Is the locomotion of crawling human infants different from other quadruped mammals?

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Abstract Crawling on hands and knees is an early pattern of locomotion of human infants using two functional segments for the fore limbs and one for the hind limbs and as such it offers an interesting way of studying quadrupedalism in one of its simplest form. In this contribution we investigate how crawling human infants compare to other quadruped mammals especially primates. For this we present quantitative data on both the gait and kinematics of seven 10-month-old crawling infants. We found that crawling on hand and knees is very close to the locomotion of non-human primates in terms of their quite protracted arm at touch down, the coordinations between the spine movements in the lateral plane and the limbs, the relatively extended limbs during locomotion and the strong correlation between stance duration and speed of locomotion that is observed in most mammals. However important differences with primates are found, such as the choice of a lateral sequence walking gait, which is similar to most non-primate mammals and the relatively stiff elbows during stance as opposed to the quite compliant gait of primates. In conclusion despite infants crawl only for a short period and have a limb geometry very different from other mammals, their locomotion is surprisingly similar to that of other primates with several features resembling the locomotion of other quadruped mammals. These finding raise the question of the role of both the mechanical structure of the body and neural control on the determination of these characteristics.

Keywords: infant locomotion, crawling, gait, kinematics, quadruped locomotion

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1. Introduction

Despite the wide diversity among quadruped mammals, several basic principles of locomotion are common to most of them in terms of gaits, kinematics, and neural control (Fischer et al., 2002; Grillner, 1975; McMahon, 1984; Orlovsky et al., 1999; Vilensky, 1987). It is thus possible to get insights from animal locomotion by studying these common principles because they emphasize fundamental principles governing locomotion from the neural as well as the mechanical perspectives.

For example most mammals use similar gaits that change for different speeds. They use symmetrical gaits such as walk, trot and pace at slow and moderate speeds (Hildebrand 1965, Hildebrand 1967) and asymmetrical gaits at high speeds (Hildebrand 1977). In vertebrate quadruped locomotion, the duration of stance phase is directly related to the locomotion speed while the swing phase stays almost constant for most speeds (McMahon, 1984; Vilensky, 1987). Mammals also share many kinematic similarities. They have similar periods of flexion and extension of the shoulder and hip, two period flexion/extension of the more peripheral joints, and lateral and sagittal movement of the spine (Fischer et al., 2002; Grillner, 1975; Shapiro et al., 2001; Vilensky, 1987).

However primate locomotion can be distinguished from other quadrupeds in several ways. Whereas most mammals use a lateral sequence walking gait (swing sequence: left-hind (Lh), left-front (Lf), right-hind (Rh), right-front (Rf)), primates use mainly a diagonal sequence gait LhRfRhLf (Hildebrand, 1967; Vilensky and Larson, 1989). Even if lateral sequence walking can be observed, the diagonal sequence is always the dominant one (Shapiro and Raichlen, 2006). It has been suggested that this gait was first evolved for fine branch locomotion (Schmitt and Lemelin, 2002). Primates also have a more protracted arm at touch down (over 90° relative to horizontal body plane) than other mammals (Larson et al., 2000), a quite compliant gait characterized by important elbow yields during stance, longer steps and longer contact times and relatively extended limbs during stance (Schmitt, 1999). However the exact reason for these differences remains controversial.

There are two main motivations for investigating human infant crawling dynamics. First, infants have a crawling posture that is different from other quadrupeds and not optimized for quadrupedalism. Indeed, crawling infants have only two functional limb segments for the fore limb (arm and forearm) and one for the hind limb (since knees are on the ground during stance). Secondly, the scapula is not aligned with the shoulder. Consequently, the study of infant crawling is the study of quadrupedalism in a mechanically simple and non-optimal form. All the gait characteristics of infants common to other mammals would suggest that these are independent of the functional limb geometry of the quadruped and therefore emphasize the importance of the neural control and the constraints imposed by quadrupedalism in the emergence of these common characteristics. Second, primate locomotion differs from other quadrupeds in several aspects (Larson et al., 2000; Schmidt, 2005; Schmitt and Lemelin, 2002) and it is not known how it is related to young human infant's locomotion. Indeed, although Hildebrand (1967) gives a direct comparison of the interlimb coordination between primates and infants and shows that that infants use lateral sequence walks that differ from primates but are similar to most other quadruped mammals, there is no data for the specific kinematics of the limbs.

The development of crawling is similar to other motor skills, as sitting, cruising and walking. The ability is a result of improved posture, neuromuscular control and experience. The importance of postural and neuromuscular control is reflected by the fact that at the very onset of crawling, infants use hands and knees immediately in an optimal way. The right hand starts (Adolph et al. 1998)) the locomotion. However, the crawling technique is highly variable, in other respects depending on clothing (Burnside 1927) or friction (Adolph et al. 1998). The infant prefers a crawling pattern that fits the environmental conditions. In the past, several studies have mapped up crawling stages and crawling patterns (Burnside 1927; Gesell 1939), and the refined neural control with age (Forssberg 1980; Gesell 1939 ; McGraw 1941). These characteristics show a high variability with age and with environmental conditions. More recent studies have emphasized the strong role of experience. For example, cross-cultural studies show that training before the crawling onset gives an earlier start (Bril et al ;1989). It has been shown that at the onset of locomotion like cruising and walking, the postural systems involved in the perception-action loop are not perfect yet. In cruising, (7-12 months) the infant wobble, which is decreased with experience. (Haehl et al. 2000). Similary, Adolph (2000) has suggested a sway model for locomotion.

Despite the importance of infant crawling there are very few studies of the biomechanical properties of this mode of locomotion. Before standing and walking on two feet, many human infants start to locomote on four limbs. Infants start crawling at around 9 months (Goldfield, 1989) and continue until they start walking. Infants may have very different strategies for crawling (Adolph et al., 1998), using either three or four limbs, the belly touching the ground or not, with different types of limb coordination, but their most common gait is a walking trot with alternated locomotion on the hands and knees (hereafter called "the standard crawling gait").

Burnside (1927) and Hildebrand (1967) were the first to report quantitative data on interlimb coordination during crawling on hands and knees. They found that the coordination pattern is between a walking trot and a lateral sequence walk. Hildebrand also reported a difference in the durations of stance between hands and knees (hand stance is between 120-130% longer than for the knees) which is high compared to other quadrupeds. He also remarked that the concept of gait for human infants is less meaningful than for other mammals due to the unsteadiness of infant locomotion. In a more recent study, Patrick et al. (2009) tested 26 human infants and 7 adults in various conditions (treadmill and normal ground) and among their observations we can note that the crawling pattern was mainly restricted to a lateral sequence walk and they never observed symmetric running patterns. They reported gait transitions in infants crawling but these transitions were smooth variations of the ipsilateral phase lag (between the fore and hindlimbs), which can be related to the unsteadiness nature of infant crawling.

There are almost no studies of the kinematics of infant crawling. Although Mucino et al. (1987) and Niemitz (2002) reported kinematic data on infants for the different limbs, their experiments were only done on one and two infants respectively, and no extensive analysis of these data or comparisons with other mammals was done. Moreoever, to the best of our knowledge, there are no quantitative studies available about the crawling gait in human infants that combine both gait analysis (i.e. footfall patterns) and kinematic data of joint movement as compared to what is known in mammals.

In this study, we are therefore interested in providing such an analysis and answering two main questions. First, despite the simple and non-optimized limb geometry of the human infant,

how is its crawling gait different from the gait of other quadrupeds (in terms of kinematics and interlimb coordination)? Second, how does this locomotion relate to non-human primate locomotion? The aim of the present study is to give a detailed description of the standard crawling gait of human infants and to compare its characteristics with other quadrupeds and especially primates. These comparisons will be done in terms of 1) the basic limb kinematics, 2) the relation between speed of locomotion and swing/stance durations, 3) the preferred footfall sequences and 4) the coordination between the limbs and the spine.

2. Methods

Subjects

Nine healthy infants, 9 to 11 months old, participated in the study. They were selected as crawlers practicing the standard gait using hands and knees in an alternated fashion (see Table 1). Three of them were measured twice (A, A1, and E in Table 1). We had to discard two of them for the analysis because the collected data were not complete (not shown in Table 1). On most trials these two infants only made one step and stopped. The following discusses the results obtained with seven infants, three of them measured twice. They were all healthy infants (4 boys, 3 girls), full term with normal birth weight, and according to parents without any complications or illnesses during the neonatal period .

Procedure

The study was performed in accordance with the ethical standards specified in the 1964 Declaration of Helsinki and was approved by the ethics committee of Uppsala University. When the parents came to the lab they were informed about the experiment and signed a consent form. They obtained a gift certificate of value 10 € for participation. The parents undressed the infants and 18 small markers (diameter 4 or 8 mm respectively) of reflective material were attached to the skin on the joints or close to them. Three markers were put on the spine (neck, thoracal and lumbal). The subjects wore a hat on which three markers were attached (1 midsagittal, 2 coronal). The markers on the wrists and knees were glued to a velcroband. This gave stability to the critical parts that were close to the floor during locomotion. One disadvantage was that the knee markers were just above the joint. The remaining markers (elbows, shoulders, hips and feet) were attached with double-sided tape used for skin electrodes. When all 18 markers were properly attached the infant was encouraged to crawl on a rug (polypropylene, size 230 x 170 cm) placed on the floor. The parent and one experimenter were sitting on the floor on opposite sides of the rug using attractive toys to catch the infant's attention. A second experimenter sitting close to the rug handled the measurements and observed the infant's behavior. Each trial was videorecorded in synchrony with the measurements.

Measurements

A motion capture system, 'Proreflex (Qualisys)', was used to measure the movements in 3-D space. Data was collected at 240 Hz for 12 s periods sampled with external pre-triggering. In close synchrony with the measurement sessions, a video camera monitored the infant during the trials. Five Qualisys cameras were used, two were placed on ceiling stands and three were placed on the floor so that the crawling area was covered. When the infant showed intention to start crawling, the measurement was started by the second experimenter. Usually between 20 and 40 trials per infant were recorded The trials that were taken into account were those containing at least one complete gait cycle. Thus valid trials contained on average 3 complete cycles (see below for details).

Data evaluation

For each measurement, the markers were identified and their positions translated to Euclidian coordinates (Qualisys software) with an accuracy of 0.5 mm. These raw data were then processed (Matlab, Mathworks) in order to interpolate for missing data over small time intervals (<200ms) and to remove high frequency noise. In order to do that, we used two consecutive methods. First we interpolated the missing data using a piecewise cubic Hermite interpolation. We did not perform any extrapolation of the data at the beginning and end of each time series. Then, in order to remove the noise, we smoothed the data using a locally weighted scatter plot smoothing. It used least squares linear polynomial fitting with 20 data points for each local smooth calculation (span of 83 ms).

Swing - Stance measurement

In order to study steady state crawling and to have comparable data, we selected only the crawling sequences in which the infant was crawling straight toward a goal without stopping to do something else. Only complete gait cycle sequences were taken into account. Thus a stance phase was always measured between 2 swing phases. Table 1 shows the final number of complete cycles obtained for each infant that were used in the analysis below. The swing phase of the arms/legs was defined as the phase during which the hands/knees were moving forward.

In order to calculate the onset of the swing phase, we calculated the squared time derivative of the positions of hands and knees. The threshold was defined as the value just above the maximum value found during the middle of the stance phase averaged over all the stance phases (Figure 1). We always used the videos to check the consistency of the measures and correct them when necessary (i.e. to exclude wrong swing measurements).

Kinematic measures

Five different degrees of freedom (DOFs) were chosen for study: the angle of the shoulder in the sagittal plane, the elbow of both arms, the hip in the sagittal plane, the knee for both legs, and the spine angle in the horizontal plane. Figure 1 shows the different degrees of freedom, the shoulder and hip joints have an angle of 0 when they are vertical. The elbow and knee joints are taken to be 0 when they are completely flexed (note that it is physically impossible). These measurements are compatible with other kinematic studies (e.g. Larson et al. (2001)) and therefore necessary enable comparison with previous studies.

In this study we calculated the median movement of the different DOFs. In order to calculate the median values for each infant, we first separately scaled the swing and stance phases for each trajectory by means of local linear interpolation and then calculated the median value of all the data set for each point in time. We set the duration of the swing to 40% of a complete cycle and the stance to 60% which correspond to a typical value for the crawling gait. This scaling allows to compare the limb kinematics between different crawling gaits with different stance and swing durations.

For the case of the DOF of the spine, this median movement was rescaled in the same way as for the joints, except that it was centered on 0°. Furthermore, the movements were separated into 4 different phases in two different manners. In a first manner, we used the swing phase of the left arm, the period when the 4 limbs were on the ground, the swing of the right arm, and the period when the 4 limbs are on the ground again. In a second manner we used the same information, except that the separation was done with reference to the swing of the legs (swing of right leg, complete support, swing of left leg and complete support). This allowed us to show the coordination of the spine with the four limbs. A positive value for the spine angle means that the spine is folding in the left direction (Figure 1).

Statistical measures

In this study, we use the median and interquartile range estimators instead of the mean and standard deviation as the former estimators are more robust against noise and outlier values (Morgenthaler, 2001). Non parametric tests that do not require a Gaussian distribution of the data were used to evaluate the results. Whenever needed, we used Spearman correlation tests and Wilcoxon rank sum tests. The level of statistical significance was set to 5%.

Limitations and strengths of the study

The main limitation of this study is the small number of infants that were analyzed. However, as will be shown below, our data is consistent with previous findings on the crawling gait of infants (lateral sequence walking gait) and generally our results are consistent among all the infants. Thus we think that we are yet able to capture the main characteristics of the standard crawling gait. Another limitation is the restriction of our study to one gait whereas it is known that infants can adopt different strategies to locomote. Thus our results cannot generalize to every crawling

behavior and we cannot infer general principles from the developmental perspective. On the other hand, we think that this study has several strengths. It is the first quantitative study that combines both kinematics and gait/timing information for crawling infants and that includes the study of the spice movement in the horizontal place. Second our method to collect data is quite precise since we captured the 3-dimensional joint motions at a 240 Hz rate, which is, to the best of our knowledge the first time that data is collected at such a high rate for crawling infants.

3.   Results

Gait analysis

Swing and stance durations

The crawling gait is a symmetric gait that resembles a trot gait in terms of the temporal symmetries between the limbs. It means that diagonally opposed limbs move almost in synchrony (trot) and are half a period out of phase with the contralateral limbs (symmetric gait). Thus the left arm is synchronized with the right leg and they are half a period out of phase with the other two limbs. The swing phases of the ipsilateral limbs never overlap. Figure 2 shows the typical footfall sequence of this gait.

To quantitatively characterize this gait, we first calculated the percentage of the cycle period by which the left arm, and the left leg footfall precedes the right arm, resp. right leg footfall, which gives us an indication on the symmetry of the gait. For all infants we found values around 50% indicating the symmetry of the gait. Then in order to fully characterize the gait, we calculated the mean duty factor (stance period of the hind legs as a percentage of the stride duration) and the diagonality (the percentage of the cycle period by which the left hind footfall precedes the left fore footfall) of the gait for each infant as defined by Hildebrand (Hildebrand, 1965). For all infants the duty factor was comprised between 50 and 70% and the diagonality between 33 and 40%. Thus all infants had a gait between a walking trot and a lateral sequence diagonal couplets walk (diagonal couplets mean that the gait is closer to a trot than to a pace, see Hildebrand (1965) for more details) in agreement with what was found in previous studies (Burnside, 1927; Hildebrand, 1967; Patrick et al., 2009). As pointed out by these authors, infants crawling is different from other quadruped locomotion in terms of the discrepancy between the fore and hind limbs duty factor. Our data confirms that. We found that the duty factor of the fore limbs is on average is 8% higher than the duty factor of the hind limbs. More specifically for 5 infants we found a statistically significant difference (p<0.05) and no statistical difference for 2 infants (one of which had a slightly smaller, but not statistically significant, duty factor for the fore limbs than for the hind limbs).

The median duration of the arm swing is between 300 and 446 ms for the 7 infants, the median duration of the leg swing is between 354 and 554 ms. The variability of the swing phase (the ratio of the interquartile range of the swing duration to its median duration for each infant) has a median of 16%. Compared to this, the median duration of the stance of the arms for the different infants varied between 367 and 1035 ms, and the median duration of the stance of the

legs between 373 and 975 ms. The variability of the stance duration (ratio of the interquartile range of the stance duration with its median duration for one infant) has a median of 28%. Interestingly we see a small variability in the duration of the swing phase both within each measured infant and between all the infants whereas the variability of the stance duration is much more pronounced for each infant and especially between infants.

Relation between speed and cycle duration

The crawling velocity was estimated from the positions of the markers located on the spine during each crawling sequence. Figure 3 shows the cycle frequency, 1/stance duration and 1/swing duration as a function of the velocity. We find a strong linear relation between the frequency of the cycle and the speed of the infants (r = 0.86, p<0.001). A strong linear relation was also found for the inverse of the stance duration (r = 0.82, p<0.001) and speed of locomotion. No significant correlation with the swing duration (r = 0.11, p=0.34) was found.

Kinematics

Kinematics of the arms

Figure 4 shows the median kinematics of the forelimbs for each infant. The shoulder is flexed at the beginning and extended at the end of the swing, before touch-down. The arm posture is quite protracted at touch-down, with joint angles between 14-39° for the different infants (Md = 24°). The shoulder during stance is mainly moving from the flexed posture to an extended one to allow the body to move forward. Lift off occurs at joint angles between -10 and -34° (Md = -26°). We also note that the movement of the limbs is qualitatively the same for every infant, only the total excursion angle changes. It ranges between 39 to 72° with a median total excursion angle of 46°.

The elbow joint is extended at the beginning and end of the swing phase while it is flexed at mid-swing. The total excursion during swing ranges between 16 and 45° (Md=36°). During stance the elbow moves much less (3 to 15° among the infants, Md = 11°) and stays mostly at a quite extended position (median position between 135 to 170°, Md=151°). The fore limb is quite extended during stance as compared to other mammals (Larney 2004) and the movement of the elbow is small.

No correlation between the speed of locomotion and the amplitude of movement of the shoulders was found (correlation < 0.15 and p > 0.7).

Kinematics of the legs

Figure 5 shows the median angular values of the legs for each infant. During swing, the hip joint mainly flexes with a slight extension before touch down of the knee, at touch down the hip is very much protracted with an angle between 26 to 64° (Md = 44°). During stance the hip is

extended, with an angle at lift off between -31 to 5° (Md = -11°). This behavior is qualitatively similar to the movement of the shoulder joints (in the sense of flexion and extension patterns) although the extension before touch down is less visible as compared to the arm movement. Qualitatively, the movements of the legs are similar for all the infants, except that the amplitudes are different. The total excursion range is 52 to 75° (Md 57°).

The knee is always on the ground during stance where it is mainly used as a pivot around which the hip rotates. The median amplitude of the movement of the knee is 35°. It is observed in Figure 5 that the knee flexes during swing and extends during stance mainly to follow the movement of the hips.

As for the arms, we did not find any significant correlation between the amplitude of the hips and the speed of locomotion of the infants (correlation < 0.25 and p-values > 0.5).

Kinematics of the spine

Figure 6 shows the median movement of the spine in the horizontal plane for each infant. It also shows the coordination between the limbs and the spine. First we notice that during the swing phase of the left arm and right leg, the spine is moving from a positive angle to a negative one (same values in magnitude) and is doing the opposite movement during the swing of the right arm and left leg. When the 4 limbs are on the ground, the spine is then almost stationary. The spine thus performs an oscillation that is synchronized with the swing phase of the limbs. The maximum curvature of the spine is attained for all the infants during the stance phase of the arms, which also corresponds for most infants but one to the stance of the opposite leg (see vertical arrows in Figure 6). The median amplitude of this movement is 23° with interquartile range of 9°.

Stick figures of a typical crawling sequence of an infant can be seen in Figure 7. This shows both the typical kinematics and limb coordination pattern of the crawling sequence.

Changes in crawling with experience

Figure 8 shows the average speed of locomotion as a function of the number of days since the onset of crawling. We can see that the correlation between experience and speed of locomotion is high (r = 0.71, p = 0.021), indicating that the speed of locomotion increases with experience. Thus we should also expect changes in the duration of stance, as we pointed its relation with speed in the previous section.

Three of the infants were seen twice with approximately a month interval (see Table 1). The variations of the durations of stance and swing and the speed of locomotion are shown in Figure 9. We notice that infants A. and Al. have a significant decrease in stance and swing durations and that the major decrease is stance duration, which is more than twice the variation of the swing duration. As expected we notice for these infants a major increase of speed. Infant E. did not show significant changes in swing and stance duration and we found that speed did not change much either. We also compared the limb kinematics of the infants for the second session

but no significant change in the median kinematics was seen (data not shown), suggesting that with experience it is mainly the timing parameters that varies, not the kinematics.

4.   Discussion

Main gait parameters related to speed

We found that the standard crawling gait of the infants was between a walking trot and a lateral sequence diagonal couplets walk, with the legs starting to swing shortly after the arms which is in accordance with previous studies (Burnside, 1927, Hildebrand, 1967 and Patrick et al. 2009). The duty factor is between 50 and 70%. We also noticed that the stance duration varies considerably both for each infant and between the infants, and this variation is indeed related to changes in speed of locomotion. The swing duration varies little and we did not find any correlation with locomotion speed. The amplitude of the movements of the shoulders and hips are not correlated with speed. Therefore it is concluded that the main strategy to change speed is to vary the stance duration. It is interesting to note that the relations between stance duration and speed seems generic to quadrupeds independently of their functional kinematics. For example Righetti (2008, Chap. 4) showed through the physical simulation of quadruped models (robots) with different kinematic structures, including an infant like structure, that controlling the stance duration could always control locomotion speed, while swing duration had little influence on that. In other quadruped mammals it is well known that as speed increases, stance duration decreases in a similar manner (Grillner, 1975; Vilensky, 1987). It is also known that the duration of the swing phase is relatively constant for all speeds (Grillner, 1975; McMahon, 1984; Vilensky, 1987). Thus from that point of view the temporal characteristics of crawling locomotion are the same as for other quadruped vertebrates.

Kinematics

The general pattern of locomotion is qualitatively similar for all infants. However it must be noted that these infants were selected because they used the standard crawling gait (alternated locomotion on hands and knees); for infants having other gaits than the standard one, we might certainly find differences in the kinematics. The standard gait in infants as well as in most quadruped mammals consists of a single period of protraction (during stance) and retraction (during swing), with beginning of protraction at the end of swing for the most proximal joints (shoulder and hip) (Fischer et al., 2002; Grillner, 1975; Vilensky, 1987).

At touch down, we notice the quite protracted arm posture (shoulder joint angle between 14 to 39° relative to the vertical (Md 24°)) that is typical of primates (Larson et al., 2000), whereas other mammals have a more retracted posture where the shoulder joint angle is negative. At lift off, the shoulder joint is not very much retracted (Md -26°) while most species show angles lower than -50°. In addition the total shoulder excursion angle is relatively small (Md 46°). However when looking in details at primate species, infants shoulder characteristics are quite

close to the primates with the largest average body size, the Pongidae (i.e. great apes), where mean touch down, lift off and total excursion shoulder angles are 21, -33 and 55° respectively (Larson et al., 2000). Larson et al. (2001) published an extensive comparison on the hindlimb excursion angles of different mammals (including primates). Primates and marsupials show relatively high hindlimb angles at touch down (33 and 40° resp.) as compared to other species (< 27°). While at lift off the studied species all show angles lower than -17°, the highest being for primates (-29°). The total excursion angles are high for primates and marsupials (64 and 58° resp.) compared to other mammals (<52°). Compared to these data, infants have hindlimb angles at touch down that are relatively high (Md 44°) and small retraction angle at lift off (Md -11°) while the total excursion angle is high (Md 57°) and compares well with what we observe in other primates of the same weight. Finally, the hindlimb excursion range is much higher than that of the shoulder for infants, which is something that we observe also in Pongidae and koalas but not in other mammals (Larson et al., 2001). It is interesting to point out that in that perspective, infants have a general limb kinematics that is really close to great apes.

The elbow joint performs a single flexion and extension during swing which shorten the length of the arm to allow the limb to move forward and remains straight during stance. The swing part corresponds well to the movement of the elbow joints of other mammals. The stance part is different, however, since a flexion/extension of the limb was also expected during this phase as in many other mammals, and especially in primates which use a relatively compliant gait with a quite important elbow yield (Schmitt, 1999). Compliant gaits are generally characterized by a large elbow yield during stance, longer step length and longer contact times. They involve an increase in metabolic power (McMahon, 1985) that implies an increased effort of the muscles of the joints. The crawling gait is not compliant in contrast to other primates. However it seems that compliant gait of primates is tightly connected to arboreal locomotion and primates seem to use less compliant gaits on ground than on branches (Schmitt, 1999). We also noted that infants crawl with a quite extended forelimb, which is characteristic of large animals (including primates) with relatively weak limb bones since such a posture reduces bone stresses (Rubin and Lanyon, 1982). One might speculate that infants choose a gait that reduces bone stresses and metabolic power.

During standard crawling, the forelimb is quite extended and consists of two functional segments and the hindlimb of only one functional segment making the length of the forelimb (distance between the shoulder and the hand) greater than that of the hindlimbs. This difference in limb length can explain the differences in the excursion angles of the fore and hindlimbs as was suggested by Larson et al. (2001), perhaps to keep a similar step length between the longer and shorter limbs. This limb difference could also explain the quite protracted fore limb at touch down, since a retracted limb would lead either to an unstable gait if the elbow did not yield (since the center of mass would go out of the support polygon) or to the reduction of the visual field if the elbow yielded.

Lateral sequence footfalls

We know that the footfall sequence during quadruped walking in primates is generally a diagonal sequence gait (left-hind (Lh), right-front (Rf), right-hind (Rh), left-front (Lf)) while other non-primate quadrupeds use a lateral sequence gait (LhLfRhRf sequence) (Hildebrand,

1965, Hildebrand, 1967 and Vilensky, 1987). Despite some primates and especially their infants can also choose a lateral sequence gait (Vilensky and Larson, 1989), the diagonal sequence gait is the dominant one (Shapiro and Raichlen, 2006). The crawling gait of infants is thus closer to non-primate quadrupeds, since infants only use a lateral sequence gait. This result is consistent with previous findings on crawling infants (Burnside, 1927, Hildebrand, 1967 and Patrick et al. 2009). We must note that this lateral sequence gait is not merely characteristic of human infants but also of adults, as was reported by Patrick et al. (2009).

It is interesting to note that the gait chosen by infants is the most stable pattern of coordination possible. Indeed Gray (1944) showed that the lateral sequence gait (non-primate) is the only pattern of coordination where the projection of the center of mass on the ground stays in the support polygon[1] when at least three feet are on the ground. When at least two limbs are on the ground, this pattern of coordination then minimizes the duration of phases where the projection of the center of mass is outside the support polygon and certainly increases stability.

A lateral sequence gait close to the trot implies that the hand will start to swing just before the diagonal leg, thus giving some precedence to the swing of the hand. We also observed that during the experiments, infants were spontaneously starting to crawl toward a goal or an object with the hand directed toward the object as if they were trying to reach it. Adolph et al. (1998) also mention that infants initiate locomotion with the hands. Thus we suggest that since infants reach for and manipulate objects all the time with their hands and since the fore limbs are the only visible limbs, it could also explain the preference of the fore limbs for the start of swing, i.e. the start of locomotion. That may indicate a visual-motor coupling with the purpose to direct the infant to goals. Further experiments would be needed to confirm this hypothesis.

Spine kinematics

The spine makes a periodic lateral undulation during locomotion that is synchronized with the limbs, with maximum amplitude reached just after ipsilateral hind limb touch down. The observation of a standing wave has already been made for many tetrapods, from salamander (Ashley-Ross, 1994; Frolich and Biewener, 1992; Ijspeert et al., 2007), lizards (Carrier, 1990; Ritter, 1996; Ritter, 1995) to primates (Strepsirhines) (Shapiro et al., 2001). For strepsirhines the maximum amplitude curvature of the spine is reached after ipsilateral hind limb touchdown and for the lizards it is reached before (except for very low speeds). As hypothesized by Shapiro et al. (2001), the difference in the timing of the maximum curvature in lizards and these primates could come from their respective gait. Lizards use a lateral sequence walking gait while primates use a diagonal sequence walking gait. However we found that infants have maximum curvature of the spine similar to primates but a different gait. A tentative explanation would be that these differences are due to the limb geometry of the crawling infants, having long fore limbs compared to hind limbs which is different from the strepsirhines studied by Shapiro. If the spine movements

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[1] The support polygon is the area delimited by the limbs that are on the ground, for example when three limbs are on the ground this polygon is the triangle created by these limbs. In mechanics it is known that if the projection of the center of mass on the ground is located inside the support polygon then the body is (statically) stable under gravity otherwise the body is not stable and an action is required to keep the body balanced (taking a step for example). This stability criterion is valid for bodies that do not accelerate, it remains very good indicator for bodies with low acceleration.

and gait of infants were closer to slowly walking lizards than primates, an increase in their speed would lead to a maximum curvature happening before the end of swing. More experiments both on human and non-human primate infants using sometimes a lateral sequence gait would be needed to further compare gaits and spine movements and explore further explanations. For example, one question that could be explored is whether infants use different mechanisms to adjust speed and posture, keeping posture by modifying the swing-spine dynamics on one hand and adjusting speed by varying stance duration on the other hand.

Development of the gait through experience

It seems that, apart from stability, the main experience dependent parameter is the duration of stance phase. The swing phase remains rather constant with experience. The crawling speed is related to experience, and the crawling gait of infants becomes faster when the complete support phase (where the four limbs are on the ground) is shorter. It means that infants begin with a gait in between a walk and a walking trot and tend to a perfect walking trot with more experience. Interestingly we can find similarities with the development of the gaits of other quadrupeds. Indeed, in several rodent species lateral walking appears first closely followed by trotting, and more specialized gaits (asymmetric or biped gaits) develop only later (Eilam, 1997).

Conclusions

Despite the facts that humans crawl for only a short period in development, they can adopt many different strategies for locomotion (instead of the standard crawling gait) and that they have a mechanical structure that is not optimized for quadrupedalism, we found that the infant standard crawling gait shares many similarities with other quadruped mammals and especially with non-human primate gaits. The four main characteristics that are similar to primate locomotion are: a positive correlation between stance duration and speed (this is common to most mammals), the quite protracted limb at touch down, the relatively extended arms during locomotion and the coordination of the spine with touch down of the limbs. However the crawling gait is different from primates in at least two important aspects: first infants use lateral sequence footfalls which make their pattern of coordination closer to non-primate mammals and second they have a relatively stiff elbow during stance while primates use a compliant walking gait. These differences could be related to stability (for the gait) and to reducing joint torques (for the stiffness), however the reasons for these differences remain an open question.

In conclusion, infant using a standard crawling gait have gait and kinematic characteristics that are very similar to other quadruped mammals although they have a very different functional limb geometry. Two main, non exclusive, hypotheses may explain these differences. The first hypothesis is that these similarities reflect common principles in the underlying control mechanisms (Bernstein 1967). The second hypothesis is that these similarities are essentially due to mechanical constraints. Indeed, mechanical constraints related to stability, closed kinematic chains, power consumption, etc. might not leave much choice on possible stable and energy-efficient locomotion patterns. Further experiments as well as modeling (or robotics) approaches

that study quadruped locomotion with different mechanical structures would help in testing these hypotheses.

Acknowledgements

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Table 1. Data of birth, experience of crawling[2], number of complete steady crawling cycles that were extracted from the experiments for each limb and body mass the day of the experiment for the seven infants[3].

Infant name	Age [days]	Experience [days]	Numbers of complete cycles				Body mass [kg]
			Left arm	Right arm	Left leg	Right leg	
A.	253-296	28-71	17-6	16-12	13-2	16-7	7-7.5
Al.	273-301	21-49	12 - 5	10 -8	10 -6	Nov 7, 2009	11 -12
E.	286-332	15-61	16-5	15-6	8 -6	10 -6	9.5-10
J.	290	59	6	5	5	5	9
M.	304	39	12	13	11	13	11
O.	319	89	1	5	4	2	10.5
V.	290	21	13	7	10	3	10

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[2] i.e. the number of days since estimated start of crawling
[3] Note that A., Al. and E. were seen two times.

(a) Limbs angles schematic

(b) Spine angle schematic

(c) Position of the markers

(d) Marker data example
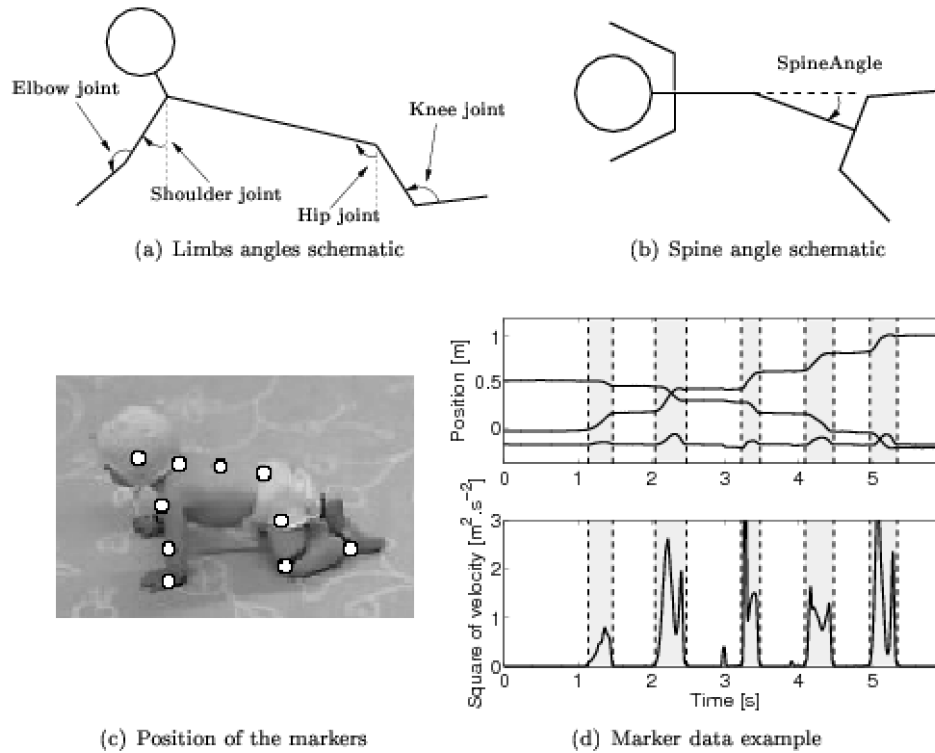
Figure 1 - a) Schematic (not based on real data) of the joint angles in sagittal plane that were measured. We measured the shoulder, the elbow, the hip and the knee joints. The arrows show the positive angles. The shoulder and hip joint were measured relative to the vertical. b) Schematic of the spine angle made by the three markers on the spine measured in the lateral plane, the arrow shows the positive direction of the angle. c) Snapshot of a crawling infant together with the position of the markers that were used to calculate the different angles. d) Typical trajectory of the hand in x-y-z directions (upper graph, the lower line is the z direction, while the middle and upper one are respectively the y and x directions) during crawling with the corresponding velocity profile of the hand (here we show the square of the velocity). The vertical lines show the separation between the swing (gray) and stance (white) phases.
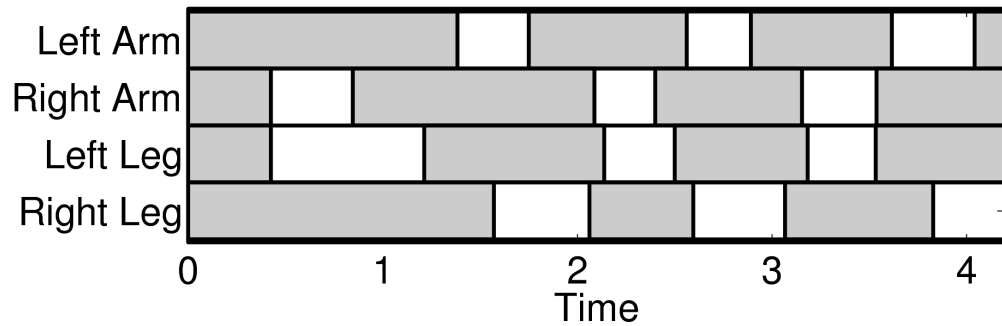
Figure 2 - Typical footfall sequence (real data) of the infant standard crawling gait. The dashed boxes show the stance phases and the white ones the swing phases. In this case the infant starts to crawl when the right arm swing first. We notice on this graph the long stance durations, the walking trot gait and the fact that the arms swing slightly before the diagonal limbs.
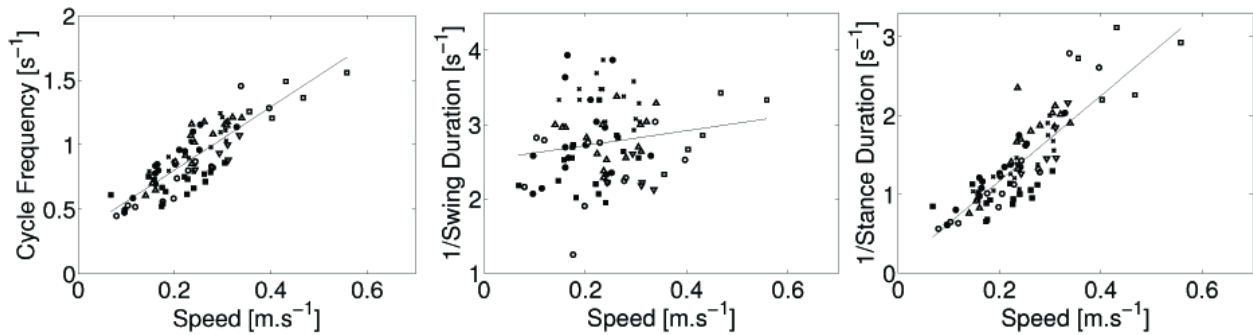

Figure 3 - Cycle frequency, 1/stance duration and 1/swing duration as a function of the speed of locomotion for all subjects: ● for A. ○ for Al. ◆ for E. ◇ for J. ■ for M. □ for O. and for × V. The regression lines are also showed. We see on this graphs the stong linear correlation between speed and cycle frequency and 1/stance duration, while there is little correlation between 1/swing duration and speed of locomotion.
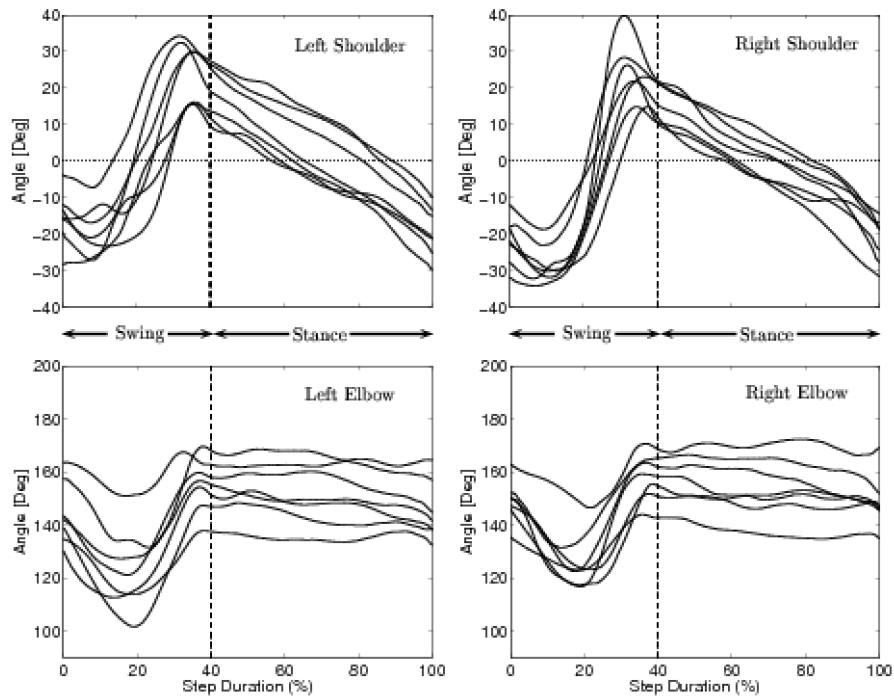
Figure 4 - Median fore limbs kinematics for each subject. The trajectories were rescaled into normalized swing and stance phases, as explained in the Methods section. The vertical dashed line indicates the touch down of the hand. We notice the same pattern of movement for all infants, with flexion/extension patterns for the shoulders, elbow flexion and extension during swing and little elbow yield during stance.
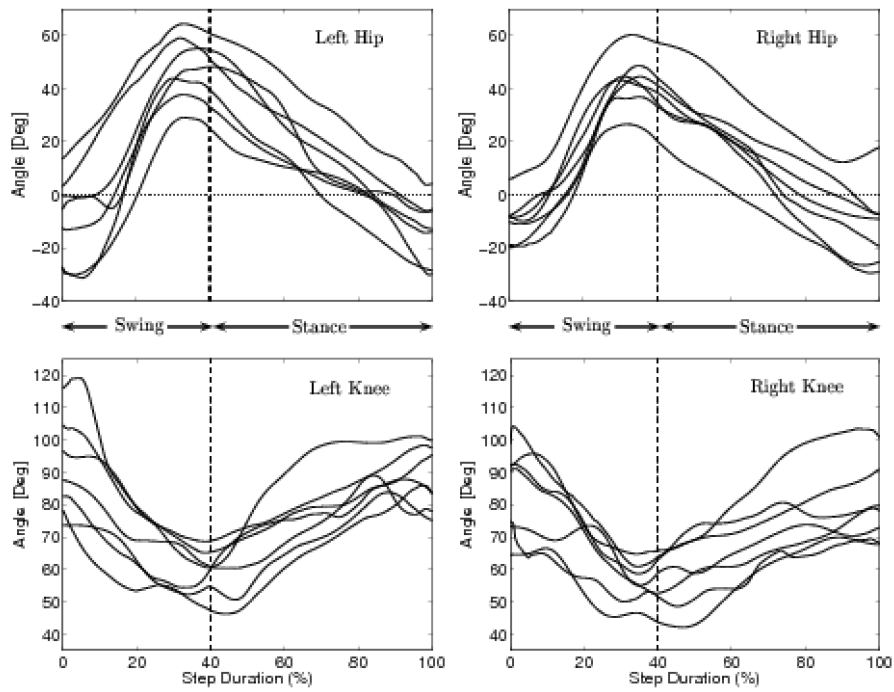
Figure 5 - Median hind limbs kinematics for each subject. The trajectories were rescaled into normalized swing and stance phases, as explained in the Methods section. The vertical dashed line indicates the touch down of the knee. We notice the same pattern of movement for all infants. The hip joints do a flexion and extension during the cycle. We also notice the flexion/extension of the knee.
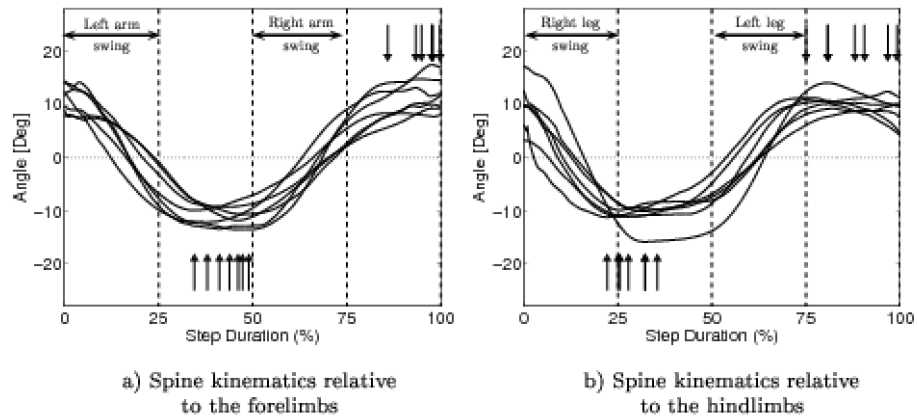
Figure 6 - Median movement of the spine for each subject. Figure a) shows the spine movement relatively to the fore limbs and figure b) relatively to the hind limbs. The vertical arrows show the maximum curvature of the spine. The vertical bars delimit the stance and swing phases. We notice the synchonization between spine movements and the limbs, specially the movement of the spine during the swing of the arms and the maximum curvature during the stance.
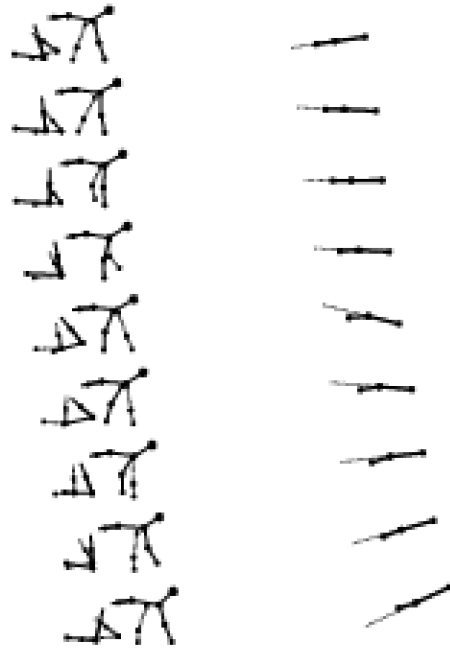
Figure 7 - Stick figures from real data of a typical crawling sequence (100 ms apart). The left graph shows the lateral view of the infant, the dashed line representing the left limbs. The right graph shows the spine movement of the same sequence from a top view, the dashed line here is an artificial extension of the front segment of the spine to help to see the curvature of the spine. We notice the maximum curvature during the stance of the arms.
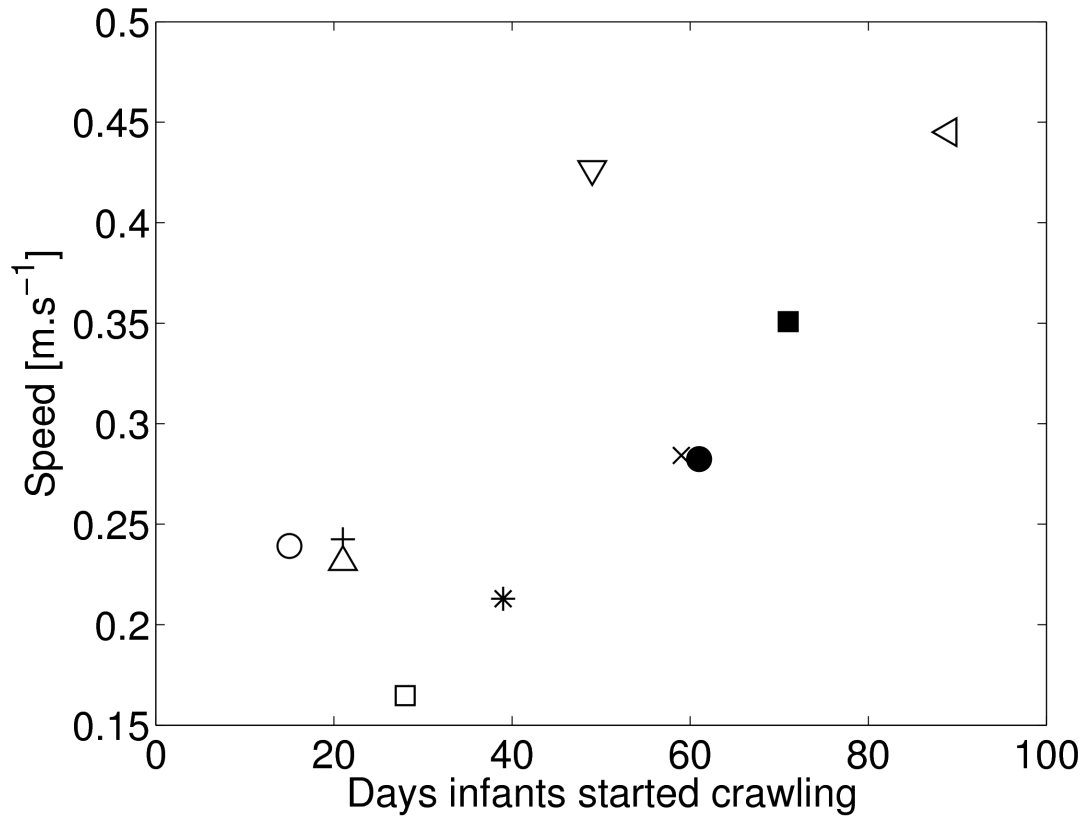
Figure 8 - Median speed of locomotion as a function of the number of days of crawling. □ and ■ represent infant A. for experiment 1 and 2 respectively. ◇ and ◆ are for Al., ○ and ● for E., × for J., ★ for M., ◁ for O. and + for V. We notice the linear correlation between the experience in crawling and the speed of locomotion.
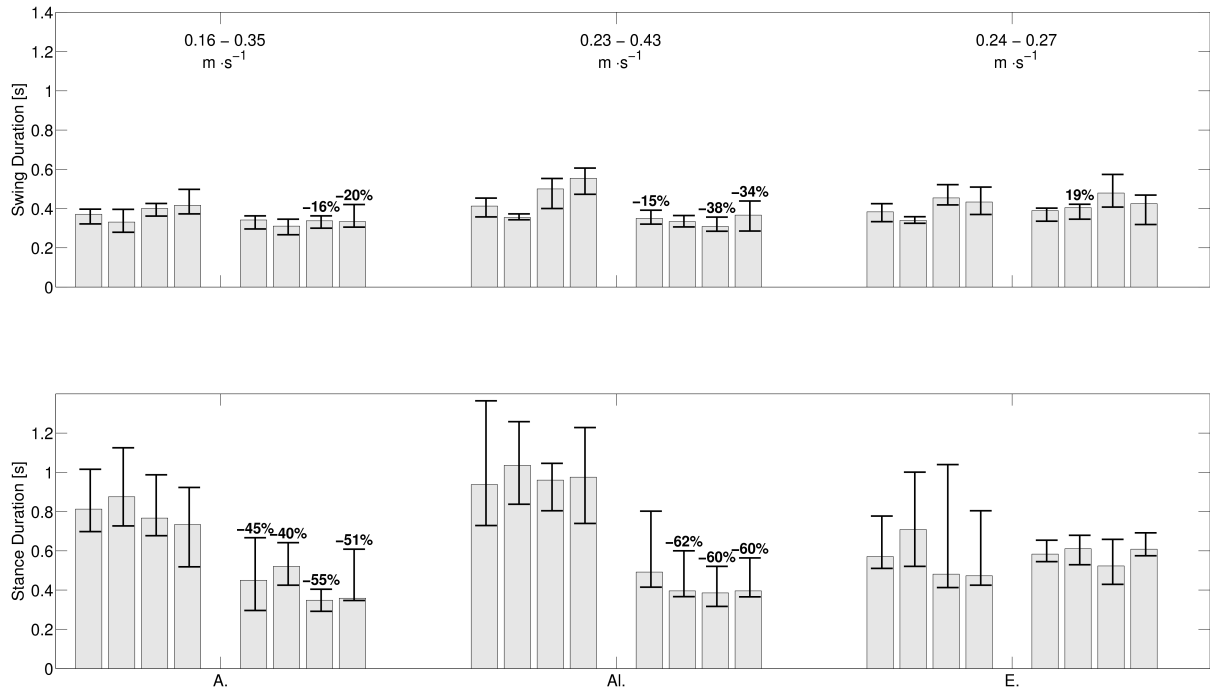
Figure 9 - Changes in swing (top figure) and stance durations (bottom figure) for the three infants measured twice. The left set of bars corresponds to the first experiment, the right one corresponds to the second one. Each group of four bars represent the median durations of the left arm, the right arm, the left and right legs respectively. We also show the interquartile range as error bars for each subject. The numbers on top of the bars represent the variation of median duration, we show only the statistically significant variations. On the top figure we also show the average locomotion speed for the 1st and 2nd experiment for each infant. We notice for A. and Al. the strong decrease in stance durations together with the increase in speed, while for infant E. there is no significant change in stance duration and no significant change in speed either.