phase) in all groups of subjects. A: correlation coefficient between VM path data in children and corresponding ensemble average in adults. B: relative position of main peak of VM (same parameter as in Fig. 4B). C: mean initial directions of VM path. IWK, intermediate walkers (see Table 1). Asterisks denote significant differences (P < 0.05).
and remarkable change in the initial foot direction (Fig. 6) with body weight unloading. These performance changes with level of unloading were observed in all toddlers who were just beginning to walk independently. Intermediate walkers (1.5–5 mo after walking onset) showed only partial improvement in foot trajectory characteristics (Fig. 7).

**Methodological considerations**

Sensory signals interact with central rhythm-generating centers in a complex manner (Pearson 1995). Afferent activity helps to shape the motor patterns, control phase-transitions, and reinforce ongoing activity. In stance, load-detecting afferents, both from muscles and skin, facilitate the center for the generation of extension and inhibit that for flexion. In toddlers, the foot shape and ossification of the soft bones of the feet are still immature at the age of 1 yr (Bertsch et al. 2004). During limb loading, a variety of receptors can be activated, such as Golgi tendon organs, cutaneous receptors of the foot, and spindles from stretched muscles (Duyzens et al. 2000). A number of cutaneous reflexes participate in the fine control of foot positioning in animals (Guertin et al. 1995; Schouenborg and Weng 1994) and humans (Aniss et al. 1992; Van Wezel et al. 1997; Yang and Stein 1990; Zehr and Stein 1999). Even though the spatio-temporal distribution of load on the soles of the feet may be generally important in the regulation of locomotion, we have previously found that it does not appreciably affect the endpoint trajectory constraints in adults (Ivanenko et al. 2002): in the limit cases of 95% BWS and 100% BWS with surrogate contact, detection of ground contact at the forefront was sufficient to trigger the central program for accurate endpoint control in adults. These findings suggest that an idiosyncratic distribution of load on the soles (Bertsch et al. 2004; Hallemans et al. 2004) and nonplantigrade stepping in toddlers were not the primary reason for the observed adaptive difference between toddlers and adults (Fig. 5).

One could argue that the enlarged vertical foot displacements at high levels of BWS in toddlers (Fig. 4) were a simple result of changes in the trunk motion influenced by an experimenter who supported the child. However, this is unlikely because of the following reasons. First, the same unloading procedure in older children and adults did not affect significantly the foot path (e.g., Figs. 4–6). Second, the amplitude of the vertical hip oscillations in toddlers throughout the gait cycle did not change significantly with BWS. Also, the mean trunk angle varied similarly with weight support between the groups of children. Finally, the foot path relative to the instantaneous hip position showed similar behavior (Fig. 6) as in space (Fig. 5A). In addition, when holding the trunk under the arms, i.e., at low levels of trunk support (BWS < 20%), leg and foot movements were similar to those during unsupported stepping (Ivanenko et al. 2005), making unlikely the contribution of simple sensory contact of the hands with the child’s trunk. As a final point, the observed phenomenon (Figs. 4 and 6) was not caused by the aftereffect of transient load changes (Lam et al. 2003b) because it persisted over all (from 2 to 5) consecutive steps performed at high levels of BWS. Therefore, we believe that the unusual forward foot overshoot in toddlers was caused by the nonspecific reduction of gravitational load during stance.

**Effect of body weight unloading on foot trajectory control in toddlers**

What is special in toddler gait? When children start to walk independently, their gait is characterized by considerable trunk oscillations revealing postural instability (Assaiante et al. 1993; Bril and Brenière 1993; Roncesvalles et al. 2001), wide swinging arms (Sutherland et al. 1980), high interstep variability (Clark et al. 1988), and immature foot trajectory characteristics and intersegmental coordination (Cheron et al. 2001a,b; Ivanenko et al. 2004, 2005). In particular, early stepping typically manifests itself in shorter step lengths, disordered vertical hip displacements, nonplantigrade gait (lack of the heel-to-toe roll-over pattern), and a single peak foot lift during swing. One may argue that this evolutionary adopted pattern (nonplantigrade gait with a high foot lift) is beneficial for toddlers as an optimal starting point strategy (Ivanenko et al. 2007) to avoid stumbling and falls and for reducing the effect of involuntary foot drag and the lack of dorsiflexor activity, which has been observed at the stance-to-swing transition during treadmill stepping in young infants (Yang et al. 2004).

The phenomenon may possibly reflect flexor-biased pattern generation (Yakovenko et al. 2005) in infants that is replaced by mature control with walking experience. For instance, the flexion reflex and the placing reflex seem to be important components of infant’s stepping (Forssberg 1985; Zelazo et al. 1972). An early form of locomotor-like alternating kicking and stepping movements is present at birth and even prenatally in humans (Thelen 1981; Zelazo 1983). Hip flexion dominates in an early period of infancy during supported neonatal stepping (≤4 wk after birth), throughout the first year up to the beginning of independent walking (Forssberg 1985; Lamb and Yang 2000; Okamoto et al. 2003; Pang and Yang 2001; Thelen 1981; Yang et al. 1998). The relative hyperflexion in hip and knee is slightly reduced compared with the neonatal stepping but it is still present before the onset of independent walking (Forssberg 1985). Indeed, the amplitude of thigh movements is relatively higher with respect to that of shank and foot movements, resulting in the wider gait loop in toddlers and by the larger contribution of the second eigenvector (PV2 in Fig. 4) (see also Cheron et al. 2001a,b). Moreover, several aspects of infant stepping, including the vertical movement of the hip joint and of the foot, the shape of the gait loop, and the bursts of EMG activity on foot placements, all suggest that toddlers implement a mixed locomotor strategy, combining forward progression with elements of stepping in place (Ivanenko et al. 2005). This hypothesis is also consonant with the finding that toddlers had not yet learned to use transverse pelvic rotation in leg-pelvis coordination to increase speed of walking (Holt et al. 2006).

In addition to the idiosyncratic foot trajectory characteristics during unsupported stepping, our data indicate that toddlers adapt differently than adults and older children to variations in load (Figs. 5A, 6, and 7). At low levels of BWS (<30%), foot trajectory characteristics were similar to those during unaided stepping, in agreement with our previous results (Ivanenko et al. 2005). However, at higher levels of BWS, the “flexor-biased” (or stepping-in-place) component of swing initiation (Figs. 5A and 6) decreased significantly with limb unloading resulting in alternating swing movements of the legs with an overshoot at the end of swing. If one accepts the terminology...
of motor primitives or stereotypies in infants (Thelen 1981), there was a switch from the stepping-in-place motor component during unsupported walking to the kicking component during walking at high levels of BWS.

We do not know the exact nature or transmission mechanisms of the information that shapes the foot trajectory and its variation with foot unloading in toddlers. It has been hypothesized that the infant population provides a good subject pool for studying the afferent control of walking in the human, before cerebral influences are fully developed (Yang et al. 1998), and some of the adaptive mechanisms we found may reside in subcortical structures. For instance, spinal cats cannot compensate for cutaneous denervation, whereas intact cats with normal supraspinal control can easily adapt to the lack of load-related cutaneous information (Bouyer and Rossignol 2003). Therefore we cannot exclude the possibility that the observed phenomenon reflects undeveloped supraspinal control of foot placement in toddlers because the descending pathways (Kinney et al. 1988; Paus et al. 1999; Yang and Gorassini 2006) and central conduction delays (Eyre et al. 1991) are immature at the beginning of unsupported walking.

Ankle plantarflexor activity is an important contributor to the initiation of the swing phase at the end of stance (Neptune et al. 2006), and its immaturity can possibly reorganize the locomotor program by compensating with hip flexors or performing shorter steps, as happens in patients (Nadeau et al. 2006; Ivanenko et al. 2005; Sutherland et al. 1988). The argument can be made, however, that limited muscle strength may not be the main factor for body weight perception and forward movement can be made, however, that limited muscle strength may not be the main factor for body weight perception and forward propulsion. For instance, when lifting oneself out of the water after a swim or bath, one perceives the body as being very heavy, and it can be initially very difficult to walk, even though the absolute strength of the muscles is not affected at all. This implies that body weight bearing requires appropriate postural and coordinative behavior. As for the toddler stepping, even at high levels of body weight support (requiring much less plantarflexor activity for propulsion), toddlers still move their legs differently from adults and older children (with a different dynamics and an overshoot of foot motion; Figs. 4 and 5A). Finally, toddlers are able to carry the additional heavy weights (Adolph and Avolio 2000). We instead suggest that the toddler idiosyncratic pattern may be a result of immature foot–support interactions and a lack of the appropriate pendulum behavior of the limbs and of the center-of-body-mass, rather than muscular underdevelopment. The transition to a pendulum pattern occurs within a few months of independent walking experience (Ivanenko et al. 2004) and is accompanied by rapid improvements in stability (Assaiante et al. 1993; Bril and Brenière 1993; Goodman et al. 2000; Roncesvalles et al. 2001) and other gait characteristics (Fig. 2, see also Cheron et al. 2001b; Hallemans et al. 2006; Ivanenko et al. 2005; Sutherland et al. 1988). Experience with body mass propulsion requires producing active forces in the form of escapeament pulses that may activate and complement the pendulum or spring dynamics (Holt et al. 2006), given appropriate (unsupported gait) input (Ivanenko et al. 2007). In fact, walking practice is a much stronger predictor of posture and gait improvement in newly walking toddlers than age or body size (Adolph et al. 2003; Holt et al. 2006; Ivanenko et al. 2004, 2005; Roncesvalles et al. 2001; Sundermier et al. 2001; Sutherland et al. 1988).

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REFERENCES


FURTHER READING IN TODDLERS


