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Kinematic Strategies in Newly Walking Toddlers Stepping Over Different Support Surfaces

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Dominici N, Ivanenko YP, Cappellini G, Zampagni ML, Lacquaniti F. Kinematic strategies in newly walking toddlers stepping over different support surfaces. *J Neurophysiol* 103: 1673–1684, 2010. First published January 20, 2010; doi:10.1152/jn.00945.2009. In adults, locomotor movements are accommodated to various support surface conditions by means of specific anticipatory locomotor adjustments and changes in the intersegmental coordination. Here we studied the kinematic strategies of toddlers at the onset of independent walking when negotiating various support surface conditions: stepping over an obstacle, walking on an inclined surface, and on a staircase. Generally, toddlers could perform these tasks only when supported by the arm. They exhibited strategies very different from those of the adults. Although adults maintained walking speed roughly constant, toddlers markedly accelerated when walking downhill or downstairs and decelerated when walking uphill or upstairs. Their coordination pattern of thigh–shank–foot elevation angles exhibited greater inter-trial variability than that in adults, but it did not undergo the systematic change as a function of task that was present in adults. Thus the intersegmental covariance plane rotated across tasks in adults, whereas its orientation remained roughly constant in toddlers. In contrast with the adults, the toddlers often tended to place the foot onto the obstacle or across the edges of the stairs. We interpret such foot placements as part of a haptic exploratory repertoire and we argue that the maintenance of a roughly constant planar covariance—irrespective of the surface inclination and height—may be functional to the exploratory behavior. The latter notion is consistent with the hypothesis proposed decades ago by Bernstein that, when humans start to learn a skill, they may restrict the number of degrees of freedom to reduce the size of the search space and simplify the coordination.

INTRODUCTION

When toddlers start to walk independently, their gait differs dramatically from more mature walking. Nevertheless, even though the toddler gait has immature characteristics (Assaiante et al. 1993; Bertsch et al. 2004; Bril and Brenière 1993; Cheron et al. 2001; Forssberg 1985; Ivanenko et al. 2004; Roncesvalles et al. 2001), it might be beneficial as an optimal starting point or as a transitional strategy (Ivanenko et al. 2007b). It may be adapted to the initial state of the control system, that is, undeveloped internal representations of both the support surface and the precise endpoint (foot) position in space. Indeed, evolutionary adopted nonplantigrade gait with a higher foot lift (Dominici et al. 2007; Forssberg 1985) could be a safe simple strategy for avoiding potential 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 in young infants (Yang et al. 2004). In addition, infant stepping shows some elements of an “optimal” or adultlike capacity for adaptation to speed changes and external perturbations (Lam et al. 2003a; Lamb and Yang 2000; Pang and Yang 2001; Thelen et al. 1987).

An important aspect of early motor development is exploratory learning (Bernstein 1967; Berthier et al. 2005; Bril and Brenière 1992; Goldfield et al. 1993; Thelen and Smith 1994; Von Hofsten 1993). In particular, many researchers consider variability in infants’ movements as manifestation of intentional exploration motivated by search for information. Adaptive control of movements also requires prospective control—the ability to plan actions on the basis of “perceived action possibility” (denoted as “affordance” by Gibson 1979) that couples perceptual information with the physical requirements for an action (Adolph 1995; Lee 1994). Children must detect information for affordances through the use of exploratory activity and previous experience. For instance, perceptual judgments of walking ability on slopes (2–36°) in toddlers of 14 mo are related to the length of their walking experience (Adolph 1995). Finally, during development the large number of degrees of freedom (df) needs to be controlled and Bernstein (1967) proposed that, at the beginning of learning a skill, individuals may restrict the df to reduce the size of the search space and simplify the coordination. However, little information is known about how exploratory learning in newly walking toddlers is reflected in their kinematic strategy when navigating across various realistic environments.

In adults, locomotor movements can be accommodated to various support surface conditions, such as uneven or compliant terrain, stairs, and obstacles, being accompanied by anticipatory locomotor adjustments and appropriate changes in the intersegmental coordination. In particular, limb segment rotations covary so that the three-dimensional (3D) trajectory of temporal changes in the elevation angles lies close to a plane whose orientation characterizes specific gait-dependent phase relationships between angular limb segment motions (Barliya et al. 2008; Courtine and Schieppati 2004; Ivanenko et al. 2008; Lacquaniti et al. 1999, 2002; Noble and Prentice 2008). The planar covariation reduces the effective df and may reflect a way in which the so-called telescopic limb behavior (end-point control by controlling the length and orientation of the main limb axis) is realized in human locomotion, likely by controlling the distribution of joint stiffness and thus the relative rotation of limb segments (Ivanenko et al. 2007a).

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In toddlers, the coordination pattern of the thigh–shank–foot elevation angles is more variable and departs from the mature pattern; nevertheless, the gait loop can be approximated by a single plane (Cheron et al. 2001; Ivanenko et al. 2004). Although general adaptive changes have been documented for the infant gait (Adolph and Avolio 2000; Dominici et al. 2007; Gibson et al. 1987; Jensen et al. 1994; Lam et al. 2003a,b; Pang and Yang 2001; Patla et al. 1996; Schmuckler 1993; Thelen and Cooke 1987; Thelen et al. 1987; Ulrich et al. 1990; Yang et al. 2005; Zelazo 1983), it is not known whether the intersegmental coordination can be adapted as well or represents an invariant feature of infant stepping. Spinal and brain stem control has a dominant influence on infant stepping (Eyre et al. 1991; Forssberg 1985; Kinney et al. 1988; Yang et al. 1998) and recent studies suggest that the spinal cord is capable of encoding foot position (Poppele and Bosco 2003) and correcting kinematic errors in hindlimb coordination (Heng and de Leon 2007). In view of these advances, infants may represent a unique population of human subjects to study gait adaptability, exploratory learning, and the role of central versus biomechanical constraints on the kinematics control of human locomotion.

The purpose of this study was to investigate how newly walking toddlers adjust their kinematic pattern when negotiating various support surface conditions: stepping over an obstacle, walking on an inclined surface, and staircase stepping. The ability of toddlers to step unaided when facing slopes or stairs is very limited and they may use alternative strategies (such as crawling, sliding, descending backward, or in a sitting position; Adolph and Berger 2006). Therefore to facilitate forward stepping, our toddlers walked supported by the hand, which represents a common strategy used by parents to prevent the child's falls and to give the toddlers greater confidence in walking (it is also worth noting that the arm support does not significantly change the intersegmental coordination during level-ground stepping; Ivanenko et al. 2005). In fact, all toddlers showed a great deal of exploratory locomotor activity in these conditions. Strikingly, however, in contrast to adults, toddlers tended to conserve their angular covariation pattern independent of the terrain characteristics. The preliminary results have been reported in abstract form (Dominici et al. 2009b).

METHODS

Participants

Ten toddlers within 2 wk of unaided walking experience [seven males, three females, age 10–16 mo, limb length 30.1 ± 3.6 (SD) cm, weight 10.3 ± 1.1 kg] and six adult subjects (four males, two females, age 33.8 ± 5.2 yr, limb length 80.0 ± 2.6 cm, weight 62.7 ± 8.8 kg) participated in the study. Informed consent was obtained from both the adults and the parents of the children. The experimental procedures were approved by the Ethics Committee of the Santa Lucia Foundation 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 to or lower than that of walking at home.

Protocols

All participants were tested in a large (11×14 m) experimental room. The following conditions were studied in both adults and toddlers.

1) *Overground walking.* For the recording of the 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. Only sequences of steps executed naturally by the toddler (e.g., no stop between steps and approximately constant walking speed across steps) were considered. Adults were monitored while they walked at a natural freely chosen speed along an 8-m walkway.

2) *Walking over an obstacle.* Subjects walked and stepped over an obstacle located in the middle of the walkway. A parent stood at the end of the walkway encouraging the child to walk. As in the previous protocol, in each toddler we tried to implement unsupported stepping over an obstacle in such a way that an experimenter initially held the toddler by hand and tried to leave the toddler's hand while approaching the obstacle. In all such trials, toddlers stopped before the obstacle or attempted to touch and held again the hand of the experimenter. Thus since unsupported stepping was never successful in situations with obstacles, we also recorded stepping over the obstacle while the experimenter or parent held the child by one hand and these trials were used for the analysis. Adults, on verbal instruction, were asked to walk straight ahead and stopped after they completed a nearly 8-m-long path. Two obstacle heights were used for each subject group: 5 and 7 cm for toddlers (5-cm width and 1.5-m length for both obstacles) and 13 and 19 cm for adults (13-cm width and 1.5-m length for both obstacles), which corresponds to about 0.16L and 0.23L, respectively, for both groups (where L is limb length, computed as thigh plus shank length). The order of obstacle presentation was randomized across subjects.

3) *Upstairs and downstairs stepping.* The staircase was composed of three wooden steps and starting and finishing horizontal landing platforms. Stairs were built to adult and infant proportions. For toddlers, the rise height was 5 cm ($\sim 0.16L$), the tread depth 15 cm ($\sim 0.5L$), and the step width 50 cm; for adults, 13 cm ($\sim 0.16L$), 40 cm ($\sim 0.5L$), and 80 cm, respectively. The experimenter always walked aside the subject to prevent falling. As in the previous protocol, we tried to implement unsupported stepping over staircase in each toddler. Since no toddler could step unaided, we recorded walking up- and downstairs while the experimenter or parent held the child by hand.

4) *Uphill and downhill walking (23% inclination of the support surface corresponding to 13°).* The length of the inclined surface was about 2.1L for both toddlers and adults (0.63 m for toddlers and 1.7 m for adults). Again, toddler stepping was recorded with hand support since they could not step unaided on the inclined surface.

The initial position for toddlers was about 1–2 m and for adults it was always 3 m from the obstacle/stairs/slope. Short trials (≤ 2 min, depending on fatigue) were recorded with rest breaks in between. For toddlers, parents stood in front of the child encouraging him/her to walk. Adults were instructed to approach, step over the required support surface, and continue walking at a comfortable self-selected walking speed. They were not given any instructions on how to negotiate the obstacle/staircase/inclined surface and were asked only to step over different surfaces in their usual manner with their preferred selection of leading and trailing limbs. In adults, walking in each support surface condition was repeated five times, for a total of 35 trials [7 conditions (normal walking, 2 obstacles, up- and downstairs walking, uphill and downhill walking) \times 5 repetitions per condition]. For toddlers, it was typical that several trials were recorded for each condition (on average, 9 ± 5 trials per condition). The presentation of conditions was randomized across the subjects. All walking conditions were performed in one session lasting about 1.5 h.

Data recording

Bilateral kinematics were recorded at 100 Hz by means of the nine TV cameras constituting the motion analysis system (VICON-612, Oxford, UK). Passive markers (diameter: 1.4 cm) were placed on the skin after the manual palpation of the following anatomical landmarks

(see also Fig. 1A): glenohumeral joint (GH), elbow (Elb), wrist (Wri), ilium (IL), greater trochanter (GT), lateral femur epicondyle (LE), lateral malleolus (LM), heel (HE), and fifth metatarsophalangeal joint (VM). Particular care was taken to place the VM marker in approximately the same position (on the lateral aspect of the fifth metatarsophalangeal joint) in all subjects. In the task of stepping over an obstacle (condition 2), four markers were also placed on the edges of the obstacle (two markers on each side of the obstacle), to measure its height and position in space. In condition 3, ten markers were placed on the edges of the staircase (five markers on each side of the staircase) to measure its location in space. In condition 4, four markers were placed at the beginning and the end of the inclined surface (two markers on each side), to measure its position.

Data analysis

Performance of the participants was described according to the following parameters: 1) *general gait parameters*, including: walking speed and stride length; 2) *main spatial characteristics of foot motion*, as described by: the amplitude of the foot lift and the position of the center of the foot of the trailing and leading limb relative to the obstacle or edges of the staircase; and 3) *intersegmental coordination*, assessed by using the principal component analysis (PCA) of the thigh, shank, and foot elevation angles (Borghese et al. 1996).

For the analysis of normal walking (condition 1), the steps related to gait initiation and termination were discarded and only those performed in the central section of the path were included in the analysis (typically three to six strides for toddlers and two to four strides for adults). Deviations of gait trajectory relative to the x -direction (Fig. 1B) 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. For stepping over the obstacle, three strides were analyzed: the stride preceding the obstacle (step -1), the crossing stride (step 0), and the following stride (step 1). For stair ascent and descent, all strides over the staircase were analyzed. For downhill and uphill walking, only the strides started and ended on the inclined surface were analyzed (typically one to three strides for toddlers and one stride for adults). The body was modeled as an interconnected chain of rigid segments: GH-IL for the trunk, GH-Elb for the arm, Elb-Wri for the forearm, IL-GT for the pelvis, GT-LE for the thigh, LE-LM for the shank, and LM-VM for the foot.

GENERAL GAIT PARAMETERS. Gait cycle was defined as the time between two successive foot-floor contacts by the same leg according to the local minima of the vertical displacement of the HE marker (Dominici et al. 2007; Ivanenko et al. 2007a). Walking speed for each stride was computed as the mean velocity of the horizontal (x -axis) trunk movement (km/h), the latter being identified by time course of the displacement of a virtual marker located at the midpoint between left and right IL markers. Stride length (m) was measured according to horizontal displacement of the foot marker (VM). In addition, a video clip for each trial was viewed and characterized by two examiners. In particular, we described general obstacle task performance by calculating the percentage of trials with a successful stepping over the obstacle (step over), placing the leading limb onto the obstacle (step onto), stopping before the obstacle (stopped before), and stumbling (brief contact of the leading limb with the obstacle and the following foot movement). For the stair climbing task, we described where the subjects placed the first foot (on which edges or treads) when approaching the staircase. Finally, observations were made by two examiners on unusual behavior when negotiating different support surfaces.

CHARACTERISTICS OF FOOT MOTION. The amplitude of the foot lift in the obstacle task (condition 2) was measured as the vertical foot (VM marker) displacement of the leading limb in space and in the uphill/downhill stepping task (condition 4) as the vertical displacement of the VM marker relative to the hip. The horizontal position of the center of the foot was used to characterize foot placements of both limbs relative to the obstacle or edges of the staircase. It was calculated as a virtual marker located at the midpoint between LM and VM markers. The horizontal foot position relative to the obstacle/staircase was normalized to the subject's limb length (L) calculated as thigh plus shank segment length. For the obstacle task, the spatial distribution of foot placements relative to the obstacle was expressed as the percentage of the total steps (the data for stepping using the two obstacle heights were pooled together). The latter analysis was performed for the crossing stride (step 0, the leading limb) and for the stride preceding the obstacle (step -1, both the leading and trailing limbs). For the stair climbing task, we characterized 1) percentage of placing the first foot on different parts of stairs (edges and treads) when approaching the staircase (first foot placement) and 2) total

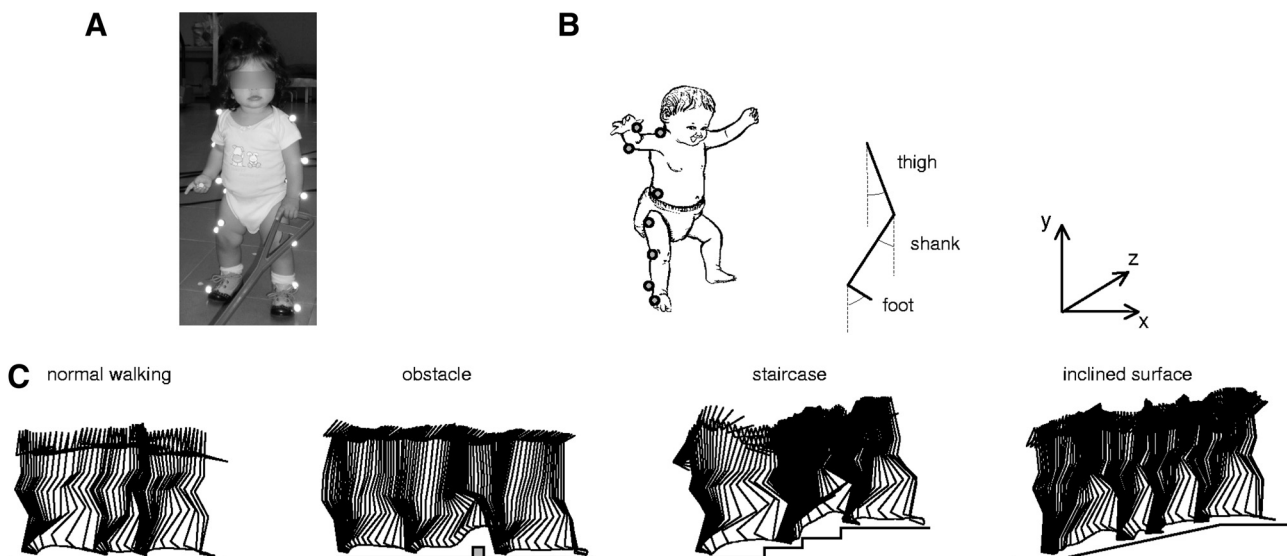


FIG. 1. Experimental setup. A: kinematic data were measured by monitoring markers placed bilaterally on specific body landmarks. The body was accordingly modeled as an interconnected chain of rigid segments. B: elevation angles of the thigh, shank, and foot segments in the sagittal x - y plane were computed relative to the vertical. C: examples of unilateral sagittal stick diagrams of one representative child are illustrated for stepping over the normal flat surface, obstacle, staircase, and inclined surface. For the latter 3 conditions, the toddler walked with the hand held in the hand of an experimenter. Photograph used with permission.

spatial distribution of all steps during stair climbing (the left and right foot placements were pooled together).

INTERSEGMENTAL COORDINATION. The elevation angle of the thigh, shank, and foot 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) (Fig. 1B). The intersegmental coordination of the elevation angles in the sagittal plane was evaluated in position space as previously described using PCA (Borghese et al. 1996; Ivanenko et al. 2007a). Briefly, 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_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_{it} , u_{is} , and u_{if} correspond to the direction cosines (projections) with the positive semiaxis of the thigh, shank, and foot angular coordinates, respectively. The first two eigenvectors u_1 – u_2 lie on the best-fitting plane of angular covariation. The third eigenvector (u_3) is the normal to the covariation plane and defines the plane orientation. The planarity of the trajectories was quantified by the percentage of total variation ($PV = PV_1 + PV_2$) accounted for by the first two eigenvectors of the data covariance matrix (for ideal planarity, $PV = 100\%$ and $PV_3 = 0$). Since the tasks were performed differently by the toddlers and the adults (i.e., toddlers often placed the foot onto the obstacle or edges of stairs; see RESULTS), in the obstacle task, we included only step over trials to compare the intersegmental coordination with a similar task performance in the toddlers and the adults. For the upstairs and downstairs tasks in toddlers, we also analyzed separately the steps landed on treads and edges.

Statistics

Descriptive statistics included means \pm SD. Statistical analyses (Student's *t*-test, ANOVA) were used to compare gait parameters (walking speed, stride length, foot lift) across conditions and subjects, after the evaluation of the normal distribution of the data. For the obstacle task, two-way repeated-measures ANOVA was used to evaluate the influence of group and obstacle height (2 groups [toddlers, adults] \times 2 heights) on the leading foot lift (dependent variable) during the crossing stride (step 0). For the uphill/downhill walking task, two-way repeated-measures ANOVA was used to evaluate the influence of group and condition on the vertical foot displacement (2 groups [toddlers, adults] \times 2 conditions [uphill, downhill]). Since the toddlers walked uphill and downhill at different speeds (see RESULTS) and the foot lift depends on the walking speed (Ivanenko et al. 2002), the selected strides at about the same walking speed (~ 0.75 km/h) were chosen for the analysis. The Shapiro–Wilk test was used as the test of normality for the spatial distribution of foot placements in the obstacle task and the distribution was also classified using cluster analysis (K-means clusters, Statistica 6.0, StatSoft). Spherical statistics on directional data (Batschelet 1981) were used to characterize the mean orientation of the normal to the covariation plane (see earlier text) and its variability across steps. To assess the variability directly, we calculated the angular SD (called spherical angular dispersion [SAD]) of the normal to the plane. Two-way factorial ANOVA was performed to evaluate the influence of group and task (2 groups [toddlers, adults] \times 6 tasks [normal walking, obstacle, stair ascent and descent, uphill and downhill walking]) on u_{3t} , u_{3s} , u_{3f} (dependent variables). Post hoc tests were performed by using the Tukey test. Reported results were considered significant for $P < 0.05$.

RESULTS

All toddlers were just beginning to walk independently and we succeeded in recording their unsupported stepping over the flat horizontal surface under laboratory conditions. The mean

walking speed was 1.4 ± 0.6 km/h and stride length was 0.72 ± 0.15 m, consistent with previous studies (Cheron et al. 2001; Halleman et al. 2005; Ivanenko et al. 2004, 2005). For each toddler, we tried to implement unsupported stepping over different support surfaces. However, in all such trials, toddlers stopped before the obstacle/stair/slope and thus failed to negotiate it. Therefore we also recorded stepping with arm support. This maneuver highly facilitated the task and all toddlers achieved task performance. In the first three sections, we describe the general gait and foot placement characteristics during stepping over different surfaces and in the last section the changes in the intersegmental coordination.

Stepping over the obstacle

While negotiating an obstacle in their travel path, adult subjects showed a typical anticipatory foot placement behavior reported previously in numerous studies (e.g., McFadyen and Carnahan 1997; Patla and Prentice 1995; Sparrow et al. 1996). The key features of lead and trail foot motion are summarized in Fig. 2. Adult subjects showed precise and systematic gait adaptations to step over the obstacle and no subject contacted the obstacle (Fig. 2A). At both heights, the obstacle was accommodated in a natural manner without abrupt adjustments to the gait pattern or any other unusual adaptations. In particular, lead foot lift increased systematically in all adult subjects as the obstacle height increased (Fig. 2B). Foot placing in step -1 was well differentiated for the leading and trailing limbs and occurred at about 1.18L and 0.33L from the obstacle, respectively (Fig. 2C; the data for the two obstacle heights were similar and therefore were pooled together; see also Sparrow et al. 1996). The leading limb crossed the obstacle (see pie charts in Fig. 2A) and contacted ground at a distance of about 0.57L (Fig. 2D).

Toddlers in about 21% of trials either refused to cross the obstacle (stopped before) or failed to do it correctly (stumbled). Interestingly, successful obstacle negotiation was often performed by the toddlers in a manner different from that of the adults, since in 52% of trials they placed the foot onto the obstacle without stopping whole body motion and only in 27% of trials they stepped over (adult subjects stepped over an obstacle in 100% of trials). Total successful obstacle negotiation (step onto and step over) was observed in about 79% of trials. We attempted to challenge the participants with two different obstacle heights ($\sim 0.16L$ and $\sim 0.23L$) and in both cases the percentage of failure trials (stopped before or stumbling) was similar ($\sim 20\%$).

In toddlers during step over trials, the two obstacle heights could not be differentiated in foot path adoption and anticipatory locomotor adjustments. The amplitude of the foot lift in the crossing stride was similar to that of the adults when normalized to the limb length (Fig. 2B, ANOVA [2 groups \times 2 conditions], $F = 0.707$, $P = 0.42$ for the effect of group). However, in contrast to adults, the foot lift (step over trials) did not depend on the obstacle height (Fig. 2B). Placing the leading and trailing limbs in step -1 (step onto and step over trials) occurred in a relatively wide range of positions and with a marked overlap in the lead and trail foot placement distribution (Fig. 2C). Leading limb placing in step 0 showed a wider spatial distribution and a clear difference from that of adults (Fig. 2D) and could not be explained by casual placements, since there were two promi-

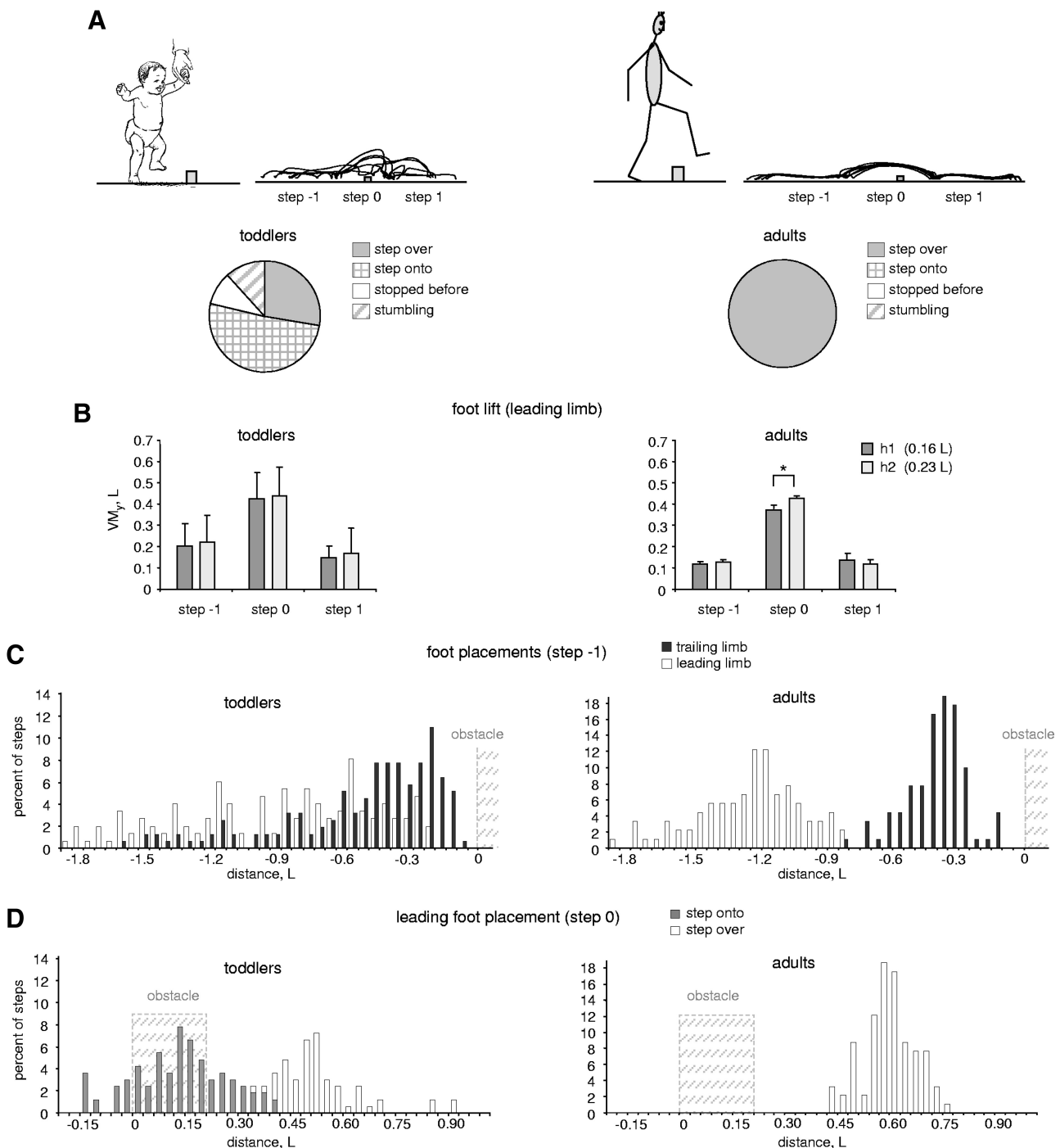


FIG. 2. Stepping over an obstacle in toddlers and adults. *A*: examples of superimposed foot (fifth metatarsophalangeal joint [VM] marker) trajectories ($n = 6$ trials) of the leading limb across 3 consecutive steps in one toddler and one adult. Step 0 corresponds to obstacle crossing. *Bottom*: pie charts showing the percentage of trials for each age group with a successful stepping over the obstacle (step over), stepping onto the obstacle (step onto), making a stop at the obstacle (stopped before), and stumbling (leading limb contact with the obstacle). The data for the 2 obstacles ($h_1 = 0.16L$ and $h_2 = 0.23L$, where L is limb length) were pooled together. *B*: maximal foot height (VM_y) of the leading limb in toddlers and adults for step -1, step 0, and step 1 during step over trials. Asterisk denotes significant difference in the foot lift between the 2 obstacles in adults. *C*: distribution of take-off distances of the leading and trailing limbs (the center of the foot) prior to obstacle crossing (step -1) as a function of the normalized (to the limb length) horizontal distance from the leading edge of the obstacle (the data for all step onto and step over trials and subjects were pooled together). *D*: leading foot placement for the obstacle crossing step (step 0) for toddlers and adults. The obstacle width is schematically indicated by the rectangle. The steps when the foot stepped onto the obstacle are marked in gray.

ment peaks in step 0 that were absent in step -1 (Fig. 2, *C* and *D*). Indeed, we analyzed whether the distribution of foot placement followed a normal distribution (Fig. 2). The distribution differed significantly from normal (Shapiro-Wilk test: $W = 0.975$, $P = 0.004$) and its kurtosis was <0 , indicating a clear bimodal distribution.

This distribution was therefore classified into two groups according to the results from $k = 2$ -cluster solution on all foot placements: the first peak occurred at $0.09L$ (corresponding to step onto trials, Fig. 2*D*) and the second peak was located at the $0.49L$ distance from the obstacle (step over trials, Fig. 2*D*) with a

similar SD (0.12L for both peaks). In contrast, in adults the results of the Shapiro–Wilk test indicated a normal distribution ($W = 0.979$, $P = 0.15$), with the mean value located at the 0.57L from the obstacle (step over).

Stair ascent and descent

Stair climbing performance differed between adults and toddlers. In adults, during stair ascent, the first foot contact occurred on the first step and ended at the same foot contact on

the third step, the contralateral foot placing was spatially shifted by one stair accordingly (Fig. 3, A–C). Stair descent started with foot contact on the first step with stereotyped alternating foot placements (Fig. 3A). The mean horizontal walking speed was equivalent during ascent and descent trials (Fig. 3D, $P = 0.8$, paired t -test), likely suggesting that adults compensate well for different biomechanical gravity- and surface-related requirements to maintain the same natural self-selected speed. Adults never stepped on the edges.

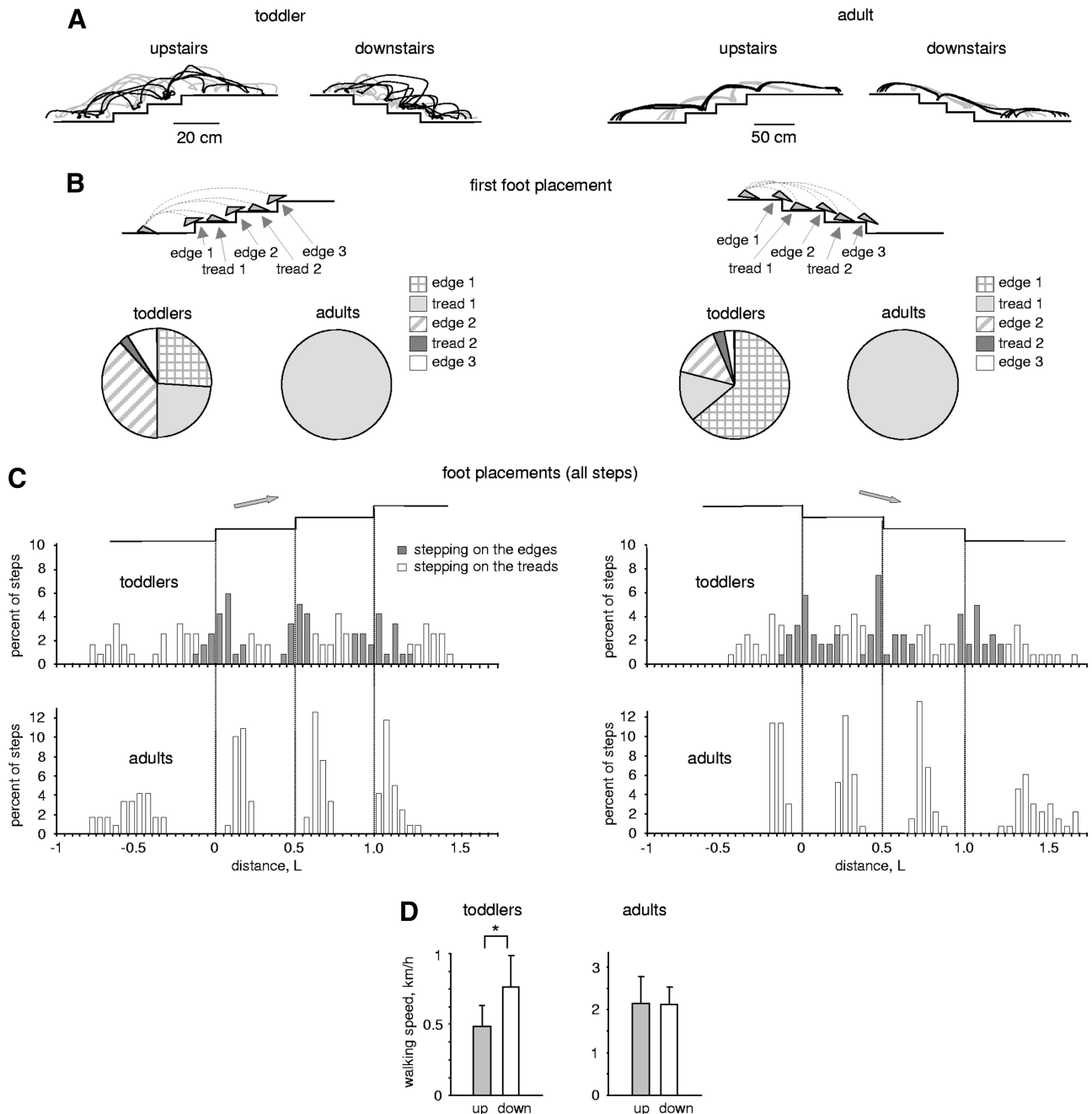


FIG. 3. Stair ascent and descent in toddlers and adults. *A*: examples of superimposed foot (VM marker) trajectories ($n = 4$ trials) in one toddler and one adult. Black, right leg; gray, left leg. *B*: pie charts showing the percentage of the first foot placement on different parts of stairs (see schematic illustration): edge 1, tread 1, edge 2, tread 2, edge 3. Stepping onto the edge or tread was determined from videos by 2 observers. *C*: spatial distribution of foot placements (the center of the foot) in toddlers and adults as a percentage of the total number of foot placements (for both legs) across all trials and subjects. Vertical dotted lines denote locations of stair edges. Distance is normalized to the mean limb length for each age group. The steps when the foot stepped onto the obstacle are marked in gray. *D*: mean (\pm SD) horizontal walking speed in toddlers and adults for ascending and descending trials. Asterisk indicates significant difference ($P < 0.005$, paired t -test).

In toddlers, the first foot contact could occur on both the treads and edges during either stair ascent or stair descent (Fig. 3B). The overall percentages of first foot placements on the edges (sum of edge 1, edge 2, and edge 3 placements in Fig. 3B) were 74 and 77% during ascent and descent trials, respectively (whereas in adults it was 0% during either ascent or descent). Furthermore, some toddlers (three) touched the edges of the stairs with the hand prior to ascending or descending and the occurrence of foot placements on the edges of the stairs was high (Fig. 3C), suggesting haptic “probing” of the support surface. Finally, there was a clear difference in the walking speed during ascent and descent trials because it was significantly higher in the former condition (Fig. 3D, $P < 0.005$, paired t -test).

Walking on the inclined surface

Figure 4A illustrates examples of foot trajectories of both legs in one toddler and one adult across four trials. In adults, foot placing was stereotyped across trials. Therefore we did not compare the spatial distribution of foot placements in adults and toddlers. Nevertheless, the results revealed a significant difference in adaptation of general gait and foot motion characteristics to uphill and downhill stepping in the two groups of subjects.

In adults, as in the case of stair climbing, the mean walking speed was similar during up and down trials (Fig. 4B, $P = 0.7$, paired t -test). However, the foot trajectory showed adaptation; the foot lift was higher during downhill walking (Fig. 4C). In toddlers, performance was basically opposite to that of adults in this task. The walking speed increased significantly during downhill trials (Fig. 4B, $P < 0.01$, paired t -test), whereas the foot path characteristics were similar in comparisons of the selected strides at the same walking speed of 0.75 km/h (Fig. 4C). ANOVA (2 groups \times 2 conditions) showed no significant effect of the group ($F = 1.53$, $P = 0.24$) and condition (uphill vs. downhill, $F = 2.70$, $P = 0.12$) on the vertical foot displacement, but a significant group \times condition interaction

($F = 16.60$, $P < 0.001$). Post hoc analysis revealed a significant difference in the foot lift between uphill and downhill walking in adults ($P = 0.01$), but not in toddlers ($P = 0.24$) (Fig. 4C). Again, information-gathering behaviors became evident in some instances: infants looked down the slope as they approached it, stopped at the edge, and generated haptic information from touching, which is consistent with previous observations (Adolph 1997).

Intersegmental coordination

The intersegmental coordination of the thigh–shank–foot elevation angles was compared across all walking conditions and was evaluated in position space using PCA (Borghese et al. 1996). In essence, the method is shown in Fig. 5A. Planar covariation of the elevation angles is directly related to the dimensionality of the original data set. In adult walking, two principal components typically account for about 99% of the total variance ($PV_3 = 0.7\%$ in the example in Fig. 5A). Figure 5, B and C illustrates the examples of planar covariation of leg segment angles for one representative adult subject and one toddler walking over different support surfaces. Three consecutive gait cycles were analyzed and plotted for each case.

In adults, planar covariation holds for different support surface conditions ($PV_3 \approx 0.7\text{--}1.7\%$, Fig. 5B, Table 1) and the orientation of the covariance plane changes systematically across conditions. The orientation of the plane reflects phase relationships between the elevation angles of the leg segments, and therefore the timing of the intersegmental coordination (Bianchi et al. 1998), and is characterized by the u_3 vector of the covariance matrix (normal to the plane). Figure 6A (right panel) illustrates a clear systematic change in the u_{3t} component (projection of the u_3 vector to the thigh axis) reflecting rotation of the normal to the plane. This rotation in 3D (thigh–shank–foot elevation angles space) can be seen in Fig. 6B (right panel) that shows the spatial distribution statistics of the normal to the plane (u_3) for each condition. Each circle on the sphere surface corresponds to the projection of the mean

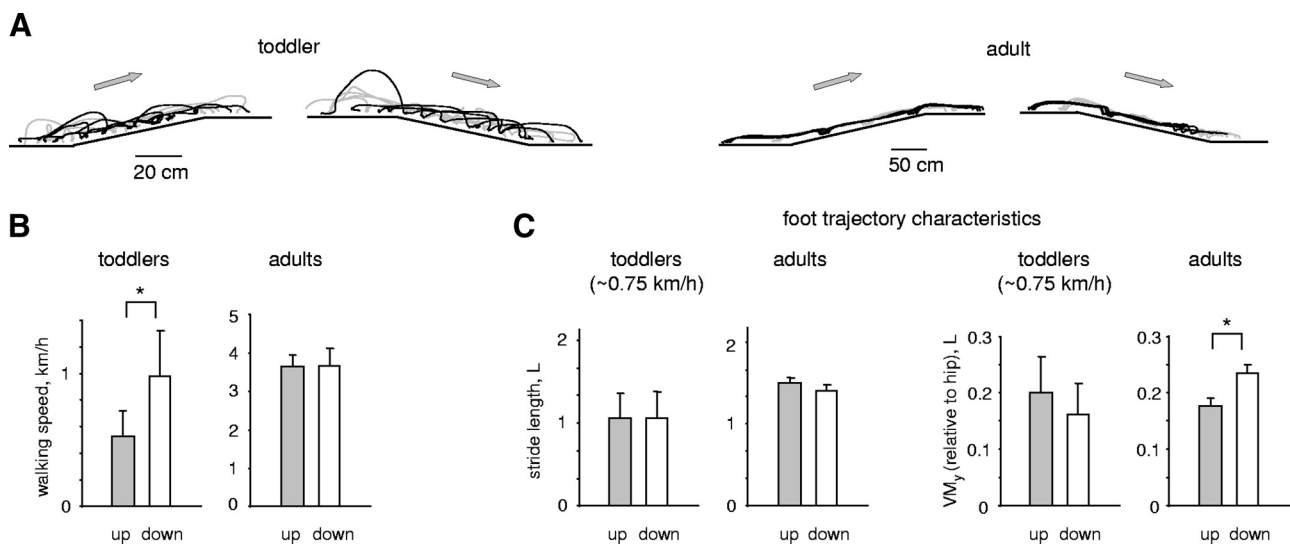


FIG. 4. Walking on inclined surfaces in toddlers and adults. A: examples of superimposed foot (VM marker) trajectories ($n = 4$ trials) in one toddler and one adult. Black, right leg; gray, left leg. B: mean (\pm SD) horizontal walking speeds in toddlers and adults during walking up and down inclined surfaces. C: foot trajectory characteristics in toddlers and adults: stride length and vertical foot motion (peak-to-peak VM_y displacements relative to the hip). For toddlers, we selected steps up and down the inclined surface at matched walking speeds (~ 0.75 km/h). Asterisks indicate significant differences ($P < 0.05$).

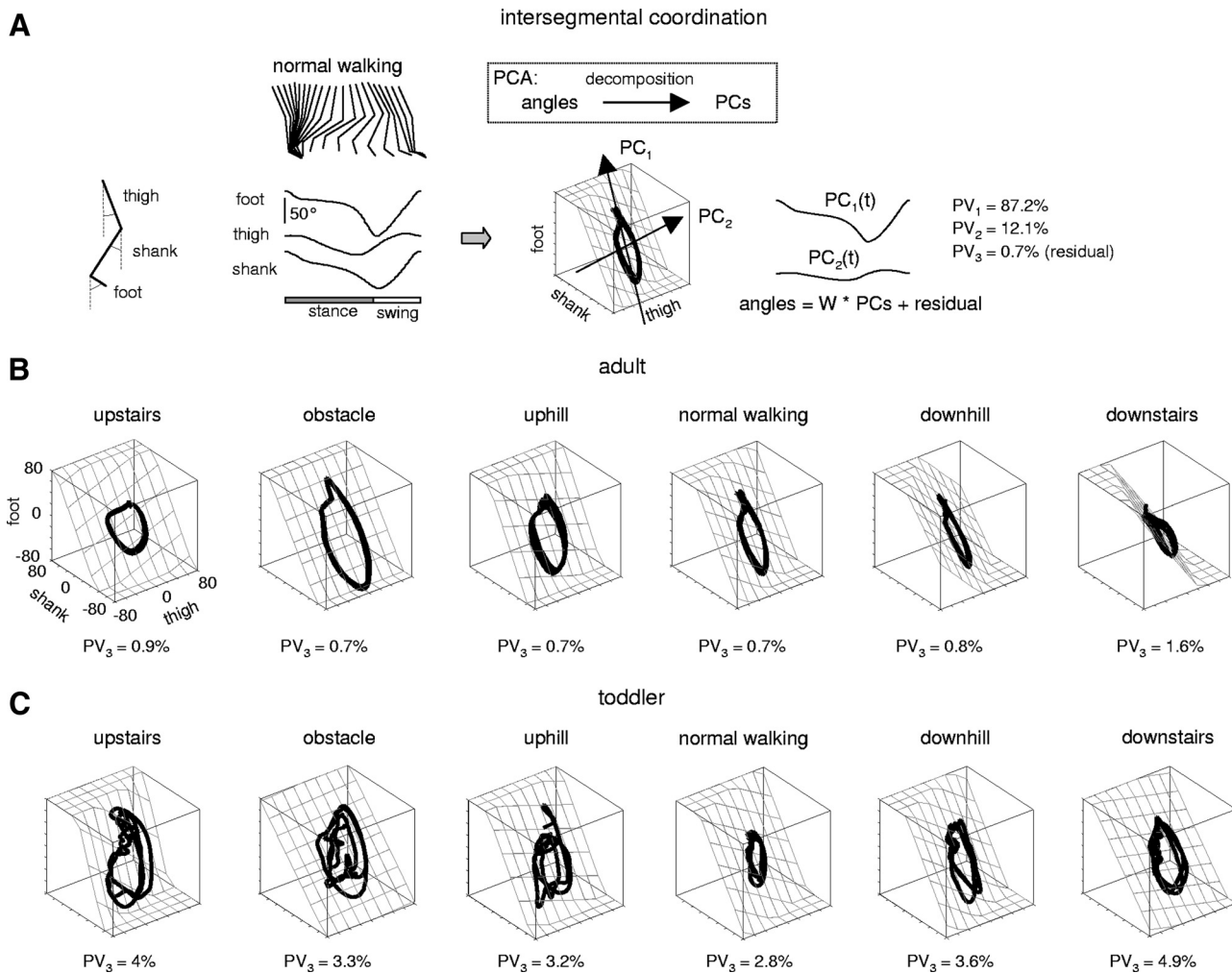


FIG. 5. Planar covariation of elevation angles during stepping over different surfaces. *A*: principal component analysis (PCA) of elevation angles in one representative adult subject during normal walking. From *left to right*: schematic illustration of elevation angles, stick diagram, and thigh, shank, and foot elevation angles of the right leg, corresponding 3D trajectory in segment angle space (gait loop) along with the interpolated plane and the directions of PCs (black arrows), and 2 principal components (PC₁ and PC₂). Gait cycle path (gait loop) progresses in time in the counterclockwise direction, heel strike and toe-off phases corresponding roughly to the top and bottom of the loop, respectively. The interpolation plane results from orthogonal planar regression. *B*: gait loops and interpolation planes during upstairs, obstacle, uphill, normal walking, downhill, and downstairs conditions in one representative adult. *C*: gait loops and interpolation planes in one toddler. Three gait cycles of the right leg were superimposed and processed for each condition. Percentage of total variation explained by the 3rd PC (PV₃) is indicated for each condition. Note higher PV₃ values and less variation in the covariance plane orientation across conditions in the toddler than in the adult.

plane normal (the center of the circle) onto the unit sphere. The mean plane normal was calculated as the mean normal of individual planes. The radius of each circle corresponds to the SAD across subjects. The mean radius of the circles across all conditions was $5.7 \pm 2.1^\circ$ (range, $3.9\text{--}9.2^\circ$). There was a tendency for the normals to intersect the unit sphere along an arc and for upstairs and downstairs conditions the planes rotated in the opposite directions with respect to the level walking plane.

In toddlers, at the onset of independent walking, the gait loop during normal walking departs from the mature pattern

(Fig. 5*C*, *fourth panel*) and the index of planarity (PV) is smaller in toddlers than that in adults (96.5 ± 0.8 vs. $99.3 \pm 0.2\%$, $P < 0.01$ unpaired *t*-test), consistent with previous studies (Cheron et al. 2001; Ivanenko et al. 2004). For the obstacle task in toddlers, we included only the step over trials to compare with a similar task performance in the adults. For the upstairs and downstairs tasks in toddlers, all steps were pooled together since we did not find differences in the u_{3t} parameter between steps landed on treads or edges: $u_{3t} = 0.23 \pm 0.11$ and $u_{3t} = 0.19 \pm 0.07$, respectively, for upstairs and $u_{3t} = 0.28 \pm 0.08$ and $u_{3t} = 0.32 \pm 0.10$ for downstairs

TABLE 1. Planar covariation of the thigh-shank-foot elevation angles (PV₃ parameter, \pm SD) in adults and toddlers during walking over different support surfaces

| | Upstairs, % | Obstacles, % | Uphill, % | Normal Walking, % | Downhill, % | Downstairs, % |
|----------|---------------|---------------|---------------|-------------------|---------------|---------------|
| Adults | 1.7 ± 0.5 | 1.2 ± 0.4 | 1.4 ± 0.9 | 0.7 ± 0.2 | 0.7 ± 0.2 | 1.3 ± 0.4 |
| Toddlers | 4.0 ± 1.3 | 3.3 ± 1.1 | 3.2 ± 1.0 | 3.5 ± 0.8 | 3.6 ± 0.7 | 4.9 ± 1.9 |

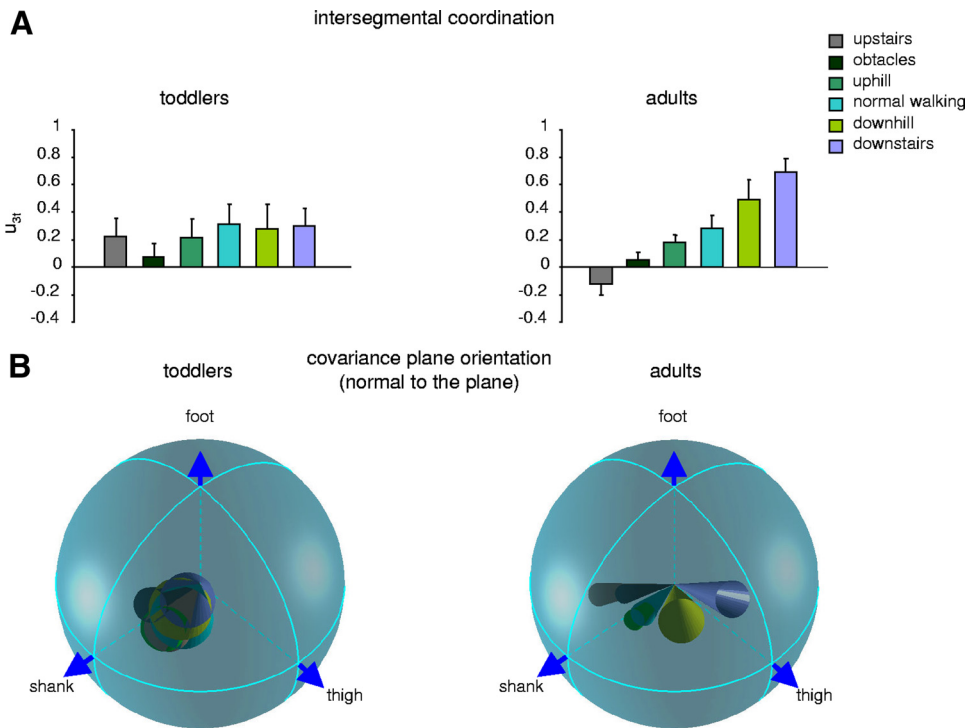


FIG. 6. Orientation of the covariation plane during walking over different surfaces in toddlers and adults. *A*: changes in the u_{3t} parameter (projection of the normal to the thigh axis, mean \pm SD). Note different plane orientations in different walking conditions in adults and similar plane orientations in toddlers. For the obstacle task in toddlers, we included only the *step over* trials (*step onto*, *stopped before*, and *stumbling* trials were excluded) to compare with the same task performance in the adults. For the upstairs and downstairs tasks in toddlers, all steps were pooled together since we did not find differences in the u_{3t} parameter between steps landed on treads or edges. *B*: spatial distribution of the normal to the plane for each condition. Each circle on the sphere surface corresponds to the projection of the mean plane normal (the center of the circle) onto the unit sphere whose axes are the thigh, shank, and foot. The radius of the circle corresponds to the spherical angular dispersion (SAD) across subjects. The angles of cones correspond to 2 SADs, accordingly. The foot and thigh semi-axes are positive and the shank semi-axis is negative.

($P > 0.05$ for both conditions, unpaired t -test). It is also worth noting that, when comparing similar task performance between the two groups (landing on treads), the u_{3t} numbers for steps landed on treads in the toddlers (0.23 ± 0.11 and 0.28 ± 0.08 for upstairs and downstairs, respectively) were significantly different from those in the adults (-0.12 ± 0.08 and 0.69 ± 0.10 , respectively, $P < 0.0002$).

The planar covariation was weaker in toddlers than that in adults across all support surface conditions (Table 1), although the gait loop could still be approximated by a single plane. The step-by-step variability of plane orientation, estimated as the angular dispersion of the plane normal (Dominici et al. 2007), was considerably higher in toddlers ($SAD = 11.4 \pm 2.3^\circ$, averaged across conditions) than that in adults ($5.7 \pm 2.1^\circ$) (Fig. 6*B*). In striking contrast with the adults, we did not find any systematic rotation of the covariation plane across conditions in the toddlers (Fig. 6, *A* and *B*). Only during the obstacle task, did the plane orientation tend to be orthogonal to the thigh axis (smaller u_{3t} parameter, Fig. 6*A*), although it is overlapped with other conditions (Fig. 6*B*). Factorial ANOVA (2 groups \times 6 tasks) showed that the group ($F = 8.402$, $P < 0.00001$) and task ($F = 16.54$, $P < 0.000001$) significantly affected u_{3t} , u_{3s} , and u_{3f} parameters and there was a significant group \times task interaction ($F = 6.632$, $P < 0.000001$). Post hoc analyses revealed a significant difference in the u_{3t} parameter between the adults and the toddlers for the upstairs, downstairs, and downhill tasks ($P < 0.05$ for all three tasks)—that is, a significant rotation of the covariation plane in the adults relative to that in the toddlers for these conditions (Fig. 6, *A* and *B*).

DISCUSSION

The aim of this study was to compare the characteristics of stepping over nonhorizontal surfaces in adults and newly walking toddlers. The analyses revealed several remarkable

differences between these two groups. The foot path and placements were much less accurately controlled in toddlers (Figs. 2, 3*C*, and 4*C*). In particular, in addition to a noticeable percentage of stumbling steps, the foot lift during successful obstacle crossing was not dependent on the obstacle height (Fig. 2*B*) and the leading and trailing limb placements relative to the obstacle were variable as opposed to those in adults (Fig. 2*C*). Overall, the results suggest prominent exploratory haptic foot placement behavior and a simpler strategy in intersegmental coordination in newly walking toddlers, consisting in the maintenance of an approximately constant planar covariance of angular segment motion, whereas in adults the covariance plane systematically rotated across support surface conditions (Figs. 5 and 6). We discuss the findings in the context of their functional significance.

Coordination strategy in toddlers stepping over different support surfaces

Unlike the infants' ability to generate coordinated adultlike "reactive" motor responses to sensory or mechanical limb perturbations (Lam et al. 2003b; Lamb and Yang 2000; Pang and Yang 2001; Thelen et al. 1987), the covariation pattern in toddlers is strikingly resistant to changes in the support surface characteristics (Figs. 5 and 6). The latter behavior may reflect both "reactive" and anticipatory adjustments. Unsupported stepping was not successful in our toddlers during stepping over obstacles/stairs/inclined surface so that they walked with hand support. However, it is unlikely that hand-holding significantly changes the covariation pattern since it does not change the intersegmental coordination during level-ground stepping (Ivanenko et al. 2005). Appropriate planar covariation might be necessary both for gait optimization (Bianchi et al. 1998; Ivanenko et al. 2004) and for maintaining stability (Cheron et al. 2001), which differs considerably in walking and standing

because the former necessitates appropriate lower limb coordination. Another argument in favor of its functional significance is that, in contrast to adults, toddlers did not compensate for the velocity of the forward body motion: the walking speed markedly increased and decreased when stepping down and up, respectively (Figs. 3D and 4B). In line with previous studies, the aforementioned differences may indicate that toddlers need to learn the “rules” of walking in the gravity field (Holt 2006; Ivanenko et al. 2007).

Indeed, the ability of young children (aged 14–30 mo) to walk unsupported over different terrains is limited, with greater failure rates than those in adults (Adolph and Berger 2006; Patla et al. 1996). Our toddlers were just beginning to walk independently (within 2 wk of unsupported walking experience) and could not step unaided over nonlevel support surfaces. The planar covariance of the elevation angles of the lower limb segments is weak and variable at the time of the first unsupported steps (Cheron et al. 2001; Ivanenko et al. 2004). The parallel development (similar time constants) of trunk stabilization, planar covariation of the elevation angles (Cheron et al. 2001), and the gravity-related pendulum mechanism of walking (Ivanenko et al. 2004) suggests that a dynamic integration of a gravity-centered reference for equilibrium and forward propulsion emerges rapidly after the onset of independent walking.

In adults, the full limb behavior in all gaits can be expressed as the 2 degree of freedom (df) planar motion for each gait, plus the rotation of the planes about a defined axis (1 df) (Ivanenko et al. 2007a). This extends the analysis to a full 3 df spatial control of locomotion, in which the third dimension may determine the gait pattern or its adaptation to different support surface conditions. In toddlers, the maintenance of a roughly constant planar covariance (Figs. 5 and 6) reduces flexibility of the kinematic pattern and thus restricts the manifold of angular segment motion. It is also worth noting that the planar covariance was similar in toddlers when landing the foot either on treads or on edges of stairs. Therefore we suggest that this coordination strategy is consistent with the exploratory learning hypothesis of Bernstein (1967) according to which children learn by first reducing the degrees of freedom.

The fact that stepping over the same terrain could be performed using different covariation patterns in adults and toddlers (Fig. 6) strongly supports the idea that the origin of the planar covariation law is not purely biomechanical, but to a great extent depends on the neural control and learning (Barliya et al. 2008; Ivanenko et al. 2008). We recently showed that the 2 df of the covariation plane may represent limb length- and orientation-related angular covariances. For instance, a linear combination of in-place angular covariances (e.g., during stepping in place) with limb orientation covariance could predict actual intersegmental coordination in different gaits (Ivanenko et al. 2007). Limb length and orientation components also have central representations in the activity of spinocerebellar neurons (Bosco and Poppele 2000). Furthermore, a separate limb length (foot lift) control is associated with a particular muscle activation synergy in both healthy subjects (Ivanenko et al. 2005) and spinal cord injury patients (Ivanenko et al. 2003). Finally, there is also developmental evidence supporting separate maturation/control of limb length and orientation. For instance, kicking (Dominici et al. 2007; Thelen 1981) and foot lift (“flexor-biased” locomotor component; Forssberg 1985;

Ivanenko et al. 2005) movements are considered as motor primitives or stereotypes in young infant behavior. Thus the basic elements of the locomotor pattern are innate to humans, although safe bipedal negotiation of the environment seems to require their appropriate integration that develops over time (McFadyen and Carnahan 1997). At the onset of independent walking, effective stepping over different support surfaces is learned with a simple exploratory learning strategy of reducing the degrees of freedom that need to be adjusted and controlled (freezing orientation of the mean covariance plane, Fig. 6).

Exploratory foot placement behavior in toddlers

In the context of traveling in a cluttered environment over different surfaces, toddlers often tended to place the foot onto the obstacles or edges of stairs that we interpret as a part of haptic exploratory repertoire. Even taking into account step-by-step variability, the characteristics of the footfalls could not be fully explained by random or casual placements. It was most evident in the obstacle task in which a spatial distribution of the leading limb footfalls had two prominent peaks corresponding to the “step onto” and “step over” strategies (Fig. 2D). For the stair task, the occurrence of foot placements on the edges of the stairs was also high (Fig. 3). Furthermore, in many cases toddlers touched the edges of the stairs with the foot prior to ascending or descending, suggesting haptic “probing” of the support surface without moving the body forward. In contrast, all adults demonstrated stereotyped foot placement characteristics (Figs. 2, 3, and 4). It is worth mentioning that the adult subjects did not have special instructions except for “stepping forward until the end of the walkway.” Likely, their stereotyped behavior was based on the everyday life experience with staircase/obstacle stepping and anticipatory feedforward control of foot placements as one travels over uneven terrains.

Vision plays a major role in navigation through structural environments. Adults have been found to fixate on the obstacle for the last two steps prior to the obstacle, but not the step over the obstacle, suggesting that the nervous system can process visual spatial information in a feedforward control mode to facilitate safe foot placement (Patla 1997). Young children show inconsistency in selecting an appropriate strategy (Patla et al. 1996) and further studies on the role of fixation when approaching an obstacle will advance our understanding of the relationship between visual exteroceptive input and perceptual judgment of the environment in toddlers. For instance, infants simultaneously look and take a probing step when peering over the brink of the descending slope (Adolph and Berger 2006). Nevertheless, the usage of visual information is greatly influenced by cognitive factors and infants may even neglect obvious obstacles (e.g., toys located on the floor) when walking in a play area. The occurrence of the first steps at around the age of 1 yr is approximately coincident with the appearance of a new “geometric” mechanism of joint visual attention (looking where someone else is looking or pointing; Butterworth 1998). Improved cognitive capacity to generate different associations (Zelazo 1983) may in turn be accelerated by underlying changes in information accessibility due to the enhanced freedom to explore the world beyond the territory at hand when starting to walk.

These perceptual and cognitive aspects were not an intended focus of the current study. We do suggest, nevertheless, that

“haptic” foot exploratory placements (Figs. 2 and 3) and simplified kinematic strategy of limb segment motion (Fig. 6) can be viewed as a process of learning to gain control over movement, calibrating the sensorimotor space (Adolph and Berger 2006; Bernstein 1967; Berthier et al. 2005; Chen et al. 2007; Konczak and Dichgans 1997), and integrating the visual, kinesthetic, and effector system properties in the coherent locomotor body schema (Dominici et al. 2009a).

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