Interlimb coordination in human crawling reveals similarities in development and neural control with quadrupeds

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ABSTRACT

The study of quadrupeds has furnished most of our understanding of mammalian locomotion. To allow a more direct comparison of coordination between the four limbs in humans and quadrupeds, we studied crawling in the human, a behavior that is part of normal human development and mechanically more similar to quadrupedal locomotion than is bipedal walking. Interlimb coordination during hands-and-knees crawling is compared between human infants and adults, as well as to interlimb coordination of quadrupeds. Mechanical factors were manipulated during crawling in order to understand the relative contributions of mechanics and neural control. Twenty-six infants and seven adults were studied. Video, force plate and electrogoniometer data were collected. Belt speed of the treadmill, width of base, and limb length were manipulated in adults. Influences of unweighting and limb length were explored in infants. Infants tended to move diagonal limbs together (trot-like). Adults additionally moved ipsilateral limbs together (pace-like). At lower speeds, movements of the four limbs were more equally spaced in time with no clear pairing of limbs. At higher speeds, running symmetrical gaits were never observed, although one adult galloped. Widening stance prevented adults from using the pace-like gait, while lengthening the hind limbs (hands-and-feet crawling) largely prevented the trot-like gait. Limb length and unweighting had no effect on coordination in infants. We conclude that human crawling shares features with both other primates and non-primate quadrupeds, suggesting similar underlying mechanisms. The greater restriction in coordination patterns employed by infants suggests their nervous system has less flexibility.
INTRODUCTION

There has been renewed interest in both the behavior and the underlying mechanisms surrounding interlimb coordination in quadrupedal locomotion, perhaps fueled by our improved ability to study intersegmental circuitry. While considerable progress has been made towards the understanding of commissural circuitry in the spinal cord responsible for coordination of homologous (left and right) limbs (reviewed in Kiehn 2006), much less is known about circuitry coordinating the ipsilateral limbs (Falgairolle et al. 2006). Recent studies suggest an asymmetry in the relationship between the pattern generators for the fore- and hindlimbs, which could guide the search for coordinating circuitry (Ballion et al. 2001, Juvin et al. 2005, Akay et al. 2006). Although the arms are not essential to walking in humans, the motion of the arms during walking is typically coordinated with that of the legs (Craik et al. 1976, Donker et al. 2001). Indeed, in many rhythmic limb behaviors in humans, the frequencies of arm and leg movements maintain an integer relationship, consistent with these movements being controlled by coupled oscillators (Wannier et al. 2001). Further, rhythmic activity of one limb pair affects electromyographic and reflex activity of the other pair (Zehr and Haridas 2003, Frigon et al. 2004, Huang and Ferris 2004) suggesting important neural linkages between the arms and legs (Dietz et al. 2001, Haridas and Zehr 2003).

Mechanisms of interlimb coordination in humans and quadrupeds could be more directly compared by studying human crawling, during which mechanical constraints are more similar to that of quadrupeds. If the coordinating circuitry is indeed similar, one would predict that humans and quadrupeds would respond in the same way under various situations. For example, quadrupeds show distinct forms of coordination at different locomotor speeds, such as walking at
slow speeds, trotting or pacing at faster speeds, and galloping at top speeds (reviewed in Grillner 1981). Coordination has also been correlated with morphology in quadrupeds. Short-legged animals use trot-like coordinations in which the diagonal fore- and hindlimbs move together, while long-legged animals may use pace-like coordinations in which the ipsilateral fore- and hindlimbs move together (Hildebrand 1976). Finally, coordination changes as a function of stability. Less stable conditions require coordinations that allow either 3 limbs (tripod) or diagonal limbs for support. All these conditions can be manipulated and tested in the human.

Interlimb coordination during crawling in humans has attracted relatively little attention in the literature. Early papers based on film records describe coordination in crawling from a small number of infants executing a small number of steps (Hildebrand 1967– 6 infants, 12 sequences; Burnside 1927 – 2 infants, 14 cycles). More recent studies are limited in scope regarding interlimb coordination (Freedland and Bertenthal 1994, Adolph et al. 1998 – both quantified initiation of swing phase only), making it difficult to compare with studies in quadrupeds. Studies of older children and adults crawling again are scarce. Interestingly, the limited studies indicate the types of coordination employed to be different between crawling on hands-and-knees (Muybridge 1955, Wannier et al. 2001), and hands-and-feet (Muybridge 1955, Hildebrand 1967, Sparrow 1989, Sparrow and Newell 1994), except at higher speeds of locomotion (Sparrow and Newell 1994). There are no studies that have explored coordination across a full range of locomotor speeds during hands-and-knees crawling.

In this paper, we asked whether infants and adults, being of quite different morphology and at different stages of development, show the same patterns of interlimb coordination. We identify
the response of interlimb coordination of both groups to increasing speed and compare this to that of quadrupeds. Since differences in coordination were found between infants and adults, we manipulated mechanical factors including the width of the base of support, functional limb length, and weight-support, to determine if adults and infants make the same changes to coordination as predicted by animal morphology. If the abilities are different between adults and infants, then portions of the nervous system that develop later in life (Yakovlev and Lecours 1967, Huttenlocher 1994) likely play a role in the behaviors that are unique to adults.

METHODS

Subjects

Data from 26 infants and 7 adults were included in this study. All experiments were performed with the informed, written consent of the adult subjects or parents of the infant subjects in accordance with the Declaration of Helsinki Guidelines on Human Experimentation, and with local ethical board approval. Infants ranging in age from approximately 7 to 13 months were recruited from New Mothers’ groups in local public health clinics. Adult subjects were recruited by word of mouth.

Experimental procedures

All crawling is on hands and knees, unless stated otherwise. Infant data were taken from undisturbed crawling sequences on the treadmill and/or over ground. Adults were tested on the treadmill only, because it is difficult to obtain sufficient number of steps over ground in a small laboratory.
INFANTS CRAWLING UNDISTURBED. Over ground crawling sequences were generally limited to 3 to 6 steps in order to ensure that the resolution of the video image was sufficient to determine effectively stance and swing of the limbs. Treadmill sequences varied in length for infants, depending on crawling proficiency and how agreeable the infant was to crawling on the treadmill. Belt speed for infant treadmill sequences was set at 0.22 m/s, the slowest possible for our forceplate-instrumented treadmill (Gaitway treadmill, Kistler Instruments, Amherst, NY). A body harness held by an examiner was used to ensure the safety of the infant on the treadmill; infants supported their own weight during analyzed sequences of crawling.

INFANTS CRAWLING UNWEIGHTED. Infants are generally less stable than adults (i.e., fall more often). We reduced the constraint of stability by unweighting five infants as they crawled on the treadmill. Coordination was compared between cycles in which they supported most of their own weight, and those when the examiner supported through the harness as much of the infant’s weight as was possible without cessation of crawling. The per cent body weight supported by the infant was determined from forceplates beneath the treadmill belt.

ADULTS CRAWLING ON THE TREADMILL – SEVERAL SPEEDS. Adults crawled for approximately 1 - 2 minutes at a time. Each trial included changes in treadmill belt speed and consisted of several crawling sequences at a variety of constant belt speeds. Overall, belt speed ranged from 0.22 to 1.34 m/s. For most trials, belt speed changed −0.1 – 0.2 m/s at a time, the changes in speed being spaced in time with the aim of collecting ten steps at each speed. To achieve crawling at the fastest belt speeds employed, the trial commenced with a moderate belt speed at which the subject felt comfortable. Belt speed was then increased more rapidly to approach the fastest
speeds without overtiring the subject. Cognitive tasks such as counting by 4’s, political
geography, reciting the alphabet backwards, or recounting of recent events were employed to
maximize the automaticity of crawling. Kneepads and socks prevented irritation of the skin.

ADULTS CRAWLING ON THE TREADMILL – MIDLINE OBSTRUCTION AND SLOW SPEEDS. We wished
to explore the mechanical effects of width of support and very slow treadmill belt speeds on
interlimb coordination. Five adults were tested crawling on the treadmill at belt speeds of 0.45
m/s and 0.13 m/s, with and without a foam obstruction fixed along the midline of the treadmill
belt. The midline obstruction forced the subjects to assume a wider support than normal. The
actual width of the foam obstruction (~0.1 to 0.15 m) was adjusted to accommodate the size of
the subjects in order to force a wide stance at the knees. Hands were forced to the edges of the
treadmill belt. Each trial lasted 1-2 minutes, sufficient duration to collect at least 10 full steps
under each condition.

CRAWLING ON HANDS AND FEET. To investigate the effect of limb length on interlimb
coordination, we studied the same five adults crawling on hands and feet at one or three treadmill
belt speeds (0.45 – 0.80 m/s). Hands-and-feet crawling effectively increases the functional
length of the legs compared to hands-and-knees crawling. Two infants who spontaneously crawl
on hands and feet over ground were also videotaped. Five steps were recorded for one of the
infants and 24 steps were analyzed for the other.

Data collection
All trials were videotaped at 30 frames/s (Samsung Digital-Cam SC-D353, Samsung Electronics Co., Ltd.); videos were subsequently captured onto computer (Adobe Premiere 6.0, Adobe Systems Incorporated). A second camera (JVC GZ-MG50U, Victor Company of Japan) allowed simultaneous video recording of side and front profiles of adults crawling with the midline obstruction. All video recordings were de-interlaced to 60 fields/s offline (VirtualDub © Avery Lee).

To identify key anatomical landmarks on the video recording, reflective markers were taped over the shoulder (lateral to the acromion), elbow (lateral epicondyle), wrist (ulnar styloid process), hip (greater trochanter), knee (lateral joint line), ankle (lateral malleolus), and on the trunk (lateral midline). For subjects videotaped in front profile, additional markers at the midline of the knees, wrists, and shoulders were applied. Snugly fitting clothing helped ensure minimal shifting of the markers during movement.

Twin-axis electrogoniometers (Penny and Giles, Biometrics, Blackwood Gwent, UK) were positioned bilaterally over the hip for all subjects except adults crawling with the midline obstruction and infants crawling on hands and feet, and across the knee for 17 subjects (13 infants and 4 adults). Goniometer signals were amplified and low-pass filtered on-line at 30 Hz using custom-made analogue gain filters. Surface bipolar EMG recordings were also obtained bilaterally from some subjects, but will not be presented in this paper.

All signals were digitized on-line at 2000 s⁻¹ (Axotape, Axon Instruments, Foster City, CA). Analogue signals were recorded on VHS magnetic tape (A.R. Vetter, Rebersburg, PA) for back-
up. Video and analogue data were synchronized with a digital counter, which advanced an LED counter in view of the camera(s) (resolution 1/100th s), and emitted a 5 V pulse at 1 Hz. The time indicated by the LED will be called the synclight time.

Most treadmill trials were performed on a Gaitway treadmill (Kistler Instruments, Amherst, NY) instrumented with forceplates. Adult trials exploring the effects of midline obstruction and very slow belt speeds made use of a Biodex treadmill (Isokinetics Inc., De Queen, AR), which could be run at slower speeds than the Gaitway. The left side of the subject faced the camera for all treadmill sequences. Occasionally the infant’s right side faced the camera for over ground crawling.

**Data analysis**

Data were analyzed off-line. Stance and swing for all four limbs were determined from video played frame-by-frame (Peak Motus, Peak Performance Technologies, Centennial, CO). If we could not identify the occurrence of a particular stance or swing event within a span of 3 frames then the event was omitted.

For infants, step cycles from all acceptable sequences were analyzed. An acceptable sequence consisted of at least two complete consecutive cycles with no stops or perturbations. A change in speed during a sequence was acceptable. For over ground crawling, the first and last steps of each sequence (starting and stopping) were omitted.
Due to the large number of steps in adult trials, only a subset was analyzed. Pilot work indicated that 10 steps were sufficient for treadmill speeds below 0.36 m/s and 7-8 steps sufficed for treadmill speeds at or above 0.36 m/s, because the step-to-step variability decreased with increasing speed. Occasionally less than 7 steps were collected at higher speeds (> 0.89 m/s) to avoid overtiring of the subject. For one subject there were obvious changes in coordination pattern, so attempts were made to record and analyze a range of speeds across coordination patterns. In addition to these sequences collected at constant belt speeds, a few sequences during which there was a change in treadmill speed were also analyzed in attempt to capture changes in coordination. Finally, to reduce sampling bias as much as possible, three steps were randomly selected from the middle of at least every other constant-speed sequence for each of the four adult subjects tested at a variety of treadmill belt speeds; only the relationship between ipsilateral limbs was determined for these steps.

After marking of stance and swing, subsequent calculations and data manipulations were performed using custom-written software routines (Matlab®, The MathWorks, Inc., or SigmaPlot 2000, SPSS Inc.). A step cycle was defined in relation to stance of the left leg, with one cycle being from the initiation of stance of the left leg to the next occurrence of the same event (LLst to LLst). The instantaneous rate of crawling was determined for each step cycle, and was calculated as the inverse of the duration of the cycle.

INTERLIMB COORDINATION. We define coordination to be the relative timing of events between the four limbs. We defined limb pairing to be the initiation of stance by 2 limbs close together in
time, i.e. in-phase, as occurs with some types of coordination (referred to as “couplets” by Hildebrand (1976)).

Figure 1 illustrates measurements used to describe interlimb coordination. The limb-contact pattern, commonly referred to as footfall patterns for quadrupeds, shows the timing and duration of stance (solid lines) and swing (spaces) phases for each of the limbs. Timing of initiation of stance and swing events for each limb was expressed as a function of the left leg cycle, ‘a’ in the top graph of Figure 1. For example, in the figure, initiation of stance phase in the left arm occurred at a time interval ‘b’ after initiation of stance in the left leg. We expressed this delay as a percentage of the cycle duration in the left leg, and call this a phase lag (100*b/a). The occurrence of these phase lags for each of the limbs can then be expressed in histogram format (see Results, Figure 2).

(Figure 1 near here)

The phase lag between stance of the left arm and stance of the left leg, henceforth called ipsilateral phase lag, was the main variable for quantifying interlimb coordination in symmetrical gaits. Symmetrical gaits are those in which the movements of the homologous limb pairs (i.e., left and right arm, left and right leg) are equally spaced in time (Hildebrand 1976). If, in addition to this left-right symmetry, duration of stance in forelimbs is equal to that in the hindlimbs, then the ipsilateral phase lag is sufficient to fully quantify the coordination (Hildebrand 1976). The more similar the stance phase duration between fore- and hindlimbs, the more sufficiently ipsilateral phasing alone describes interlimb coordination. Ipsilateral phase lags close to 50% indicate that limbs enter stance alternately, and describe a trot-like gait, in which it
is the diagonal limbs that enter stance together (Figure 1 top graph). Ipsilateral phase lag values close to 0% or 100% indicate that ipsilateral limbs enter stance nearly synchronously, and describe a pace-like gait (Figure 1 bottom graph). The whole spectrum of trot to pace is a continuum of the relationship between ipsilateral limbs (Hildebrand 1989). Values midway between pace and trot (i.e. 25%, 75%) indicate no pairing of limbs, the four limbs entering stance equally spaced in time (Figure 1, middle graph).

**Statistics**

Descriptive statistics include mean and standard deviation (sd) for normal distributions, and median and interquartile (iq) ranges otherwise. For comparative statistics, parametric tests (e.g. T-test, paired T-test, One-Way Analysis of Variance (ANOVA)) were applied when distributions passed tests of normality and equal variance. Otherwise, non-parametric tests (e.g. Wilcoxon Signed Rank test, Kruskal-Wallis One-Way ANOVA on Ranks) were employed. Kuipers test for two samples (Batschelet 1981) was used to compare histograms of interlimb coordination between infants crawling over ground and infants crawling on the treadmill. Significance level was set at 0.05 for all statistical tests.

**RESULTS**

We characterized hands-and-knees crawling in 13 infants crawling over ground (age: mean ± sd 10.0 ± 1.2 months). Five of these infants also crawled on the treadmill, along with six additional infants (9.5 ± 0.7 months). Initially four adults crawled on the treadmill at a variety of belt speeds (age 28.5 ± 5.4 years). Data from these subjects constitute the bulk of the data presented here. To answer questions stemming from investigation of these original 19 infants and 4 adults,
we collected limited data from additional subjects (7 infants and 3 adults). Coordination patterns
during unweighting on the treadmill were determined for five infants (10.9 ± 1.7 months), and
during hands-and-feet crawling for two infants (10.3 and 9.4 months). Five adults, including two
from the original study, were tested crawling on the treadmill at two different speeds with and
without a midline obstruction, and during hands-and-feet crawling (34.2 ± 11.9 years). Finally,
we videotaped the front profile of 5 infants (10.0 ± 2.2 months) during over ground crawling in
order to compare width of stance with that of adult subjects.

The median rates of crawling were similar across subject groups, at about 1 cycle per second.
Infants crawling over ground exhibited the greatest range of rates, and infants crawling on the
treadmill exhibited the narrowest range, being restricted to the 0.22 m/s belt speed. All steps
collected from infants as well as the vast majority of steps from adults could be classified as
“symmetrical” (Hildebrand 1976), or “alternating” (Grillner 1981). One adult demonstrated a
few cycles of galloping, a non-symmetrical gait, at a treadmill belt speed of 1.30 m/s.

**Interlimb coordination in symmetrical gaits**

For infants, diagonal limbs tended to swing together. The histograms in Figure 2A present the
timing of the initiation of stance (black bars) and swing (grey bars) in each limb, as a function of
the left leg cycle. Note that the bottom graph only has swing phase indicated because the
horizontal axis is defined by the stance phase of the left leg (delineated by vertical dotted lines).
Data from all infants crawling over ground are shown together, because all infants demonstrated
the same pattern. The homologous limbs enter stance alternately (e.g., black bars for right leg
occur around 50% of left leg cycle). Diagonal limbs, illustrated by the top two graphs and
bottom two graphs of Figure 2A, initiate swing at about the same time (compare grey bars from diagonal limbs). In contrast, the arm usually enters stance slightly before the diagonal leg (black bars in LEFT ARM lead those of RIGHT LEG). Consequently, there is a longer stance phase (and shorter swing phase) in the arm than the leg (paired T-test, p<0.05). Infants crawling on the treadmill demonstrated coordination very similar to that of infants over ground. Six of the seven distributions from treadmill crawling (not shown) were not statistically different from those of over ground crawling (Kuiper’s test for two samples). The stance phase of the arm was again significantly longer than that of the leg (Wilcoxon Signed Rank test, p<0.05).

(Figure 2 near here)

Adults exhibited a greater variety of interlimb coordination than did the infants. Two adults showed a trot-like coordination similar to the infants, in which the diagonal limbs tended to enter stance close together in time (compare Figure 2A&B). A third adult showed a pace-like coordination, in which it was the ipsilateral limbs that were more closely paired (Figure 2C, compare black bars from right side of body, and black bars from left arm are close to 0% of horizontal axis). The fourth adult showed both trot-like and pace-like coordinations (Figure 2D). As with the infants, the stance phase of the arm was longer than that of the leg in all subjects (Wilcoxon Signed Rank test, p<0.05). Across subject groups, the duration of the stance phase of the arm, normalized to that of the leg, was not significantly different between subject groups (Kruskal-Wallis ANOVA on Ranks, p > 0.05; medians and (iq ranges): infants over ground: 116.7% (100.0%-133.2%); infants treadmill: 114.0% (102.7%-128.1%); adults: 115.2%(109.7%-120.7%).
The influence of speed of crawling on coordination

Since coordination patterns are known to be speed dependent in quadrupeds (Grillner 1981), we further examined the coordination as a function of crawling rate and of limb duty cycle. Ipsilateral phase lag for individual steps from all infants crawling over ground was first plotted against the instantaneous rate of crawling in Figure 3A. There was a weak relationship between rate of crawling and ipsilateral coordination, with a greater occurrence of phase lag values around 25% (no limb pairing) at lower compared to the higher rates. Adults did not show a linear or consistent relationship between the rate of crawling and the coordination of ipsilateral limbs. Because individual adults preferred different coordinations, their data are sub-grouped according to preference of coordination. Figure 3B shows the ipsilateral phase lag for the 2 individuals who showed a preference for a trot-like coordination (filled circles, i.e., same individuals as Figure 2B), and the subject who preferred pace-like coordination (open circles, i.e., same individual as Figure 2C). Figure 3C shows the fourth individual who exhibited a wide range of coordination patterns. Interestingly, at rates around 1 Hz, ipsilateral phase lags around 30% were less common in the adults (few data points in this region in Figure 3B&C)

(Ipsilateral phase lag near here)

Ipsilateral phase lag illustrates the pairing of the limbs, but it also illustrates the sequence by which the limbs make contact with the ground (Hildebrand 1976). Most of the ipsilateral phase lags fell between ~0% and 50%, describing lateral sequence gaits, in which the first limb to make contact after the left leg is the left arm. At rates around 1 Hz, there were a few steps from adults that showed ipsilateral phase lags of >50%, which describe a diagonal sequence, in which the first limb to make contact after the left leg is the contralateral arm.
The duty cycle of a limb is also related to the speed of travel, and is commonly used to describe locomotion of quadrupeds. To compare our coordination patterns with those of other mammals, we next plotted the ipsilateral phase lag against duty cycle. As noted above, there was a large difference in duration of stance of the forelimbs compared to stance of the hindlimbs (also observed by Hildebrand, who commented that it was, “the greatest discrepancy […] noted for any animal” (Hildebrand 1967)). Therefore, instead of plotting ipsilateral phase lag against the duty cycle of the hind leg (as would become Hildebrand’s method), we chose to adopt Cartmill’s method, which is an extension Hildebrand’s method taking into account differences in stance duration between fore- and hindlimbs (Cartmill et al. 2002). According to their predictions, the duty cycle of the forelimb is most important in animals using trot-like gaits, whereas that of the hindlimb is most important during pace-like or diagonal sequence gaits. Thus, we plotted ipsilateral phase lags >25% and <50% (trot-like) against the duty cycle of the forelimb, and those <25% (pace-like) or >50% (diagonal sequence) against the duty cycle of the hindlimb. To compare our data with the model, we eliminated step cycles that deviated too much from a symmetrical gait. Removing cycles in which the phase lag between homologous limbs was less than 45% or greater than 55% reduced our data sample, but gives us a more accurate picture. While ipsilateral phase lag showed no overall pattern of change with increasing rate of crawling, plotting this same phase lag against relevant duty cycle now reveals some interesting relationships (Figure 4). At higher duty cycles (and therefore slower crawling velocities (Hildebrand 1966, Grillner 1975)), adults used coordinations with little pairing of limbs, or with pairing of the diagonal limbs. As duty cycle decreased (and speed increased), coordinations became more discretely trot-like or pace-like. The adult data showed the same shape as
Cartmill’s data for non-primate quadrupeds (Figure 4, lower two prediction lines of model), but was shifted with respect to his prediction lines. Notably, there are a number of cycles with no limb pairing at moderately fast speeds. Infants (Figure 4, open circles) were more clustered around the prediction line for animals, typically shorter-legged, that generally use trot-like gaits (Figure 4, middle prediction line).

(Figure 4 near here)

Another interesting observation from this plot is that duty cycles of less than 50% (i.e., running) were rarely observed in our subjects. “Running” can be defined as locomotion in which there is a whole-body aerial phase. Whole-body aerial phases were never observed during symmetrical gaits in our subjects. Double-limb flight in only one of the homologous pairs (half-run) was rare.

**Mechanical influences on coordination patterns**

To determine if mechanical factors might account for the differences observed between infants and adults, we manipulated speed, width of support, and functional limb length in adults, and load and functional limb length in infants. At the comfortable belt speed of 0.45 m/s, unobstructed crawling produced coordination patterns ranging from pace-like to trot-like in adults (Figure 5A, filled circles), in agreement with the data in Figure 3B&C. When the treadmill belt was slowed to 0.13 m/s, the preference was for no limb pairing (Figure 5A, open circles).

(Figure 5 near here)
Introduction of the midline obstruction forced a wider stance at the hands and knees. This was quantified as the ratio of support width/shoulder width, expressed as a percentage (Figure 5D). Without the obstruction, adults assume a width of support at the arms that is approximately equal to the width of the shoulders, while the knees are considerably closer together (left bars in Figure 5D). In comparison to adults, infants use a wider support base in relation to their shoulder width for both the arms and legs (right bars in Figure 5D). The obstruction widened the support width in adults making the ratios not statistically different from those of the infants (middle bars in Figure 5D). Interestingly, the widened width of stance constrained the coordination in adults to be trot-like at the faster belt speed (compare filled dots in Figure 5A&B), more similar to the infants. There was no effect of the obstruction on coordination at the slower speed, coordination remaining largely without limb pairing.

Unweighting of infants during crawling should reduce the role of stability in selecting interlimb coordination patterns. From five infants, we analyzed a total of 100 steps of crawling in which the infant took most of its full weight (mean 80%, Figure 5C, open triangles), and 73 steps in which the infant supported only a mean of 35% of its weight (Figure 5C, filled triangles). Crawling patterns were the same whether there was weight support or not (T-test, p>0.05).

Crawling on hands and feet extends the functional length of the hindlimbs compared to crawling on hands and knees. On hands and feet, five adults showed little limb pairing to pace-like coordinations at a range of treadmill belt speeds (Figure 6, filled triangles). By contrast, the two infants showed more trot-like coordination, similar to their hands-and-knees crawling (Figure 6, open triangles).
**Characteristics of galloping observed in one adult subject**

One adult subject used a gallop at the highest treadmill speed at which she was tested (1.30 m/s). One complete cycle of rotary gallop (LL RL RA LA) was recorded in one sequence, and transverse gallop (LL RL LA RA) was recorded in another sequence. The difference in these two forms of gallop lies in the order in which the forelimbs strike the ground. The treadmill was stopped at the initiation of the gallop to ensure the safety of the subject, allowing completion of little more than one cycle in either sequence. Limb contact patterns from one of the sequences, demonstrating transition to a rotary gallop, are shown in Figure 7A. Gallop cycles were characterized by a deviation from alternating stance between the two legs, and near synchronous stance of the two arms with one another. Consequently, there was at least one ~200 ms period of double flight for both the legs and the arms. The cycle of rotary gallop (Figure 7A) included an approximately 50 ms moment in which all four limbs were off of the treadmill. For both types of gallop, the duration of the swing phase became longer than that of the stance phase for the legs, but not for the arms.

**Transitions between coordination patterns**

Transition to a gallop occurred from a pace-like symmetrical gait. Quantification of the instantaneous rate of crawling during the transitions, as well as the relative phase relationships between limb pairs is shown step-by-step for both sequences of transition in Figure 7B. The
phase lag between legs changed by about 20 percentage points over one step cycle, while stance of the arms, alternating during symmetrical gait, became near synchronous over two cycles. At the same time, ipsilateral phasing changed from near synchronous to alternating.

Transitions within symmetrical gaits, between different categories of the continuum of coordinations, were common during individual crawling sequences and much more gradual than the transitions to gallop. Over 19% of infant sequences over ground, 21% of infant treadmill sequences, and 22% of adult sequences demonstrated a change in ipsilateral phasing greater than or equal to 10% over the course of the sequence. Examples of crawling sequences exhibiting some of the larger transitions are illustrated in Figure 7C&D. The maximum change in ipsilateral phasing from one step to the next was 14-15% for both infants and adults. Changes in ipsilateral phasing could occur with or without changes in treadmill speed. Conversely, a change in treadmill speed may or may not be associated with a change in coordination. There did not appear to be any consistent correlation between step-to-step changes in ipsilateral phasing and step-to-step changes in any of the following: rate of crawling, phasing between limbs of homologous pairs, duration of stance or swing for any of the four limbs.

**DISCUSSION**

This paper is, to our knowledge, the most extensive study of interlimb coordination of crawling in human infants and adults. Adults showed considerable flexibility in the coordination of ipsilateral limbs, from strictly alternating movements of the limbs (trot-like) to near synchronous movement (pace-like). These different patterns of coordination in adults could be altered by mechanical factors such as the size of the support base, speed of locomotion, and functional limb
length. In contrast, infants showed more restricted coordination in spite of mechanical changes. Hence, the neural options available to infants may be more restricted. Running symmetrical gaits were not observed in either infants or adults, although one adult galloped. Transitions between coordination patterns occurred smoothly over a number of steps for symmetrical gaits, and over one or two steps for the transition to galloping, as occurs in quadrupeds. The similarity in coordination between humans and other quadrupeds suggest the organization of underlying circuitry for these movements may be quite similar.

**Coordination patterns of humans share characteristics with other mammals**

The coordination patterns exhibited by our subjects fall directly within those reported for non-primate quadrupeds (Hildebrand 1967). Both infants and adults used lateral sequence gaits almost exclusively, consistent with previous reports of crawling in infants (Burnside 1927, Hildebrand 1967) children (Hildebrand 1967) and adults (Sparrow 1989, Sparrow and Newell 1994, Bajd et al. 1995). Lateral sequence gaits are used preferentially, if not exclusively, by the large majority of quadrupeds (Hildebrand 1976). The most notable exception is non-human primates, which usually use diagonal sequence gaits (Hildebrand 1967, Hildebrand 1976, Vilensky and Larson 1989). The reason for this difference between non-human primates and other quadrupeds remains controversial (Kimura et al. 1979, Demes et al. 1994, Larson et al. 2000, Shapiro and Raichlen 2005, Cartmill et al. 2007, Vilensky and Larson 1989), and is beyond the scope of this paper.

Although largely differing from non-human primates in sequence of limb contact, our subjects resembled non-human primates in other ways. Most notably, humans generally did not use
running symmetrical gaits, but rather only walking gaits and, occasionally, half-runs, just like other primates (Hildebrand 1967, Vilensky 1983, Vilensky 1989, Vilensky et al. 1991). Even our galloping subject did not use a running symmetrical gait but instead transitioned from a walking gait directly to a gallop, as has been reported for monkeys (Vilensky 1983, Hurov 1985, Vilensky et al. 1991).

Both non-primate mammals (Grillner 1981) and non-human primates (Vilensky et al. 1991) often use different patterns of interlimb coordination at different speeds of locomotion. It appears that humans, especially adults, also share this characteristic. Very slow treadmill speeds (0.13 m/s) induced coordinations with no clear pairing of limbs in our adults (Figure 5A). This is consistent with the fact that locomotion at lower speeds requires gaits offering higher stability such as the no-pairing coordinations (Hildebrand 1989), in which the individual may spend a great proportion of the step cycle in a tripod support. At intermediate treadmill speeds, many patterns were possible (Figure 3B&C), with adults showing preferences for some patterns at certain rates of crawling (Figure 3B), but the ability to use intermediate coordinations (Figure 3C). Describing gait in terms of duty cycle provides another way to represent locomotor speed. As with other mammals (Cartmill et al. 2002), limbs were most closely paired at the smaller duty cycles, producing in adults trot-like and pace-like gaits, with less pairing at higher duty cycles (Figure 4). At duty cycles of about 60%, it appears that many options are available. The model of Cartmill, Lemelin and Schmitt (Cartmill et al. 2002) assumes that quadrupeds will select coordination patterns maximizing the polygon of support. When bipods are necessary, longer-limbed animals will select pace-like gaits over trot-like. Our data suggests that limb length is a factor in humans (discussed later). The deviation of our data from Cartmill’s model (Figure 4)
suggests that minimizing bipedalism may not be as crucial in humans as in other mammals. It seems that other factors must additionally play a role.

At very fast speeds, quadrupeds often gallop (non-symmetrical gait). To our knowledge, there has been no previous mention of galloping during quadrupedal locomotion in human infants or adults. Here, we documented two sequences of such a behavior. The observed periods of double- and quadruple-flight, and the longer swing duration compared to stance are common characteristics of galloping in quadrupeds (Grillner 1981). It is not unusual for animals that gallop to use both rotary and transverse gallops in a continuous sequence of locomotion (Grillner 1975, Wetzel et al., 1977). Both forms of gallop were seen here. Interestingly, the subject did not intend to gallop and was simply trying to remain on the treadmill as the speed increased. Thus, the transition happened automatically without conscious effort.

**Adults demonstrate greater flexibility in coordinating ipsilateral limbs than infants**

Our results in infants agree with those of two earlier studies indicating that infants tend to move diagonal limbs as a pair, employing trot-like gaits (Burnside 1927, Hildebrand 1967). With a much greater number of subjects and cycles, we also report a higher incidence of coordinations with no limb pairing. Interestingly, most other infant quadrupeds also tend to use no-pairing or trot-like coordinations (Peters 1983 – cats; Jamon and Clarac 1998 – rats; Hildebrand 1967, Shapiro and Raichlen 2005 – monkeys; but c.f. Nakano 1996 – monkeys). Hence, human infants show similar coordination to those of other young quadrupeds.
Our adults showed greater flexibility in coordination compared to our infants. All previous reports of hands-and-knees crawling in human adults indicate pairing only of diagonal limbs in trot-like coordinations (Burnside 1927, Muybridge 1955, Bajd et al. 1995, Babic et al. 2001, Wannier et al. 2001). In contrast, our data demonstrated that adults are also capable of pairing ipsilateral limbs (pace-like gaits) and galloping. This flexibility was not seen in the infants.

*Do mechanical or neurological factors account for the differences between adults and infants?*

Mechanical factors might partially account for the differences between infants and adults. Infants have proportionately smaller limbs than do adults. Short- or medium-legged animals tend to adopt gaits offering greater stability (Hildebrand 1976, Walker 1979, Williams 1981, Hildebrand 1989). These gaits encompass gaits with no pairing of limbs, as well as gaits in which diagonal limbs are in-phase (trot-like), providing a diagonal line of support across the body during bipods (Hildebrand 1989). In contrast, pace-like gaits offer less lateral stability as bipods are formed by ipsilateral limbs, and are generally used only by longer-legged (e.g., cursorial) animals, which can place the limbs closer to the midline of the body (Hildebrand 1976, Hildebrand 1989). The infants in our study employed a wider stance with respect to their shoulder width than did the adults, placing their limbs further from the midline. The poorer balance of infants relative to adults furnishes an additional reason to select these more stable gait patterns (Hildebrand 1989). Further support for this line of reasoning is seen in our adults. Longer-limbed and well balanced, the adults may be freer to use the less stable pace-like coordination. However, when midline support was prevented (Figure 5B), or an element of
instability was introduced with very slow treadmill speeds (Figure 5A), adults avoided the use of pace-like gaits.

In longer-limbed animals, pace-like gaits offer an advantage over trot-like gaits in that the ipsilateral limbs can avoid mutual interference (Hildebrand 1989). During hands-and-feet crawling, which increases the functional length of the legs, adults largely avoided trot-like coordinations, perhaps to avoid this mutual interference. Interestingly, when limb length was changed volitionally by some infants (i.e., hands-and-feet crawling), the coordination remained the same, in direct contrast to the adults.

If more stability were provided to infants during crawling (i.e., by supporting some of their weight), we expected that they might be freer to adopt other coordinations. Unloading infants by up to 88% of their body weight did not produce a greater range of coordination patterns than was observed when the infants fully supported their own weight. Interestingly, altered mechanical environments such as during immersion in water (Bekoff and Trainer 1979, Cazalets et al. 1990), or air-stepping (Vilensky et al. 1989) also did not seem to alter the coordination pattern in other infant quadrupeds. The ability of an animal to vary phasing between ipsilateral limbs during symmetrical gaits is evidence that the neural coupling between these limbs is flexible (Grillner 1981). Thus, it appears the coordination options available to infants are more restricted, and may reflect the immaturity of the nervous system. Many parts of the nervous system could be implicated, since immaturity is widespread at this age (Yakovlev & Lecours 1967; Huttenlocher 1994).
Transitions between coordination patterns suggest sharing of elements in the circuitry for different forms of crawling

Within a sequence of crawling, variation in phasing of the ipsilateral limbs occurred frequently in both adults and infants. We defined a transition as a change in phasing between the ipsilateral limbs by at least 10% in a locomotor sequence. Examples shown in Figure 7 illustrate the continuous nature of these transitions. There are no pauses in the movement, and the changes occur gradually over a number of cycles. More abrupt transitions were seen in the subject who galloped. The ways in which the transition occurred has similarities to run-gallop transitions in quadrupeds (Miller et al. 1975, English and Lennard 1982), and walk-gallop transitions in primates (Hurov 1985, Vilensky et al. 1991). The abrupt change in phasing between the legs (over one step cycle) accompanied by more gradual changes between arms and between ipsilateral limbs (distributed over two step cycles) that we saw here has been beautifully illustrated in the cat (English and Lennard 1982). In simpler vertebrates, smooth transitions in coordination characterize rhythmic movements in which there is a sharing of circuitry between the movements (Stein 2005). While we know little about the circuitry involved in human crawling, it certainly exhibits the same type of transition between different forms of coordination.

Conclusions

In summary, humans show the same types of interlimb coordination during locomotion as those shown by other non-primate quadrupeds, suggesting common underlying circuitry. At the same time, the lack of running symmetrical gaits better resembles locomotion of non-human primates. Adults show flexibility in coordination both spontaneously and when the crawling mechanics are
altered. This is not evident in infants, so the immaturity of the neuromuscular system seems to constrain the options available to the infant. Transitions between different coordinations occur smoothly in a sequence of cycles, suggesting considerable sharing of circuitry for the different forms of coordination.
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Figure 1. Examples of coordination illustrated with limb contact patterns. Sequences of limb contact from 3 different subjects: 1 infant (trot-like), and 2 adults (no limb pairing, and pace-like) crawling on the treadmill. Time is represented horizontally, with periods of stance (solid lines) and swing (spaces). In the trot-like gait, the diagonal limbs enter stance close together in time. In the pace-like gait, the ipsilateral limbs enter stance close together in time. There is said to be no limb pairing when the initiation of stance in all the limbs are equally spaced in time. Ipsilateral phase lag, the primary measure of coordination, is the delay between left arm contact and the preceding left leg contact (b), expressed as a per cent of the cycle duration of the left leg (a).

Figure 2. Coordination of limbs during symmetrical hands-and-knees crawling. Histograms describe the incidence of initiation of stance and swing (vertical axis) for each of the four limbs with respect to the step cycle of the left leg (horizontal axis). Data is from infants crawling over ground (A, 94 cycles from 13 infants), and adults crawling on the treadmill (B, C and D). Two adults showed a trot-like coordination (B, 194 cycles), one showed a pace-like coordination (C, 177 cycles), and one showed all forms of coordination (D, 225 cycles). Initiation of stance of the left knee occurs at 0% and 100% of the step cycle (vertical dotted lines). Grey bars: swing; black bars: stance. Bin width: 2%.

Figure 3. Effect of rate of crawling on ipsilateral phase lag. Data are individual cycles from infants crawling over ground (A, 94 cycles) and adults crawling on the treadmill (B, C). Adult data is divided into those who showed a specific preference for one form of coordination (B, trot-like coordination: two subjects, filled circles, 224 cycles; pace-like coordination: 1 subject, open circles, 188 cycles), and the one subject who did not (C, 242 cycles). Infants showed a weak, linear relationship between rate of crawling and pattern used (r²=0.17, p<0.05). Adults showed no simple relationship with crawling rate.

Figure 4. Coordination in human crawling compared with quadrupeds. The ipsilateral phase lag is plotted against duty factor of the leg for phase lags <25% or >50%, and against duty factor of the arm for phase lags between 25% and 50%, in accordance with the model presented by Cartmill et al. (2002). Prediction lines from the Cartmill model are superimposed on our data. The top prediction line describes typical non-human primate behaviour. The bottom two prediction lines fit data from non-primates, but is shifted from the model.

Figure 5. Mechanical influences on patterns of coordination. A) Unobstructed crawling of five adults at 0.45 m/s exhibited a wide range of coordination patterns (filled circles, 99 cycles). Slowing the treadmill to 0.13 m/s restricted crawling to coordinations with little or no pairing of limbs (open circles, 100 cycles). B) An obstruction along the midline limited adults to largely trot-like coordination at the higher speed (filled circles, 50 cycles), and had little effect on coordination pattern at the lower speed (open circles, 50 cycles) compared to A. C) Unweighting of infants by 43 to 88% (filled triangles, 73 cycles) did not change coordination patterns used compared to when infants supported most (66-87%) of their own weight (open triangles, 100 cycles). D) The midline obstruction imposed upon the adults forced a significantly
wider stance at both the arms and the legs (indicated by an asterisk (*)); resultant stance widths were similar to those of infants during undisturbed over ground crawling (ANOVA with Tukey test post-hoc). Bars are mean±s.d. across subjects. Stance width was normalized to shoulder width.

**Figure 6.** Ipsilateral phase lag in hands-and-feet crawling. Two infants crawling on hands and feet (open triangles, 29 cycles) demonstrated the same coordination patterns as infants crawling on hands and knees (i.e., Figure 3A). Five adults crawling on hands and feet showed predominantly no clear pairing of limbs, or pairing of ipsilateral limbs (filled triangles, 161 cycles).

**Figure 7.** Crawling sequences with transitions in phasing between limbs. **A)** Limb contact patterns showing transition from pace-like cycles into a rotary gallop. The arrow indicates the beginning of the transition. The graphs in **B** demonstrate the changes in rate of crawling and phasing between limb pairs (legs, arms, ipsilateral) that occurred during the two sequences in which the subject transitioned to a gallop. Filled circles represent the sequence shown in **A**; open squares represent a second sequence (not shown), in which the subject transitioned to a transverse gallop. **C)** and **D)** Transitions within symmetrical crawling sequences. Ipsilateral phase lag (vertical axis) for individual cycles was plotted for sample sequences during which there was a change in ipsilateral phasing by ≥ 10%. Plots present data from two infants crawling over ground (**C**), and two adults on the treadmill (**D**).
Trot-like

ipsilateral phase lag ~ 47%

1 second

No limb pairing

ipsilateral phase lag ~ 25%

1 second

Pace-like

ipsilateral phase lag ~ 11%
A GALLOP SEQUENCE

B TRANSITION TO GALLOP

C INFANTS: SYMMETRICAL

D ADULTS: SYMMETRICAL