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What Does Prone Skateboarding in the Newborn Tell Us About the Ontogeny of Human Locomotion?

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The crawling behavior of sixty 2-day-old newborns was studied while they were supported prone on a mini skateboard and on a pediatric mattress without additional support. Analyses of the number and types of limb movements and their characteristics, the coactivation of limb pairs, and the displacement across the surface, revealed that newborns can crawl with locomotor patterns similar to those documented during quadrupedal locomotion in animals and human adults. This was particularly apparent on the skateboard. This discovery suggests that locomotor circuitry underlying quadrupedal locomotion develops during fetal life. Drawing upon other evidence for a quadrupedal organization underlying bipedal gait, we argue that early quadrupedal training may enhance interventions designed to hasten the onset of independent walking.

Bipedal Versus Quadrupedal Locomotion in Humans

Efficient bipedal locomotion and the upright posture of modern humans are unique among living primates. Using functional anatomy, energetic calculations, and evolutionary psychology, studies of fossil hominids have contributed significantly to our understanding of the evolution of upright posture and bipedal locomotion (Niemitz, 2010). However much less is known about quadrupedal locomotion in present-day humans, even though the vast majority of human infants crawl long before they learn to walk (Adolph & Robinson, 2013) and the emergence of this crawling has been demonstrated to have crucial consequences for

multiple developmental domains (Anderson et al., 2013; Anderson et al., 2018; Campos et al., 2000). It is relevant to note here that the terms crawling and creeping have been used interchangeably for decades in motor development research. However, when we use the term crawling, we refer to what is now commonly called “hands-and-knees crawling,” with the belly supported above the floor. Historically, the term “creeping” was used to refer to this type of prone locomotion and the term crawling was used to refer to a manner of prone progression in which the belly stayed in contact with the floor, what researchers and clinicians now refer to as “belly-crawling.”

Infants are not the only ones to crawl; even without practice, adults retain remarkable crawling capacities that can be recruited on demand (Cole, Vereijken, Young, Robinson, & Adolph, 2018). With training, adults can even become crawling experts, literally running on four limbs or climbing at impressive velocities, as demonstrated in many online video clips (;). Perhaps the most puzzling

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observation is that even upright bipedal locomotion is not free of quadrupedal mechanisms, with the arms oscillating as pendulums in concert with the legs (Canton & MacLellan, 2018; Dietz, 2002; Dietz & Michel, 2009; Zehr, Hundza, & Vasudevan, 2009). Coordinated movements among the arms, legs, and trunk have also been highlighted as evidence that the functional spinal neuronal networks underlying adult walking have a quadrupedal organization (Falgairolle, de Seze, Juvin, Morin, & Cazalès, 2006). According to Falgairolle et al. (2006), “while there has been a progressive increase in locomotor system complexity during evolution, many basic features have been preserved across the spectrum from lower vertebrates through to humans” (p. 305). This suggestion has received further empirical support recently from a study by La Scaleia et al. (2018) showing evidence of alternating arm–leg oscillations when newborns engaged in supported upright stepping on a moving treadmill belt or on a stationary surface of support. Though these alternating oscillations were sporadic, they showed the same diagonal coupling between the upper and lower limbs that has been documented in adult walking, with the peak forward movement of the upper arm coinciding with the end of the stance phase on the ipsilateral leg. The authors claim that these findings provide evidence for the presence of a neural coupling between the upper and lower limbs during locomotion at birth. We believe this coupling would be even more evident if the experimenter did not restrict the movement of the arms by holding the newborn under its armpits, a technique widely used in infant stepping studies. We hypothesize that supporting the newborns at the trunk, as was done in Barbu-Roth et al.’s (2009, 2014) stepping studies, would reveal a more robust quadrupedal pattern in the upright position.

In line with these suggestions about the neural circuitry underling walking, it is interesting to note that even though the bodies of modern adults have been sculpted by evolutionary pressures for bipedal propulsion, evidence suggests that newborns are not born with a morphology suited for bipedalism. For example, Thelen and Ulrich (1991) have noted that newborns are biomechanically unsuited for upright locomotion because they have large heads and trunks and proportionally small and weak limbs. In contrast, some characteristics of the newborn’s morphology appear much more suited to quadrupedal locomotion because its top-heavy characteristics are less problematic in the prone position as the demands on support and balance

mechanisms are negligible. In addition, walking proficiency and efficiency continue to improve over several years as anthropometric changes are induced by growth, maturation, and practice locomoting in the upright posture (Ivanenko, Dominici, & Lacquaniti, 2007; Mangione, Gomez, & Senegas, 1997; Shefelbine, Tardieu, & Carter, 2002). On the flip-side, it is interesting to note that habitual quadrupeds, like circus bears and elephants can be taught to locomote bipedally for extended periods despite having a morphology more poorly suited to bipedal locomotion. Similarly, cats and dogs can walk on their hind limbs if provided appropriate support or trained extensively (Rossignol, Dubuc, & Gossard, 2006). These findings suggest that the neural circuitry underlying quadrupedal locomotion can be adapted to bipedal locomotion, even in animals whose morphology is poorly suited to bipedalism.

The aforementioned observations raise an interesting question: have we underestimated the newborn’s capacity to engage in quadrupedal locomotion and have we underestimated the contribution early quadrupedalism makes to the development of later bipedal and quadrupedal locomotion? Answering this question is pivotal for understanding how human infants start to propel themselves and what factors shape the acquisition of independent mobility and future locomotor behavior. This question has assumed even greater importance following recent discoveries that suggest neonatal stepping is a precursor of mature bipedal locomotion, because neonatal stepping and mature bipedal locomotion can be modulated by optic flows that specify forward and backward translation across a surface (Barbu-Roth et al., 2009, 2014), and therefore appear to be regulated by the same sources of information, and because the onset of independent walking is hastened considerably if stepping is trained daily from birth (André-Thomas & Autgaerden, 1966; Zelazo, Zelazo, & Kolb, 1972).

Until very recently, most of the studies on newborns’ locomotor skills had focused on their early capacity to “walk,” that is, to perform alternated steps forward when they are supported in an upright posture with their feet touching a rigid surface. Curiously, little is known about quadrupedal locomotor activity at birth. The focus on neonatal stepping is probably due to researchers’ natural fascination with a behavior that is a defining characteristic of the human species. However, this bias implies that newborn upright stepping is the primitive form of walking, whereas it is quite possible that upright stepping is the manifestation of

quadrupedal locomotion, as suggested by the recent findings of La Scaleia et al. (2018) discussed earlier, but that the quadrupedal pattern has been hidden by the practice of inadvertently interfering with arm movements or ignoring arm movements when newborn stepping is tested. This suggestion is also consistent with the idea expressed by several authors that early stepping, kicking, and crawling might all be part of the same locomotor pattern expressed in different postures and contexts (Barbu-Roth et al., 2009, 2014; Thelen, Bradshaw, & Ward, 1981; Thelen & Fisher, 1982; Thelen, Fisher, & Ridley-Johnson, 1984). For example, Thelen et al. (1981) argued that the similarities in the morphological and temporal structure of infant supine kicking and upright stepping suggested that the leg movements in both forms of behavior might be under the control of a central locomotor pattern. Following Thelen et al.'s (1981) suggestion, and after observing arm movements correlated with leg movements during air stepping in human newborns, Barbu-Roth et al. (2009, 2014) speculated that early crawling, stepping, kicking, and swimming movements might all share the same neurological substrate, consistent with the common core hypothesis for the control of rhythmic human movement (Zehr, 2005). Recent studies on neonatal prone locomotion have also suggested that stepping could be the partial expression of crawling or swimming (Forma, Anderson, Goffinet, & Barbu-Roth, 2018).

Newborn Crawling

As noted already, very little is known about the origins of human quadrupedal locomotion, despite the beautiful descriptions of newborn crawling and swimming provided many decades ago by Myrtle McGraw (1939, 1941). Using film recordings of forty-two 11-day-old infants, immersed in water with their chin supported above the water, McGraw (1939) meticulously described how newborns produced rhythmic arm and leg movements synchronized with lateral trunk bending to propel themselves forward. According to McGraw (1941), newborns can produce similar but much less coordinated movements on land when placed prone on a mattress with their chin supported. However, she reported far fewer arm movements if the newborn crawled alone on a horizontal surface without their chin supported. Other authors, including Bauer (1926), Stirnimann (1938), and more recently Katona (1988, 1989), have reported newborns' capacity to propel themselves when prone on a surface. However, the lack of quantitative data from these

different studies prevents conclusions about whether newborn crawling is truly quadrupedal, involving coordination among all four limbs, or whether newborn crawling is primarily dominated by bipedal stepping in a prone position.

In a recent mixed qualitative and quantitative study on the crawling behavior of twenty-six 3-day-old newborns placed prone on a water mattress, Forma et al. (2018) reported that newborns could propel themselves only short distances, with most of their locomotor movements generated by the legs. Arm movements were very limited. Interestingly, Forma et al. also showed that, like upright air stepping (Barbu-Roth et al., 2009, 2014), the leg crawling pattern was already under supra spinal level control because the newborns modified their leg movements in response to optic flows projected on the mattress. The optic flows were created by a moving black-and-white checkerboard pattern that created the impression the newborn was moving forward or backward across the surface of the mattress. The modification of the leg movements was presumed to be a function of the positive feedback loop created between the visual consequences of movement created by the imposed optic flow patterns and the leg movements that would typically generate these consequences during self-initiated locomotion. This observation suggests that even in a prone position, newborns appear to move under the influence of a bipedal mechanism that is modifiable by supra spinal factors, favoring the idea that bipedal tendencies dominate quadrupedal tendencies at birth. However, Forma et al. noted that this bipedalism could also reflect the newborns' inability to raise their heads and trunks off the mattress, literally pinning their arms under their bodies and preventing efficient propulsion via coordinated arm and leg movements. Tellingly, McGraw (1939) described quadrupedal coordinated swimming movements of the arms and legs, along with propulsion, when her newborns were supported under their chin in the water. Katona also observed greater propulsion when newborns were positioned in the crawling posture for at least 3 min on a slope of 30° with their head oriented downward to minimize the effect of gravity (1989). However, studying the characteristics of propulsion in water or on a slope is difficult, especially if an experimenter is needed to support the newborn's head. Consequently, to investigate the possibility of independent neonatal quadrupedal propulsion on land, there is a need to devise a method that provides independent support for the newborn's head and trunk and frees the arms and legs to engage in propulsive movements in any direction.

The Mini Skateboard

In this study, we report on the use of such a method. The method features a mini skateboard, which conforms to the newborn's unique morphology in a way that supports a slightly flexed position of the head and encourages a natural lengthening of the spine while simultaneously raising the head and the trunk off the ground and freeing the arms. Comfortably and securely wrapped on top of the mini skateboard, the newborn can not only move its arms, head, trunk, and limbs, but also propel itself in any direction thanks to small ball-bearing-style wheels secured to the underside of the skateboard deck (see Figure 1).

Purpose and Significance of this Study

The current study sought to determine if human newborns can perform a quadrupedal pattern of locomotion that involves coordination among all four limbs and that leads to forward progression across a surface. We were especially interested to see if the newborn crawling pattern shows some evidence of the diagonal gait observed in mature human and animal quadrupedal locomotion, that is, diagonal contralateral arm–leg pairs moving in phase and ipsilateral arm–leg pairs moving out of phase. We hypothesized that newborns can make forward progression using a quadrupedal pattern of locomotion on land but, in order to fully express

this quadrupedalism, they need to be relieved from the biomechanical constraints associated with the weight of their head and trunk. To test the hypothesis, we examined prone propulsion and the characteristics of arm and leg movements of 60 newborns in two randomly-ordered conditions lasting 1 min each. In one condition, the newborns were placed prone on a pediatric mattress without any additional support for the head and trunk (Mattress condition). In the other condition, the newborns were wrapped in a prone position on the mini skateboard (Crawli condition). We expected the clearest evidence for a quadrupedal pattern of locomotion and forward progression would be found in the Crawli condition.

Our approach to the issue at hand is inspired by the dynamical systems approach to development introduced by Esther Thelen and her colleagues (e.g., Thelen & Ulrich, 1991) and the more recently elaborated relational-developmental-systems approach (e.g., Overton, 2015), in which development is considered to be multiply determined by a wide range of reciprocally interacting factors internal and external to the individual. The task and environmental contexts are particularly important determinants of behavior within these approaches. Though the current work does not examine change over time, it is grounded in the classic question about the origins of forms. Intrigued by the notion of “hidden skills” (Thelen & Ulrich, 1991), we are motivated to determine whether the newborn's

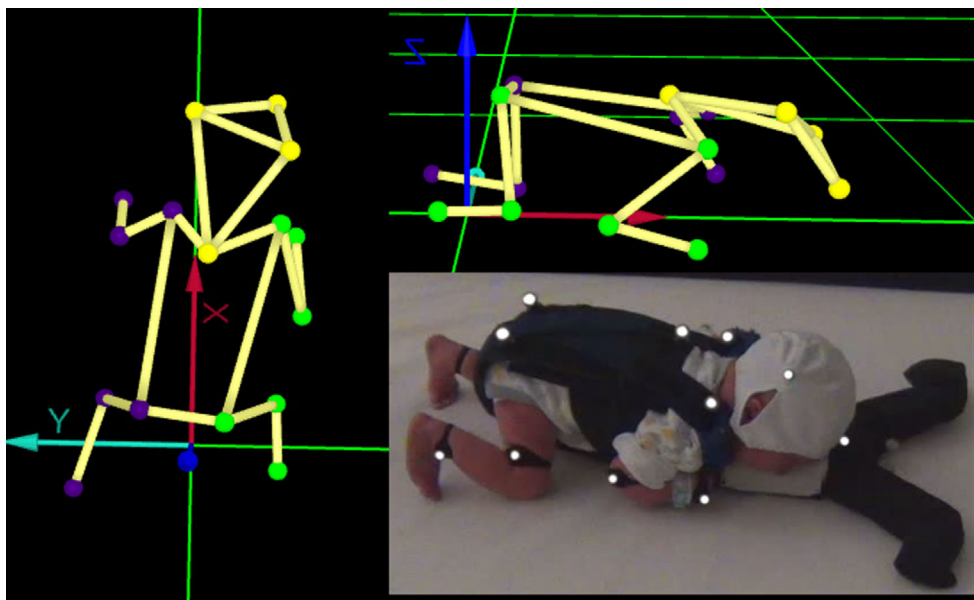


Figure 1. Two-day-old infant crawling on the Crawliskate® with motion capture markers in 3D and 2D.

capacity to engage in quadrupedal locomotion has been seriously underestimated by the field's fascination with upright bipedal locomotion, at the expense of prone locomotion, and by a failure to consider the importance of context in the expression of behavior. A clear description of the earliest forms of behavior is necessary to address other classic questions in development focused on continuity, discontinuity, variability, and the emergence of new forms of behavior. Newborn crawling is a particularly important skill because it can be used as a means to study other phenomena like the development of intentionality. If crawling is under the newborn's control and it can be facilitated with the appropriate contextual supports, then the newborn's responses to a wide range of stimuli can be studied using an approach-avoidance paradigm. Finally, newborn crawling may prove to play a vital role in early interventions designed to promote motor development, particularly the development of independent mobility. We elaborate on these ideas in the discussion.

Method

Participants

To be included in the experiment, newborns had to be born with uncomplicated vaginal deliveries, with a minimum Apgar score of 8 at 5 min after birth and no pathologies. The infants were not weighed at test but only newborns who had lost < 10% of their weight by the test day were permitted by the medical staff to participate in our study. The final sample consisted of sixty 2-day-old newborns, (32 girls, 28 boys; $M_{\text{age}} = 2.16$ days, $SD = 0.7$; mean birth weight of 3,307 g, $SD = 382$; mean term of 39.6 weeks, $SD = 1.1$; mean birth size of 50.1 cm, $SD = 1.9$; and mean birth head circumference of 34.9 cm, $SD = 2.3$). The participants were predominantly middle class and 55 (92%) were Caucasian. The other 5 (8%) were of North or Central African descent. Concerning the family characteristics, 31 subjects (51.6%) were first-born, 18 second-born (30%), 8 third-born (13.3%), 2 fourth-born (3.3%), and 1 was fifth-born (1.7%). Ninety-five percent of the families were middle class and the parents had at least a high school education and 5% were classified as low income and also had less than a high school education. The infants were recruited in the Maternity ward of the Port Royal hospital in Paris by visiting the mothers in their room 1 day after they gave birth. The mothers provided written informed consent prior to their

infants' participation in the study. The mother and her infant were escorted to our laboratory, which is located inside the Maternity. All infants were exclusively breast fed, with a mean testing time after feeding of 87 min ($SD = 107$) and tested when awake and alert: rated in Stage 3 (eyes open, no movements) on Prechtl's (1974) arousal scale just prior to testing. Data from five additional infants were collected but discarded for analysis because three infants could not reach Prechtl's Stage 3 before the next trial (two fell asleep and one was too fussy), one infant's mother asked for the testing to stop, and one mother gave her infant vitamins during the test.

Materials and Apparatus

The primary piece of apparatus was an 8 cm high \times 1 m wide \times 1.6 m long pediatric mattress placed on a 1 m high \times 1 m wide \times 2 m long table surrounded by three 5 cm high \times 5 cm wide barriers, except on the experimenter's side (see Figure S1). The table was surrounded by eight Qualysis (Göteborg, Sweden) Oqus 100 motion capture cameras that were fixed to the walls and pointed toward the center of the mattress. The capture volume was larger than the size of the pediatric mattress. Two Sony (Sony Corporation, Tokyo, Japan) Handicam HDR-CX160 HD video cameras were positioned on either side of the mattress at a height of 1.6 m so that they captured the left and right sides of the infant. The video cameras were synchronized with the motion capture cameras through the use of Qualysis Track Manager software. The other major piece of apparatus was a custom-built mini skateboard, known as the Crawliskate[®]. The Crawliskate[®] has an aluminum base that is 29 cm long and 10 cm wide and shaped like a skateboard. Inverted-V-shaped outrigger wings are attached to a plate at the front of the Crawliskate[®] that supports the newborn's head. The wings project 20 cm away from the plate and are designed to prevent the Crawliskate[®] from tipping over, while providing space for the arms to move freely. The surface that supports the newborn's trunk is inclined at 20° to ensure the newborn's head is raised and the legs are in contact with the surface. The surface underneath the trunk is constructed of a layer of high-density foam and a layer of low-density foam. Ten sets of low-friction, ball-bearing coasters under the base and the wings permit the Crawliskate[®] to move easily in any direction. The newborn is secured snugly to the Crawliskate[®] via a harness system with Velcro

straps (see the Video S1 for a demonstration of the infant and marker placement on the Crawliskate®). For a more detailed description of the Crawliskate®, see the patent PCT/EP2015/066359—WO/2016/009022 (Barbu-Roth et al., 2016).

Procedure

Upon arrival at the laboratory, the infants were undressed down to a diaper and dressed in a stretchable undergarment made in three different sizes suitable for newborns. The spherical light-reflective markers used for motion capture could not be placed directly on the skin for two reasons: (a) the newborn's skin is too sensitive and (b) the markers would have been covered by the wrapping system used to secure the newborn in the Crawliskate®. Consequently, the five trunk markers were secured to specific positions on the undergarment in the Mattress condition or on the wrapping system in the Crawli condition directly above anatomical landmarks. One marker was placed dorsal to the acromion process of each shoulder, one dorsal to each acetabulum of the pelvis, and one on the upper part of the back (closest to C7 vertebrae). Different-sized elastic bands, made from a stretchable material, were used to place eight additional markers on the limbs. Two were placed on the lateral malleoli of the ankles, two were placed on the lateral epicondyles of the femurs to mark the knees, two on the lateral epicondyles of the humerus to mark the elbow, and two to the styloid processes of the ulna to mark the wrist. The infants also wore a cap with three head markers; two were placed laterally, slightly above the ears, and one centrally, at the top of the forehead (see Figure 1).

Conditions

The infants were tested in the two randomly-ordered 1-min conditions (with a 5-min break between conditions): (a) crawling in the prone position on the mattress (Mattress condition) and (b) crawling on the mattress with the Crawliskate® (Crawli condition). During each condition, the lead experimenter (Experimenter A) stood behind the newborn, very close to the table, and a second experimenter (Experimenter B) operated a computer that was used to manage the data collection process. The computer was positioned approximately 1.5 m behind the experimental table and Experimenter A. The mother sat next to Experimenter B. She was behind the table, out of her infant's sight, and she was asked not to speak during the trial.

The overhead lights were switched off to minimize brightness and the room temperature was maintained between 23°C and 26°C.

Data Capture and Conditioning for Three Dimensional Kinematic Analyses

The 16 light-reflective markers were sampled at 60 Hz. The data were filtered with a 3 Hz Butterworth filter and gap filling was done for all gaps smaller than 15 frames using a linear interpolation. If at least one limb marker or trunk marker was tracked < 50% of the trial before gap filling, we excluded the participant from all kinematic analyses. Consequently, 12 participants were removed from the analyses of movement amplitudes, velocities, forward displacement, and the characteristics of the head movements. Twenty additional participants were removed from the analyses of the head movement characteristics because at least one head marker was tracked for < 50% of the trial.

Data Reduction

Coding the Arm and Leg Flexion and Extension Movements

We used the same method described by Forma et al. (2018) to code arm and leg movements. We isolated two types of movements using this method: (a) leg and arm steps and (b) leg kicks or arm pumps. These movements were identified via a frame by frame analysis of the video footage captured by the video cameras on either side of the infant. The steps were characterized by a movement of the hand or knee in a direction within the plane of the mattress (horizontal) that would be consistent with a flexion or extension of the limb and that would aid propulsion. The leg kicks were characterized by an initial knee flexion without concomitant horizontal displacement of the knee or flexion of the hip, resulting in the heel touching the infant's bottom. An extension movement of the knee then returned the heel to the mattress. The arm pumps corresponded to all vertical movements of the hand or elbow without concomitant horizontal movement (i.e., the hand or elbow did not move forward or backward; see Figure S2). These pumps were not observed for the legs. Without taking into consideration the timing relative to each other, flexions and extensions were pooled together in each category to calculate a total number of step, kick, or pump movements.

Duration, Amplitude, and Velocity of the Flexion and Extension Stepping Movements

Movement durations were determined from the video codings, whereas movement amplitudes and velocities were determined from the motion capture data that corresponded to each video coded movement. The durations of flexion and extension corresponded to the time between the start and the end of each coded movement. The amplitudes and velocities were determined in relation to the infant's center of mass position (approximated by the barycenter of the polyhedron outlined by the left shoulder, right shoulder, left hip, and right hip markers). The amplitudes represented the mean displacements of the two markers of the concerned limb between the start and the end of the movement. Velocities represented the peak velocities (V_{\max}) of the two markers that corresponded to each limb during the movement. Because amplitude and V_{\max} were determined from the kinematic data, they were only calculated for 48 participants. A mean value was calculated for each variable for each participant. Participants were also removed from certain analyses if they did not make any flexion or extension movements, in which case there were no values for movement duration, amplitude, or V_{\max} .

Coactivation of the Flexion and Extension of the Arm and Leg Movements

In order to analyze if the four limbs were moving together and how flexions and extensions were coactivated, we calculated several variables for each of the six possible pairs of limbs: leg pairs, arm pairs, ipsilateral pairs (left arm–left leg and right arm–right leg), and diagonal pairs (left arm–right leg and right arm–left leg). Those coactivation variables were based on whether two limbs were in motion at the same time, regardless of whether the movement was part of a step, kick, or pump and regardless of the duration of the coactivation (e.g., two limbs could be coactivated for as little as a single frame).

We calculated three measures. First, the quantity of coactivation (QC), which is the proportion of time two limbs moved together across the trial. Second, the QC deviation from the level of chance, where we randomly sampled from the distribution of all possible combinations of behavior by each limb pair, including behavior when neither limb moved, one limb moved and the other did not, and both limbs moved together. Samples were drawn for each subject and condition from the distribution 5,000 times and a frequency distribution was

created, which revealed the standard deviation of the observed QC from the 5,000 theoretical QCs. Third, we calculated the percentage of in-phase versus antiphase coupling across the coactivation periods to investigate the specific pattern of limb coactivation in terms of phasing, which is the same calculation used by Forma et al. (Forma et al., 2018). In this last calculation, the limbs were in phase if they moved in the same direction at the same time (both in flexion or both in extension) and antiphase if they moved in opposite directions at the same time (one in flexion and the other in extension). As in Forma et al. (2018), a coactivation ratio (CR) was calculated ranging from -1 for a perfect in-phase coactivation to $+1$ for a perfect antiphase coactivation and 0 for a 50/50 split. We were especially interested to see if the newborn crawling pattern shows evidence of a diagonal gait, that is, diagonal contralateral limb pairs moving in phase and ipsilateral limb pairs moving antiphase.

$$\text{CR} = \frac{\text{percentage of antiphase Coactivation} - \text{percentage of inphase Coactivation}}{2}$$

Displacement During Crawling

The effective forward displacement in the XY plane that defined the surface of the mattress (D_{xy}) was determined by the difference between the infant's center of mass position in the first frame and the last frame. If the displacement along the X axis (cephalocaudal axis) was negative, we coded the displacement as backward.

Percentage of Crawling Behavior

To estimate how many infants were able to crawl at 2 days of age, we set the same two different criteria as Forma et al. (2018). First, infants had to produce at least five flexions or extensions in the step category on each of their four limbs during the 1-min trial (20 step movements total). This criterion was set up in order to get a sufficient number of step movements to analyze the locomotor pattern. In addition, to be classified as a "crawler" they had to move their center of mass forward at least 5 cm.

Head Movements

The head movements were characterized relative to the trunk in both conditions in order to evaluate how the head was flexed forward and in line with the spine or extended backward. We extracted the

pitch of the head (rotation around the mediolateral axis) from the motion capture data in order to calculate the neck flexion (negative angle) and extension (positive angle).

Interrater Reliability

The coding of leg and arm movements was performed by a primary coder. A second coder who was blind to the purpose of the experiment coded 20% of the trials. Intraclass correlation coefficients were calculated to determine agreement between coders. To avoid the possibility of the coders comparing the crawling pattern across conditions, each trial for each infant was given a randomly assigned coded number. The coding was then performed randomly without the possibility for the coders to bias their coding with the knowledge of how the infant crawled in the other condition compared to the one that was being coded. Finally, an intraclass correlation coefficient was determined for 20% of the trials coded by the primary coder. The between-coder correlation coefficients were all high, ranging from 0.82 to 0.91 across all variables coded. The within coder correlation coefficients were equally high, ranging from 0.92 to 1. Data from the primary coder were subjected to analysis.

Data Analysis

Preserving Normality for Analyses of Steps and Kinematics

The statistical analysis was conducted with Statistica[®] software version 6.1, Stat Soft France Maisons-Alfort France. Our original plan was to analyze the data using 2 Condition (mattress, crawl) \times 2 Limb (leg, arm) \times 2 Laterality (left, right), \times 2 Movement Direction (flexion, extension) repeated measures analyses of variance (ANOVAs) on the coded number of movements and the kinematic and temporal characteristics of the movements. However, preliminary analyses revealed that the data for some of the dependent variables were not normally distributed and could not be normalized with any type of transformation. However, when the data on the coded number of steps and the kinematic variables were collapsed across categories of dependent variables and square root transformed, the distributions were normal according to the K-S test ($d = [.6, .16]$, all $p > .2$ for Steps; $d = [.6, .16]$, all $p > .2$ for Amplitude; and $d = [.7, .12]$, all $p > .2$ for Velocity). Consequently, we were able to run a 2 Condition \times 2 Limb repeated measures analysis of variance (ANOVA) on the coded

number of steps and a 2 Condition \times 2 Limb \times 2 Movement Direction repeated measures ANOVA on the movement amplitudes and velocities.

Non Parametric Analyses

The leg kick and arm pump data could not be normalized and so were analyzed using a 2 Condition \times 2 Limb \times 2 Movements type (steps, kicks/pumps) Friedman test with Wilcoxon tests to follow up on significant main effects. Similarly, the movement duration data, the head pitch data, and the displacement data during each trial could not be normalized and so they were analyzed with Wilcoxon signed-rank tests, with Bonferroni corrections when necessary.

Coactivation Analyses

The QCs and the deviations of QC from chance level were analyzed with 2 Condition \times 6 Limb Pairs repeated measures ANOVAs. The percentages of in-phase and antiphase coactivation were analyzed with a 2 Condition \times 6 Limb Pair Friedman test and Wilcoxon tests were used to follow up on significant main effects. The CRs were analyzed with a 2 Condition \times 2 Arm/Leg Pair (Ipsilateral: left arm/left leg and right arm/right leg, and Diagonal: left arm/right leg and right arm/left leg) repeated measure ANOVA.

Results

Number of Arm and Leg Steps

Note that because of the way the data were collapsed for the first analysis, steps refer to the combined number of coded flexion and extension movements that comprised each step. On the Mattress condition, newborns produced very few arm steps in comparison to leg steps (see Video S2 of an infant crawling on the mattress). In contrast, the newborns expressed a similar number of arm and leg steps in the Crawl condition (see Video S3 of an infant crawling on the Crawliskate[®]). No differences were found between the Mattress and Crawl conditions in the number of leg steps performed by the newborns (see Table 1 and Figure S3). These results were determined by a 2 Condition (crawl vs. mattress) \times 2 Limb (arms vs. legs) repeated measure ANOVA on the square root transformed number of step flexions and extensions on the 60 participants. The analysis revealed a significant interaction between Condition and Limb, $F(1,$

Table 1
Means and Standard Deviations for Each of the Variables Measured

Variables	Conditions		N	p	Sig.
	Crawli M (SD)	Mattress M (SD)			
Number of step movements/min					
Leg step	7.45 (7.6)	5.87 (7.8)	60	.269	N.S.
Arm step	8.26 (6.9)	2.36 (2.9)	60	.000	***
Number of kick and pump movements/min					
Leg kick	1.49 (1.8)	1.43 (1.6)	60	.948	N.S.
Arm pump	1.93 (1.9)	2.15 (2.7)	60	.824	N.S.
Duration of step movements					
Leg flexion (s)	0.66 (0.3)	0.75 (0.5)	44	.037	*
Leg extension (s)	1.03 (0.5)	1.08 (0.5)	43	.936	N.S.
Arm flexion (s)	0.92 (0.4)	0.75 (0.7)	39	.001	**
Arm extension (s)	0.94 (0.4)	0.67 (0.4)	41	.000	***
Amplitude of step movements					
Leg flexion (mm)	35.12 (16.3)	40.56 (14.6)	34	.106	N.S.
Leg extension (mm)	32.73 (15.4)	34.75 (14.2)	36	.930	N.S.
Arm flexion (mm)	29.45 (12.2)	20.87 (9.9)	31	.001	**
Arm extension (mm)	31.27 (14.2)	20.84 (9.4)	33	.000	***
MaxVelocity of step movements					
Leg flexion (mm/s)	149.7 (80.8)	165.8 (71.8)	35	.444	N.S.
Leg extension (mm/s)	109.5 (55.9)	124.9 (62.0)	36	.380	N.S.
Arm flexion (mm/s)	110.5 (53.8)	84.9 (38.6)	31	.003	**
Arm extension (mm/s)	104.4 (46.3)	82.7 (29.8)	33	.002	**
Coactivation ratio (CR)					
Legs CR	-0.07 (0.6)	-0.28 (0.5)	41	.045	*
Arms CR	0.11 (0.4)	0.03 (0.5)	30	.456	N.S.
AL-LL pair CR	0.18 (0.4)	0.18 (0.5)	33	1	N.S.
AR-LR pair CR	0.14 (0.4)	0.25 (0.6)	32	.439	N.S.
AL-LR pair CR	-0.17 (0.4)	-0.13 (0.5)	34	.705	N.S.
AR-LL pair CR	0.02 (0.4)	0.11 (0.5)	32	.376	N.S.
Head orientation					
Head pitch (°)	-1.50 (26.8)	8.37 (20.9)	28	.018	*
Traveled distance					
D_{xy} (cm/min)	7.47 (13.8)	-0.38 (3.3)	48	.000	***

Note. N.S. = not significant.

* $p < .05$; ** $p < .01$; *** $p < .001$, the p values are calculated from paired t tests (when the distribution is normal according to K-S test) or Wilcoxon tests (when the distribution is not normal according to K-S test). For the number of step, kick and pump movements, results are collapsed across left and right and flexions and extensions. For the duration, amplitude and MaxVelocity of the step movements, results are collapsed across left and right.

59) = 29.6, $p < .001$, $\eta^2_{\text{partial}} = .34$. Post hoc comparisons showed that significantly fewer arm steps than leg steps were taken in the Mattress condition ($p < .001$), whereas no significant difference between the number of leg and arm steps was observed in the Crawli condition.

Number of Kick and Pump Movements

A 2 Movement Type (steps or kick/pump) \times 2 Condition \times 2 Limb Friedman test revealed a

significant interaction ($p < .001$). The Wilcoxon tests used to follow up the significant interaction revealed that infants produced more leg steps than leg kicks in the Crawli condition ($N = 60$, $Z = 5.77$, $p < .001$, $\eta^2_{\text{partial}} = .56$) and in the Mattress condition ($N = 60$, $Z = 6.02$, $p < .001$, $\eta^2_{\text{partial}} = .61$). In the Mattress condition, there was no significant difference between arm steps and arm pumps, but in the Crawli condition there were more arm steps than arm pumps ($N = 60$, $Z = 4.85$, $p < .001$, $\eta^2_{\text{partial}} = .40$).

Characteristics of the Leg and Arm Steps

Amplitudes and Velocities

The arm steps were larger and faster in the Crawli condition than in the Mattress condition, the leg steps were larger and faster than the arm steps in both conditions, and the flexion movements were larger and faster than the extension movements for the legs in both conditions. These results were determined by a 2 Condition \times 2 Limb \times 2 Movement Direction (flexion vs. extension) repeated measures ANOVA on the Amplitude and peak Velocity (V_{\max}) variables. The ANOVAs revealed a significant main effect for Limb on the Amplitude variable, $F(1, 26) = 63.0$, $p < .001$, $\eta^2_{\text{partial}} = .70$, and the V_{\max} variable, $F(1, 26) = 53.0$, $p < .001$, $\eta^2_{\text{partial}} = .59$, with larger and faster leg movements than arm movements. The ANOVAs also revealed two significant interactions between Condition and Limb for Amplitude, $F(1, 26) = 24.5$, $p < .001$, $\eta^2_{\text{partial}} = .47$, and for V_{\max} , $F(1, 26) = 13.9$, $p < .001$, $\eta^2_{\text{partial}} = .34$, and between Limb and Modality for Amplitude, $F(1, 26) = 4.7$, $p < .038$, $\eta^2_{\text{partial}} = .11$, and for V_{\max} , $F(1, 26) = 33.9$, $p < .001$, $\eta^2_{\text{partial}} = .56$. The post hoc comparisons confirmed that: (a) the arm steps were larger and faster in the Crawli condition compared to the Mattress condition ($p < .001$ for Amplitude and $p = .016$ for V_{\max} ; see Figure S4), (b) the leg steps had larger and faster flexions than extensions regardless of the condition ($p = .024$ for Amplitude and $p < .001$ for V_{\max}), (c) the leg steps were larger and faster than the arm steps in the Crawli condition ($p = .013$ for Amplitude and $p = .002$ for V_{\max}) and in the Mattress condition ($p < .001$ for Amplitude and $p < .001$ for V_{\max} ; see Figure S4).

Durations

Concerning the duration of the steps, six Wilcoxon tests that were run on the step flexion and extension durations revealed (using a Bonferroni correction imposing a $p < .008$ for significant differences) that: (a) leg step flexions had shorter durations than extensions in both the Crawli ($N = 51$, $Z = 4.38$, $p < .001$, $\eta^2_{\text{partial}} = .38$) and the Mattress condition ($N = 43$, $Z = 4.23$, $p < .001$, $\eta^2_{\text{partial}} = .42$), (b) Arm steps had longer durations in the Crawli condition compared to the Mattress condition for flexions ($N = 39$, $Z = 3.21$, $p < .001$, $\eta^2_{\text{partial}} = .27$) and extensions ($N = 41$, $Z = 3.71$, $p < .001$, $\eta^2_{\text{partial}} = .34$), and (c) in the Mattress condition, leg step durations were longer than arm step durations ($N = 43$, $Z = 2.84$, $p < .004$, $\eta^2_{\text{partial}} = .19$), whereas

no significant differences were revealed in the Crawli condition between the duration of leg and arm steps, despite the differences observed in arm and leg amplitudes and velocities.

Coactivation of the Arm and Leg Movements

Quantity of Coactivation

A Condition \times Limb Pair repeated measures ANOVA on the QC revealed a Condition \times Limb Pair effect, $F(5, 110) = 6.44$, $p < .001$, $\eta^2_{\text{partial}} = .22$. Post hoc comparisons showed that a significantly higher percentage of time was spent with each pair of limbs coactivated across the trial in the Crawli condition compared to the Mattress condition (all $p < .001$) except for the Leg pairs ($p = .08$). In total, newborns displayed coactivation (i.e., two limbs moved together) on 18% of the trial duration in the Crawli condition versus 8% in the Mattress condition.

Coactivation Above Chance

The QC deviation from chance level was ranked from +0.3 SD to +1 SD above the mean calculated over the 5,000 sampling iterations (see Figure S5). All coactivations for each pair were above chance in both conditions. Despite the observation of a higher coactivation in the Crawli[®] condition compared to the Mattress condition, the Condition \times Pair effect failed to reach significance ($p = .06$).

In-Phase Versus Antiphase Coactivation

A Friedman test on in-phase and antiphase percentages of coactivation across all pairs (six in total: arm/arm, leg/leg, ipsilaterals, and diagonals) revealed a significant Condition \times Limb Pair interaction ($p < .001$). Wilcoxon tests used to follow up on the percentages of antiphase versus in-phase coactivations within each condition revealed that: (a) in the Crawli condition, the left arm–right leg diagonal pair was significantly more in phase than antiphase ($N = 34$, $Z = 2.24$, $p = .025$, $\eta^2_{\text{partial}} = .15$) and the left ipsilateral pair was significantly more antiphase than in phase ($N = 33$, $Z = 2.26$, $p = .024$, $\eta^2_{\text{partial}} = .16$) and (b) in the Mattress condition, the leg pair was more in phase than antiphase ($N = 40$, $Z = 3.31$, $p < .001$, $\eta^2_{\text{partial}} = .28$) and the right ipsilateral pair was more antiphase than in phase ($N = 32$, $Z = 2.56$, $p = .01$, $\eta^2_{\text{partial}} = .21$). A 2 Condition \times 2 Arm/Leg Pair (ipsilateral: left arm/left

leg and right arm/right leg, and diagonal: left arm/right leg and right arm/left leg) repeated measure ANOVA on the CR revealed an effect of arm/leg pair, $F(1, 35) = 13.1$, $p < .001$, $\eta^2_{\text{partial}} = .27$. Post hoc tests revealed that ipsilateral pairs, which were closest to an antiphase coactivation (moving in opposite directions), were significantly different from diagonal pairs, which were closest to an in-phase coactivation (moving in the same direction; $p = .001$).

Displacement During Crawling

Propulsion was not effective in the Mattress condition ($M = -0.38$ cm/min, $SD = 3.29$). The Wilcoxon test revealed that the Crawliskate® allowed the newborns to displace themselves significantly further from the start location ($M = 7.47$ cm/min, $SD = 13.8$; $N = 48$, $Z = 3.65$, $p < .001$, $\eta^2_{\text{partial}} = .28$). However, this displacement was highly variable among the newborns, ranging from -5.5 cm/min to a maximum of 68.7 cm/min for the Crawl condition and from -12.6 cm/min to a maximum of 6.6 cm/min for the Mattress condition. In total, during the 1-min trial, 35% of the newborns were able to perform a full and propulsive newborn crawling with the Crawliskate® (in moving at least 5 cm forward and producing at least five flexions or extensions in the step category on each of their four limbs during the 1-min trial), while only 2% were able to do so when placed directly on top of the mattress.

Head Movements

Wilcoxon tests, which were used to compare the mean pitch (rotation of the head around the medio-lateral axis) across the two conditions, revealed that the Crawliskate® encouraged the newborn to have a significantly higher forward flexion of the head, allowing the head to be relaxed and in line with the spine (mean pitch of the head = -1.5° , $SD = 26^\circ$), while the position on the mattress encouraged more head extension (mean pitch of the head = 8.4° , $SD = 20.9^\circ$; $N = 28$, $Z = 2.18$, $p < .028$, $\eta^2_{\text{partial}} = .18$).

Effects of Time After Feeding and Newborn Body Characteristics

We did not find any correlation between the newborns' anthropometric measures at birth—weight, length, and head circumference—with the number of steps, the characteristics of the steps, the

displacement across the mattress and the different coactivation variables. We checked these correlations because Thelen, Fisher, Ridley-Johnson, and Griffin (1982) have shown that relatively heavier newborns step less when supported in the upright position and we wanted to be sure that anthropometric characteristics were not influencing the number of steps taken in the prone position.

Finally, the only factor positively correlated with arm and leg steps was the delay between feeding and testing. A Condition by Limb repeated measure ANCOVA (with Delay as a covariate) on the square root transformed number of movements revealed an overall effect of Delay on the overall number of movements, $F(1, 58) = 4.99$, $p < .029$, $\eta^2_{\text{partial}} = .08$, with more movements in newborns with the greatest delay between feeding and testing, but no significant interaction with the Limb factor.

Do the Arms Actively Participate in Newborn Crawling?

It is well known that stepping movements can be passively driven by a moving surface, such as a treadmill belt. Consequently, it is possible that the higher number of arm steps observed in the Crawl condition could be passively elicited in response to the displacement of the Crawliskate®, driven by the propulsive movements of the legs. To investigate this possibility, two supplementary analyses were performed. First, we calculated the correlation between the number of arm steps and the displacement across the surface in the Crawl condition. The correlation was not significant ($r = .22$), showing that spending more time moving on the Crawliskate® did not automatically generate more arm movements. Second, we isolated a sample of 31 non-propulsive newborns who travelled < 5 cm forward in each condition and ran another Condition \times Limb repeated measure ANOVA on the number of their stepping movements. The Condition \times Limb repeated measure ANOVA on the number of their stepping movements, after a square root transformation, still revealed a significant interaction between Condition and Limb, $F(1, 30) = 12.2$, $p < .001$, $\eta^2_{\text{partial}} = .28$. Again, the post hoc tests revealed significantly fewer arm steps than leg steps in the Mattress condition ($M = 5.3$, $SD = 7.3$ for legs, $M = 2.2$, $SD = 2.4$ for arms, $p = .014$) and no significant difference between the number of arm and leg steps in the Crawl condition ($M = 5.0$, $SD = 6.0$ for legs, $M = 6.5$, $SD = 7.1$ for arms, $p = .34$). The results of this analysis are identical to the original analysis on all infants, showing that

infants performed significantly fewer arm steps than leg steps in the Mattress condition and an equivalent number of arm and leg steps in the Crawl condition. The results of these additional analyses suggest that the higher number of arm movements observed in the Crawl condition was not due to the arms being passively driven by the motion of the Crawliskate[®].

Discussion

The main purpose of this study was to determine whether humans can perform a pattern of quadrupedal locomotion at birth that leads to forward progression, with locomotion driven by all four limbs or primarily by the legs. This question has important implications for an understanding of the origins of locomotion as well as the role played by the arms in the development and control of skilled bipedal and quadrupedal locomotion. If humans are able to perform terrestrial quadrupedal locomotion at birth, this implies that the locomotor circuitry underlying quadrupedal locomotion develops during fetal life, even though that circuitry is likely primitive and will undergo considerable modification during development. In contrast, if humans are bipeds at birth, they will have to develop new neuronal circuitry to support the effective and efficient use of their arms in prone and upright locomotion. The answers to the questions raised in this study have additional theoretical and clinical relevance. From a theoretical standpoint, it is important to be able to clearly describe the earliest behaviors to address classic developmental questions related to the origins of forms, continuity and variability in development, and the emergence of new forms of behavior. One can only know if earlier behaviors are connected to later behaviors if the earlier behaviors have been described in compelling detail. In addition, failure to consider the importance of contextual support in the expression of behavior can lead to an underestimation of early competencies and a mischaracterization of development. Conversely, the provision of appropriate supports can reveal competencies that would otherwise remain “hidden” and generate new insights into how new forms of behavior emerge and how to optimize development. From a clinical standpoint, researchers and clinicians have recently highlighted the importance of starting interventions for infants at risk of motor delays as soon as possible for the ultimate success of these interventions (Lee & Gallo, 2012; Teulier et al., 2014; Ulrich, 2010). The

possibility of starting locomotor training at birth has even been proposed (Barbu-Roth et al., 2009, 2014; Siekerman et al., 2015). Against this backdrop of ideas, it is important to know if at-risk newborns should be trained to locomote quadrupedally or bipedally. The results of our study suggest that training quadrupedal locomotion may be the most appropriate strategy at birth because this form of locomotion is already active and under independent control at birth.

Evidence of Quadrupedalism at Birth

Summary of Findings

The current study showed that when tested prone and without support on a mattress, it is difficult for newborns to propel themselves forward and they primarily use their legs for propulsion, as if they were stepping bipedally in a horizontal position. This finding is consistent with the results described by Forma et al. (Forma et al., 2018), who tested newborn movement patterns in a similar context.

In contrast to the Mattress condition, testing on the Crawliskate[®] revealed a completely different picture. In this case, the newborn's head and trunk were raised upward, freeing their arms and facilitating their propulsion forward. It should be noted that, while the Crawliskate[®] raises the head, its design encourages a slight flexion of the head and a lengthening of the natural curvatures of the spine, unlike the Mattress condition, which encourages extension of the head and a shortening of the spine during crawling movements. In addition, the wheels under the Crawliskate[®] minimize friction between the abdomen and the surface, thus decreasing the forces the newborns need to generate to propel their bodies forward. Free from the biomechanical constraints that impede locomotion directly on top of a surface, the newborns demonstrated a remarkable capacity to move as quadrupeds by using an equivalent number of active arm and leg movements. Moreover, the pattern of coactivation among limb pairs on the Crawliskate[®] showed a greater tendency for the ipsilateral limb pairs, particularly on the left side, to be out of phase (one limb is in flexion while the other is in extension at the same time), similar to the movements of other young quadrupeds when placed in the water and reminiscent of the swimming movements McGraw (1939) documented in human newborns. In addition, the diagonal limb pairs, particularly the left arm-right leg pair, had a greater

tendency to move in phase (both limbs moving in the same direction at the same time), consistent with the diagonal pattern that characterizes mature hands-and-knees crawling (Adolph, Vereijken, & Denny, 1998; Freedland & Bertenthal, 1994), that is apparent in the reciprocal arm swinging with stepping during mature walking (Ivanenko et al., 2007), and that was recently observed sporadically during newborn upright stepping by La Scaleia et al. (2018). The current findings and those of La Scaleia et al. (2018) provide strong evidence for neural coupling between the upper and lower limbs at birth and suggest that the coupling that underlies mature walking and crawling is already present in the newborn.

Moreover, the fact that there were more leg steps than kicks in the Crawl and Mattress conditions and more arm steps than pumps in the Crawl but no difference in the Mattress condition is interesting in regard to the hypothetical function of leg kicks and arm pumps. As mentioned in Forma et al. (2018), leg kicks are believed to correspond to incomplete leg steps. Vertical arm pumps, in contrast, were proposed to correspond to the newborns' attempts to raise their head and trunk off the surface. Consequently, Forma et al. hypothesized that if the newborns' heads and trunks were supported, there should be a reduction in pumps, such that more arm steps than pumps would be seen. This is exactly what was observed. The leg kicks were not modified on the Crawliskate®, whereas significantly more arm steps than pumps were seen when the head and trunk were supported off the ground with the assistance of the Crawliskate®.

The effectiveness of propulsion on the Crawliskate® was also significantly higher than on the mattress, with 35% of the newborns able to move more than 5 cm and to perform at least five flexions or extensions in the step category on each of their four limbs during the 1-min trial compared to only 2% on the mattress. This result is particularly surprising given that newborns had only 1 min to adapt to the Crawliskate®. However, the variability in the displacement is important to note. This variability and the generally limited displacement could be explained by several factors. First, not all of the newborns were in the most advantageous motivational state to crawl with maximum effectiveness during the 1-min trials; those who were hungrier because of the greater delay between testing and the last feeding moved more, compared to those just fed. Second, the position of the feet on the mattress is likely important. The foot naturally

presses against the uterine wall when fetuses make pumping movements with the legs because the foot is aligned (parallel) with the uterine wall. However, newborns must reposition their feet when pushing against a surface on which they are lying prone because the feet are positioned orthogonally relative to the surface. Finally, the extended position of the trunk when lying prone, which is opposite to the newborn's naturally flexed posture, likely played a role in the amount of crawling. The effectiveness of propulsion on the Crawliskate® is a particularly important finding because it suggests the Crawliskate®, or other methods that facilitate independent propulsion, could be used in future experiments to study many other newborn competencies and preferences when newborns are tested under optimal conditions. For example, Varendi and Porter (2001) have shown that newborns will move more toward a pad infused with the mother's breast odor than to a clean pad. Would newborns also move more toward other stimuli with hedonic value, like the mother's voice or a soothing sound? Conversely, would newborns attempt to retreat from a noxious stimulus, like a rotten odor or an irritating sound? Can the amount or direction of displacement during newborn crawling be used to determine whether newborns can discriminate different stimuli? A wide range of questions like these could be addressed by assessing the extent and direction of locomotion. Moreover, an examination of these types of questions would provide additional information about whether the newborn is not only able to organize prone progression but can also steer toward a target.

What the Characteristics of Leg and Arm Movements Reveal about Newborn Quadrupedalism

Amplitude, Velocity, and Duration of the Movements

First, the Crawliskate® allows the newborn to perform not only more but also larger, faster, and longer in duration arm movements than in the Mattress condition. Second, regardless of condition, leg steps had larger amplitudes and velocities than arm steps. It is unlikely these differences are due to differences in the lengths of the legs and arms as the upper and lower limbs have very similar lengths at birth (Pomeroy, Stock, Cole, O'Callaghan, & Wells, 2014). This finding is more likely a result of the greater muscle mass, and therefore greater force generation capacity, of the prime movers of the legs compared to the arms. The legs are also described as the primary drivers within the neural circuitry

underlying quadrupedal locomotion (Falgairolle et al., 2006) and the hind limbs are well known to be more efficient at generating forward propulsion than the forelimbs in habitual quadrupeds (Manter, 1938).

The third notable finding was the asymmetrical nature of the flexion and extension movements of the legs. While no differences were found in the amplitudes and velocities of the arm flexions and extensions, the amplitudes and velocities of the leg extensions were smaller than those of the leg flexions. This finding may reflect the bias toward physiological flexion in the newborns, who most recently spent several weeks in a tightly flexed position in utero and presumably had increasingly limited opportunities to actively extend the legs. In addition, as extension is the primary propulsive movement of the legs and flexion the recovery movement, the smaller extension amplitudes and velocities must also be a function of the resistance to movement associated with the weight of the body and the friction between the body and the surface. In other words, body weight and friction would have provided greater resistance to leg extension movements than leg flexion movements, particularly in the Mattress condition. Although body weight and friction should also impede extension of the arms, the limited number of arm movements in the Mattress condition, combined with the fact that the arms make a smaller contribution to propulsion than the legs, may explain why no main effect of movement direction was found for the arms.

Finally, it is important to note that we observed that leg and arm extensions were the drivers of forward propulsions on the Crawliskate® as well as of the few forward propulsions on the mattress. This observation is theoretically important because prior research on upright stepping and supine kicking has shown that flexion movements are initiated by active muscle contraction whereas extension movements are primarily the result of passive elastic and inertial forces (e.g., Thelen & Ulrich, 1991) suggesting that it might be easier for the young infant to organize flexion movements than extension movements. The current findings show, however, that the newborn is quite capable of organizing extension movements of the legs. This is perhaps not surprising given that the fetus would have had practice extending the legs against resistance during in utero kicking or pumping—a practice that most likely contributed to the characteristics of newborn crawling observed in the current study. The description of extension movements is especially

valuable in regard to the potential clinical implications for training quadrupedal locomotion at birth in at-risk populations because our results suggest that the most effective and efficient training could be achieved by giving maximum opportunities to practice extension of the arms and legs during crawling. In addition to developing the muscles that extend the hip and knee, this type of practice might also develop the muscles associated with plantar flexion, providing one more mechanism by which practice with crawling might facilitate the development of upright walking. Sutherland, Cooper and Daniel (1980) have reported that the ankle plantar flexors play an essential role in stabilizing the whole body during the weight-bearing stance phase of upright locomotion and weakness in these muscles causes marked disturbances to gait.

Pattern of Coactivation

The final notable finding relates to the patterns of coactivation among the different limb pairs. First, it is important to note that the likelihood of seeing coactivation between pairs of limbs was higher in the Crawli condition than in the Mattress condition. It must be noted, however, that this finding must be at least partially attributable to the greater number of arm steps in the Crawli condition compared to the Mattress condition, raising the probability of observing two limbs move at the same time. Nevertheless, as the coactivations were determined relative to all movements (steps, kicks, and pumps—see methods section), it remains plausible that the Crawliskate® had an additional effect on encouraging coactivations, independent of its contribution via an increase in arm steps. Unfortunately, we do not see an obvious way of confirming this speculation at the present time. Two other findings within the coactivation analyses were noteworthy. First, the coactivations were above chance for each of the limb pairs. This finding suggests an intrinsic bias within the newborn's neuromuscular system to couple all four limbs, consistent with quadrupedalism. Second, as noted already, the nature of the couplings showed evidence of the diagonal couplings that characterizes mature hands-and-knees crawling. This was most obvious in the Crawli condition where a prevalent pattern was for the diagonally coupled left arm and right leg to move together in phase, and the left leg to move antiphase (opposite direction) to the left arm and right leg. In other words, while the left leg was extending, the left arm and right leg were flexing. This is an intriguing

finding because, when combined with the recent findings of La Scaleia et al. (2018) of sporadic quadrupedal coordination in newborn stepping, it suggests that the diagonal coupling that characterizes mature hands-and-knees crawling is wired into the nervous system during fetal development. The evidence for diagonal coupling in newborn upright stepping and crawling provides additional support for the idea that training newborn crawling at an early age might contribute to the development of upright stepping and walking in addition to the development of prone locomotor skills like hands-and-knees crawling. This idea would gain additional support if future studies revealed further evidence for diagonal coupling between the limbs during newborn upright stepping. However, we would urge researchers to abandon the traditional method of supporting the newborn under the armpits and support the infant's trunk instead so that the arms are free to move. We expect that freeing the arms would lead to a greater number of arm movements and a greater prevalence of diagonal coupling between the arms and legs. This speculation is eminently testable.

Limitations of the Study

The major limitation of this study was the short 1-min duration of the crawling tests. Since this study was designed to compare the crawling behavior of the infant on the mattress and on the Crawliskate[®], it was not possible to have longer trials because 2-day-old newborns fatigue quickly. However, we believe that in future studies more crawling behavior would be observed if the newborns had the opportunity to practice on the Crawliskate[®] for at least 2–3 min. We recommend also (a) to test the newborns at least 1 hr after feeding so they have the maximum energy for crawling and to standardize the timing between feeding and testing and (b) to provide different motivational incentives such as the mother's odor or voice to stimulate crawling. Finally, we did not measure muscle activity in the arms and legs via electromyography (EMG). Capturing EMG data would provide further insights into the nature and prevalence of coordination patterns among the four limbs. Future studies would benefit from all of these improvements.

Conclusion

This study is the first to show that newborns are able to move as quadrupeds on land as early as 2–3 days after birth. Two key innovations of the study

were: (a) the use of a device that supported the newborn's head and trunk, freed the arms to move, minimized the friction between the surface of support and the body, and yet still allowed the newborns to move independently, and (b) the use of motion capture technology to provide detailed kinematic descriptions of the quadrupedal pattern in the newborn. The findings highlight how important it is to search for optimal contexts when testing behavioral capacities. Our analyses of the number and types of limb movements and their characteristics, the coactivation of limb pairs, and the displacement across the surface, revealed that newborns are able to crawl with locomotor patterns similar to those documented during quadrupedal locomotion in animals and human adults. This discovery is important because it questions the well-established bias toward studying newborns as bipeds and it suggests that the neural couplings that are known to link the arms and legs during mature bipedal and quadrupedal locomotion develop in utero. We argue that this latter claim provides a basis for initiating training in crawling as early as birth, using a device like the Crawliskate[®], for infants at risk for locomotor delays. Given the pervasive effect that mature crawling experience has on psychological development in the second half of the infant's first year of life, it is plausible that early training in newborn crawling might have a pervasive effect on the development of the nervous system in addition to a specific effect on the development of independent mobility. These ideas clearly need to be addressed by further experimental work.

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Supporting Information

Additional supporting information may be found in the online version of this article at the publisher’s website:

Figure S1. Experimental Setup

Figure S2. Coded Flexion and Extension for Leg and Arm Step and Kick Pump Movements

Figure S3. Number of Leg and Arm Steps in the Crawli (C) and Mattress (M) Conditions

Figure S4. Amplitude and Maximal Velocity of Leg and Arm Steps in the Crawli (C) and Mattress (M) Conditions

Figure S5. Scores of Coactivations by Limb Pairs and Condition

Video S1. Demonstration of the newborn and marker placement on the Crawliskate®

Video S2. Newborn crawling on the Mattress

Video S3. Newborn crawling on the Crawliskate®