

Ontogeny of bipedal locomotion: walking and running in the chick

Gillian D. Muir*†, John M. Gosline* and John D. Steeves*‡

*Department of Zoology and ‡Departments of Anatomy and Surgery,
University of British Columbia, Vancouver, BC, Canada V6T 1Z4

1. The purpose of this study was to determine whether the production of an energy-efficient bipedal walk is an innate attribute of a precocial bird.
2. The locomotor characteristics of hatchling chicks were quantified using kinetic (ground reaction forces) and kinematic (stride length, leg support duration) measurements as the animals moved overground unrestrained. All measurements were made over a range of velocities and at regular intervals throughout the first 2 weeks of life.
3. Ground reaction force records showed that, like all terrestrial walking vertebrates, chicks undergo cyclical increases and decreases in the body's potential and kinetic energy with each step. The out-of-phase exchange of potential with kinetic energy is an efficient mechanism for the conservation of energy during walking. However, comparisons between chicks at posthatching (P) days 1–2 and P14 revealed that P1–2 chicks are unable to conserve energy because they walk with disproportionately small potential energy oscillations. During running, however, the oscillations between potential and kinetic energy are similar for both P1–2 and P14 animals.
4. P1–2 chicks also walk with a shorter stride length than P14 chicks. Examination of limb support durations shows that younger animals (P1–2, P3) spend less time in single limb support than P14 animals during walking but not running.
5. The results show that even highly precocial bipeds need to acquire the ability to walk in a controlled and energy efficient manner, although they can innately run as well as an adult. This disparity could be due to the distinct actions of the legs in these two behaviours, and the requirement for longer durations of single leg support during walking. These differences relate to constraints inherent to bipedal locomotion and many of the locomotor changes occurring in the first weeks after hatching may therefore be analogous to similar changes seen during human locomotor development.

All terrestrial walking vertebrates, including humans, use different gaits to locomote at different speeds. It has been shown that animals change gaits in order to minimize energy requirements (Hoyt & Taylor, 1981). Studies which evaluate the mechanical work of overground locomotion have defined walking and running in terms of energy exchange (Cavagna, Heglund & Taylor, 1977; Heglund, Cavagna & Taylor, 1982). During locomotion at a constant average speed, the body's centre of mass rises and falls, decelerating and accelerating with each step (Heglund *et al.* 1982). Walking gaits are energetically efficient because there is an alternating transfer between the potential and kinetic energy of the body within each stride. During walking, the leg acts as a solid strut, so that the body's centre of mass rises over the leg to reach a maximum in the middle of the

stance phase, while the opposite leg is swinging forward. Potential energy of the body is therefore greatest during mid-stance. However, the forward velocity of the body is lowest at this point and therefore kinetic energy is at a minimum. As the body moves ahead of the leg during the latter half of the stance phase, the centre of mass falls but forward velocity increases. Consequently, when both limbs are equally weightbearing (i.e. beginning of the stance phase of the opposite leg), the centre of mass is lowest and forward velocity is highest. At this point, potential energy has been converted to forward kinetic energy. As the body rises onto the opposite leg, potential energy is again recovered from kinetic energy as the body slows down. These oscillating exchanges between potential and kinetic energy thus reduce the total energy required to move at a walk.

† Present address to which correspondence should be sent: Department of Veterinary Physiological Sciences, Western College of Veterinary Medicine, University of Saskatchewan, Saskatoon, Saskatchewan, Canada S7N 5B4.

In contrast, during running, the body's centre of mass is lowest at mid-stance and highest during the suspension (airborne) phase of the stride, when forward velocity is also greatest. Potential and kinetic energy simultaneously increase and decrease within each running stride and thus exchange between potential and kinetic states is not possible. Instead of oscillating exchanges between potential and kinetic energy, running involves exchanges between elastic and kinetic energy. The leg acts as a spring during running, absorbing kinetic energy as elastic energy in muscles and tendons during the first half of the stance phase and releasing the stored elastic energy as kinetic energy during the latter half of stance (Cavagna *et al.* 1977).

What remains unclear is whether the oscillating transfer between potential and kinetic energy during walking is strictly an innate, biomechanical consequence of leg movement during walking or is a form of walking which needs to develop. Recent studies on load bearing in humans suggests that, with experience, some individuals can effectively exploit this energy exchange such that an increased load imposes little additional work (Heglund, Willems, Penta & Cavagna, 1995). Thus, it would appear that this method of energy exchange is a learned adaptation rather than a fixed or innate characteristic of walking.

This question can be investigated by examining the locomotion of animals in which apparently little locomotor development occurs. Precocial animals such as the chicken are able to locomote within hours of hatching. While the *in ovo* development of locomotor systems in the chick embryo have been well studied (Hamburger, Balaban, Oppenheim & Wenger, 1965; Hamburger & Oppenheim, 1967; Bekoff, 1976; Landmesser & O'Donovan, 1984), there are no studies which have investigated the early ontogeny of the biomechanics of overground locomotion by the hatchling chick. Birds are the only vertebrates in which bipedalism is the sole form of terrestrial locomotion; chicks are therefore useful models for human locomotion. As bipeds, both birds and humans are subject to similar postural constraints during locomotion. For example, bipeds must necessarily undergo a period of single limb support while walking and running, requiring a certain amount of balance control and muscular strength. This study has used kinetic and kinematic techniques to demonstrate that, although young chicks are innately able to run as well as adults, they must learn to walk in the controlled and efficient manner of an adult.

METHODS

Fertilized eggs were incubated at 37.5 °C and rotated four times per day. After hatching, chicks were moved to brooders equipped with food and water *ad lib*. All animals were cared for according to standards outlined by the Canadian Council on Animal Care. A total of twenty-eight chicks were used for this study.

Kinetic and kinematic data were collected from chicks as they walked overground. Chicks were encouraged to move down a 50 cm straight path, restrained by an opaque wall on the right and a clear Plexiglass wall on the left. The width of the path was adjusted to prevent the chick from touching the sides of the hallway. The ground surface consisted of balsa wood covered with a fine nylon mesh to increase traction. After each pass, the chicks were returned to the beginning of the path for a subsequent trial. Chicks underwent fifteen to twenty trials over a 10–30 min period each day.

Kinetic measurements

Kinetic (ground reaction force) data were collected from a force platform (10 cm long and 8 cm wide) built in the middle of the path and level with the surface. The force platform was modified from a basic design of Full & Tu (1990) and consisted of foil strain gauges cemented onto modified brass box beams. Output from the platform consisted of force measurements in three orthogonal directions – vertical, horizontal fore-aft (i.e. along the direction of the chick's movement), and horizontal medial-lateral. Only output from the vertical and fore-aft directions was used in this study, as horizontal medial-lateral forces were generally small (< 5–8% of vertical force) and displayed a large amount of interindividual variation. Output from the platform was linear over a range of forces from 0.1 to 4 N and the plate had a resonant frequency of 240 Hz. Cross-talk between vertically- and horizontally directed gauges was less than 5%. Data collection was triggered by the chick's body interrupting an infrared beam situated 3 cm in front of the force platform. A digital LED time display was also triggered by interruption of the infrared beam. The time clock was stopped by another infrared beam located 3 cm after the force platform. The time displayed after each pass was used to calculate mean velocity across the platform. Output from the force platform was amplified, analog-to-digital converted (RC Electronics, Inc., Santa Barbara, CA, USA) and collected on a PC.

Kinematic measurements

To facilitate visualization of the leg joints, the down on the left leg was trimmed, and markers were placed on the skin to mark the location of the ischium, the hip joint, the knee joint, the ankle joint, the distal tarso-metatarsal bone, and the toe of the third digit. Chicks were videotaped from the left side as they moved past the camera. The camera was located 1.5 m from the platform and positioned perpendicular to the direction of the chick's movement, with the camera lens level with the force platform.

Kinetic analysis

Ground reaction force records were analysed using custom-written software (G.D.M.) according to the method of Cavagna (1975). Briefly, the data in millivolts was converted to newtons (kg body mass)⁻¹. After subtracting acceleration due to body mass (i.e. 9.8 N kg⁻¹) from the vertical acceleration, acceleration in both the vertical and horizontal fore-aft directions was integrated over time to yield vertical and fore-aft velocity as a function of time (Fig. 1). Vertical velocity was then integrated over time to produce vertical displacement as a function of time (see Fig. 1). Constants for integrations of both vertical acceleration and vertical velocity were assumed to be zero – this assumption was valid because the integration was performed over an integral number of steps. The integration constant for the fore-aft acceleration was the mean velocity for each run, which was obtained from the time clock on the videotape. Kinetic energy of the centre of mass was calculated over time as $\frac{1}{2}mv^2$, where m is body mass in kilograms and v is velocity in the fore-aft direction. Kinetic energy changes represent

velocity changes only in the fore-aft direction because the actual distances moved during one stride in the vertical direction (approximately 1–2 mm) are small compared with those in the horizontal direction (approximately 150–175 mm). Hence, kinetic energy changes in the vertical direction are negligible (i.e. less than 5%) compared with those in the fore-aft direction. Potential energy changes were calculated over time as mgh , where g is the gravitational acceleration constant (9.8 m s^{-2}) and h is the change in vertical displacement of the centre of mass. Total energy as a function of time was calculated by summing potential and kinetic energy over time. Mass-specific force and energy were calculated by dividing whole body values by body mass in kilograms. To

determine quantitatively the amount of energy conserved by transfer between kinetic and potential energy, the following equation was used:

Percentage energy recovery =

$$100 \times \frac{(\Sigma + \Delta E_H) + (\Sigma + \Delta E_V) - (\Sigma + \Delta E_{tot})}{(\Sigma + \Delta E_H) + (\Sigma + \Delta E_V)},$$

where $(\Sigma + \Delta E_H)$ is the sum of the positive increments of the horizontal kinetic energy, $(\Sigma + \Delta E_V)$ is the sum of the positive increments of vertical potential energy, and $(\Sigma + \Delta E_{tot})$ is the sum of the positive increments in total energy (Heglund *et al.* 1982).

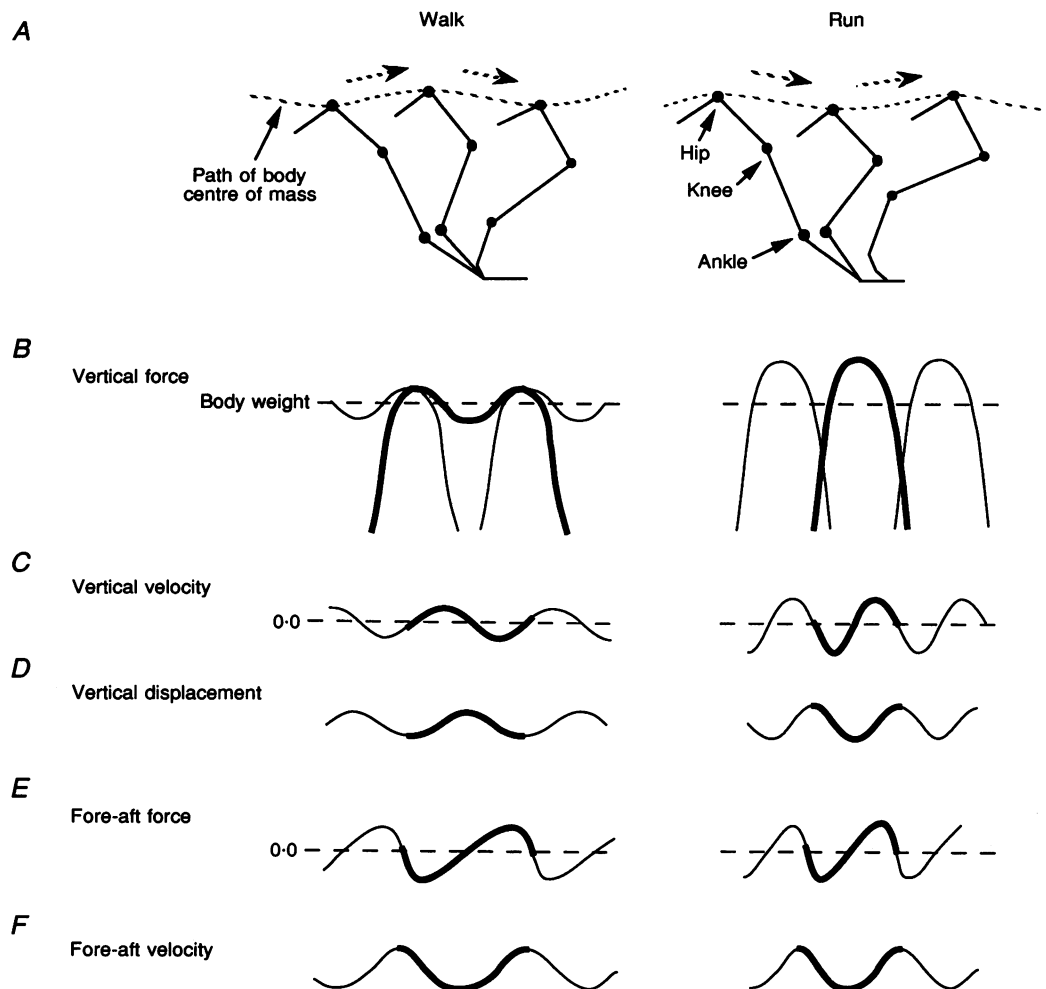


Figure 1. Diagrammatic representation of the analysis of ground reaction force records used to determine velocity and displacement of the body centre of mass in the vertical and horizontal (fore-aft) directions

The stick figures (A) demonstrate leg positions and the path of the centre of mass at the beginning, middle and end of the stance phase as the chick moves from left to right. For both walking (left column) and running (right column), oscillations in vertical force (B), as a function of time, were integrated successively to yield oscillations in vertical velocity (C) and vertical displacement (D) over time. Oscillations in horizontal (fore-aft) force (E), as a function of time, were integrated to yield oscillations in fore-aft velocity (F). Thick lines represent the portion of the traces generated during a single step. Note that while oscillations in fore-aft force (E) and velocity (F) are similar for walking and running over a single step, oscillations in vertical force (B), velocity (C) and displacement (D) differ between running and walking. Also note that the vertical displacement trace (D) mirrors the path of the body centre of mass illustrated in A.

Kinematic data analysis

Single-frame analysis was carried out on the videotapes at 60 frames s^{-1} ('V' Professional Imaging, Digital Optics, Inc., Auckland, New Zealand). Stride and step parameters collected from video included onset time of stance phase for right and left legs (onset of foot contact), onset time for swing phase (end of foot contact) and the onset time of subsequent stance phases for each limb. The position of the joint markers was digitized manually for each frame over at least one complete stride for each trial. Stride measurements and joint angles were calculated using custom-written software (G.D.M). For all stride measurements, at least five samples per chick were collected from each of data acquisition posthatching (P) days 1, 3, 5, 9 and 14. Stride length was calculated as the horizontal distance the hip joint moved between the onset of consecutive stance phases. Stride duration was the time between the onset of consecutive stance phases. Velocity, calculated as stride length divided by stride duration, was found to differ by at most 5–8% from that determined from the LED timer; consequently, the latter method was used to calculate velocity throughout the study.

In order to allow comparison between chicks of different sizes, velocity and stride length were normalized to dimensionless variables using the method of Gatesy & Biewener (1991). Stride length was divided by hip height (h) and velocity was divided by $(gh)^{0.5}$, where g is the gravitational acceleration constant (9.8 m s^{-2}). Animals run in a dynamically similar fashion at similar normalized velocities (Alexander & Jayes, 1983). Reference to these variables in the remainder of the paper refer to these normalized values.

For the remaining stride variables, duty factor was defined as the duration of the stance phase divided by the total stride duration. Single support time for each limb was defined as the time each limb was weightbearing while the opposite limb was not weightbearing (in the swing phase). Single support time was divided by stance duration to obtain the single support proportion

of stance. Least squares regression was used to determine the relationships between duty factor and velocity, as well as single support proportion of stance *versus* velocity. Slopes were compared using analysis of variance (SigmaStat, Jandel Scientific).

To compare joint angle motion throughout the step cycle, polynomial regression (SigmaPlot, Jandel Scientific) was used to calculate a representative curve for each age group. Each plot consists of joint angle data from a number of animals (one stride per individual) moving at the same velocity. In each case, a 6th order polynomial produced the best fit to each set of data for hip, knee and ankle joint angles ($R^2 > 0.80$). Maximum joint angles at initial foot contact and stride length of P1–2 and P14 chicks were compared using Student's t test (SigmaStat, Jandel Scientific). Mean measurements for each chick were calculated from at least five samples for each day of examination.

RESULTS

Ground reaction forces and energy exchange during walking

Ground reaction force patterns produced by P1–2 and P14 chickens at a walk and run were generally similar to those produced by other birds and humans (Heglund *et al.* 1982; Willems, Cavagna & Heglund, 1995; Figs 1, 2 and 5). At a walk (Figs 1 and 2), the body centre of mass rose over the leg placed on the ground and thus potential energy reached the greatest value during the middle of the stance phase. This produced a reduction in the upward vertical movement of the centre of mass at mid-stance and thus a decrease in the vertical force exerted on the ground. This is illustrated by the characteristic dip in the vertical force record which occurred mid-stance during a walking step

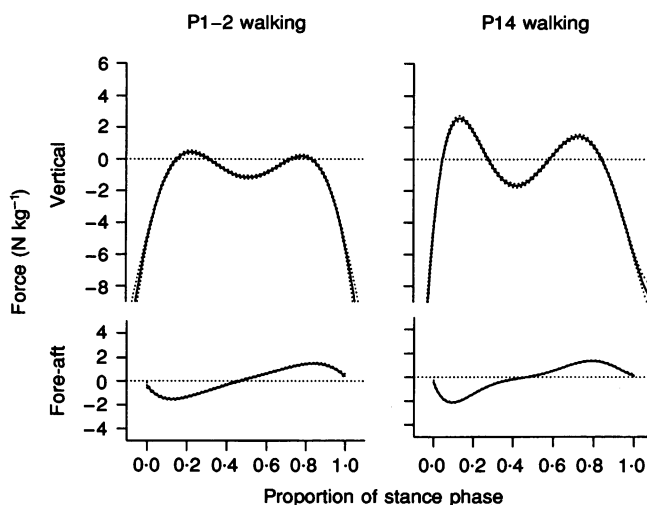


Figure 2. Ground reaction forces for a single walking step plotted against the proportion of stance duration for P1–2 chicks and P14 chicks

Chicks were moving at a normalized velocity of 0.38. Forces have also been normalized for body mass, and body weight has been subtracted from vertical force such that 0 N kg^{-1} represents body weight. Continuous lines represent a 6th order regression through data for all animals ($n = 11$ for P1–2, $n = 14$ for P14). The dotted lines alongside the continuous lines represent 99% confidence limits.

(Fig. 2). Both the P1–2 chicks and P14 chicks produced a similar pattern of vertical force, although there was a marked difference between the two in the amplitude of force oscillations within each step, especially at the beginning and end of each stance phase. In the P1–2 chicks, there was a smaller upward deflection of the force values, indicating less movement of the body downwards, at the beginning and end of each stance phase compared with P14 chicks. This corresponds with a point in the stride when the body was supported by both legs. P1–2 chicks also display a smaller downward deflection of the force record, indicating less upward movement of the body, in mid-stance compared with P14 chicks, corresponding to the time when the body was only supported by one leg.

The pattern of fore-aft forces was similar for both P1–2 and P14 chicks, and the same as those produced by other vertebrates (Heglund *et al.* 1982 and Figs 1 and 2). During

the first half of the stance phase, decelerative forces (negative force values) were produced by the ground on the body, when the limb was ahead of the body centre of mass. During the latter half of the stance phase, accelerative forces (positive force values) were produced as the body pushed ahead of the limb.

The consequences of the vertical force differences between P1–2 and P14 walking animals became clearer after force records were integrated to evaluate the energy changes occurring within each step (Fig. 3). In P14 animals, the total energy changes during each stride were reduced because potential and kinetic energy changes were out of phase and of the same magnitude. However, in a P1 animal, the total energy was dominated by changes in horizontal kinetic energy because of the small changes in potential energy within the same stride. The differences between P1 and P14 walking animals were more clearly

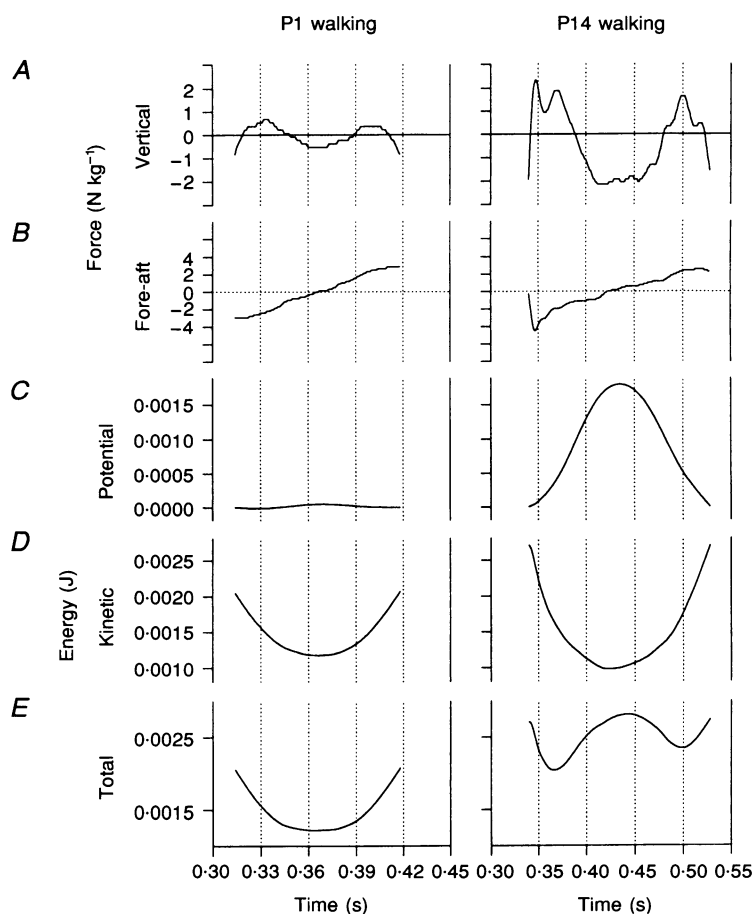


Figure 3. Representative ground reaction force records and corresponding potential, kinetic and total energy estimates for a single walking step (normalized velocity of 0.38) from P1 and P14 chicks, as a function of time

Force records (A and B) are normalized for body mass, but energy traces (C, D and E) are not. The same scale is used for both P1 and P14 animals. Note the difference in the change of potential energy (C) between P1 and P14. The efficient alternation between potential (C) and kinetic (D) energy in the P14 chick serves to reduce the change in total energy (E). However, energy conversion is not as efficient for the P1 chick, as evidenced by the lack of contribution of potential energy (C) to total energy (E).

apparent when potential energy was plotted against kinetic energy for a single stride (Fig. 4). Theoretically, a slope of -1 (beginning at the origin on the Fig. 3 plot) would indicate a walking stride where there is a 100% efficient alternation between kinetic and potential energy; the total energetic output would be zero for such a stride. Data from a single P14 walking stride approximated an efficient exchange (thin dotted loop in upper half of Fig. 4); whereas data from a P1 animal (thick continuous line in upper half of Fig. 4) has a slope of 0 indicating that there was little exchange between potential and kinetic energy.

In contrast to walking, where the body centre of mass was highest during the middle of the stance phase for each limb, the centre of mass was lowest at mid-stance during running. This produced a single peak in the vertical force record (Figs 1 and 5). During running, both P1–2 and P14 chicks produced quantitatively similar vertical force patterns. Likewise, fore-aft forces followed the same pattern during

running and walking and showed no difference between P1–2 and P14.

Integration of a single running stride from a P1 and a P14 chick revealed no differences between these two age groups (Fig. 6). Because the centre of mass was lowest at mid-stance during running, potential energy was also lowest at this point (Fig. 6C). Mid-stance also coincided with a minimum for kinetic energy (Fig. 6D). Because these two forms of energy are in phase, there is no possibility for exchange, and total body energy reflects the summation of the two (Fig. 6E). Thus, a plot of potential *versus* kinetic energy for a running stride (Fig. 4) produced a positive slope (in the lower negative quadrant of Fig. 4). Once again, there was no difference in slope between the running stride of a P1 and a P14 chick (Fig. 4).

Analysis of a number of walking strides from both age groups showed that younger animals were not as effective in recovering energy from the alternation between

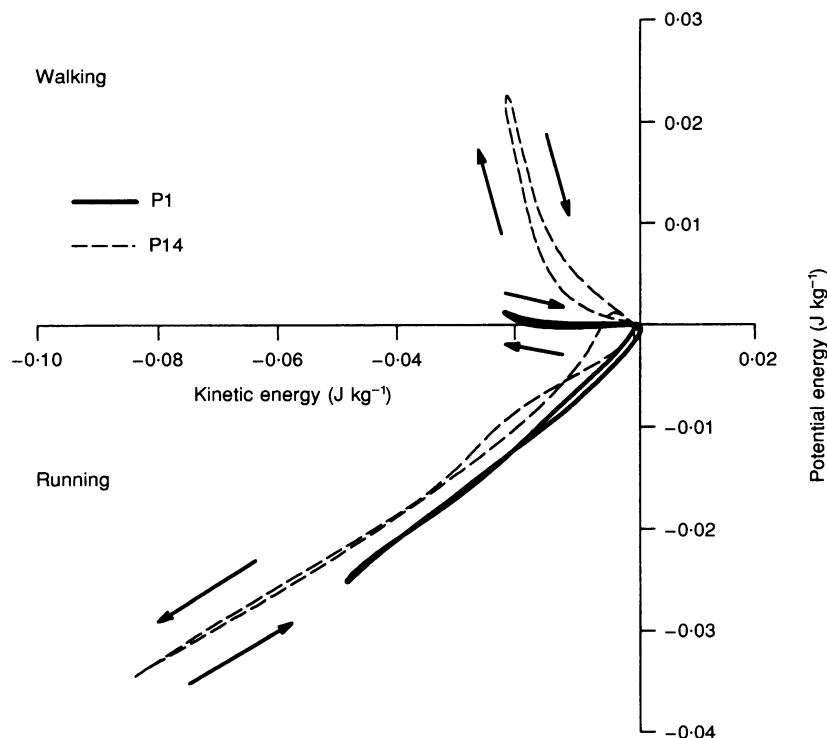
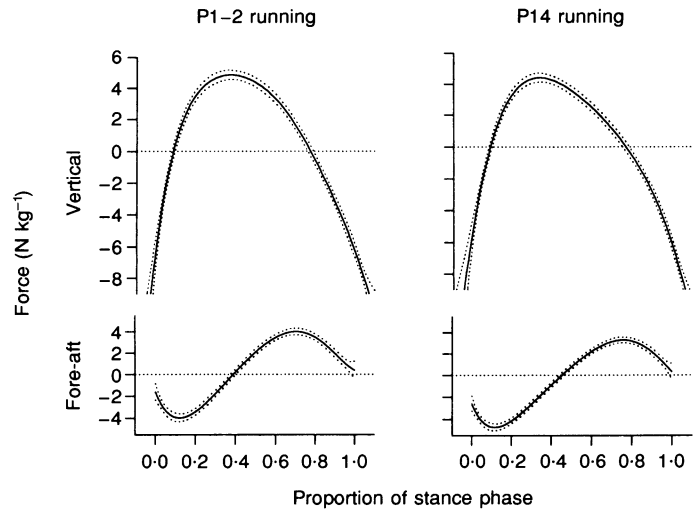


Figure 4. Potential energy as a function of kinetic energy for single steps taken from Figs 3 and 6

Both potential and kinetic energy have been normalized for body weight and initial values have been set to zero to facilitate comparison between P1 and P14 animals. The data fall only in the left quadrants because kinetic energy (horizontal axis) decreases in the first half of each stance phase and subsequently increases during the latter half of the stance phase for both walking and running. However, walking data fall in the upper left quadrant because potential energy first rises, then falls during each walking stance phase. Running data fall in the lower left quadrant because potential energy first decreases and then increases during each stance phase of running, paralleling the changes in kinetic energy. Note that, while the data of P1 and P14 running chicks do not differ in slope, data from a P14 walking step approximates a slope of -1 (100% exchange), whereas data from the P1 chick have a slope that approximates zero. The difference between P1 and P14 walking steps is due to the lack of a significant change in potential energy during walking by the P1 chick.

Figure 5. Ground reaction forces for a single running step plotted against the proportion of stance duration for P1–2 and P14 chicks

Chicks were moving at a normalized velocity of 0.9. Forces have also been normalized for body mass, and body weight has been subtracted from vertical force such that 0 N kg⁻¹ represents body weight. Continuous lines represent a 6th order regression through data for all animals (*n* = 13 for P1–2, *n* = 15 for P14). Dotted lines represent 99% confidence limits.



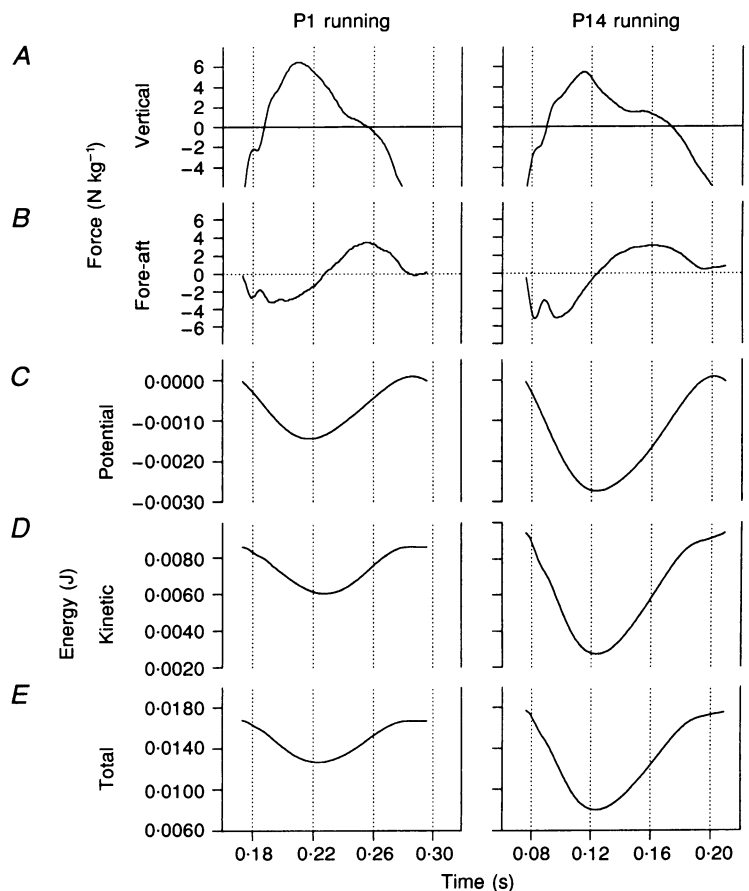
potential and kinetic forms as were older animals (Fig. 7). Figure 7 also shows that little to no energy is recovered through an exchange between potential and kinetic states during running (normalized velocity over 0.8). During walking (normalized velocities less than 0.6), older animals were able to recover on average 60% of total energy through this exchange, whereas young chicks recovered approximately one-third of this value.

Kinematic changes during the first 2 weeks post-hatching

Analysis of stride lengths and joint angle changes indicated one mechanism by which P1–2 animals may reduce the vertical movement of the body. P1–2 walking chicks had significantly shorter stride lengths (normalized velocity, 0.38) than did P14 chicks (Fig. 8). When stride length was measured at normalized running speeds (normalized

Figure 6. Representative ground reaction force records and corresponding potential, kinetic and total energy estimates for a single running step (normalized velocity of 0.9) from P1 and P14 chicks, as a function of time

Force records (*A* and *B*) are normalized to body mass, but energy traces (*C*, *D* and *E*) are not. The same scale is used for both P1 and P14 animals. Note that, unlike Fig. 3, potential (*C*) and kinetic (*D*) energy are in phase and are of the same order of magnitude and contribute similarly to total energy (*E*).



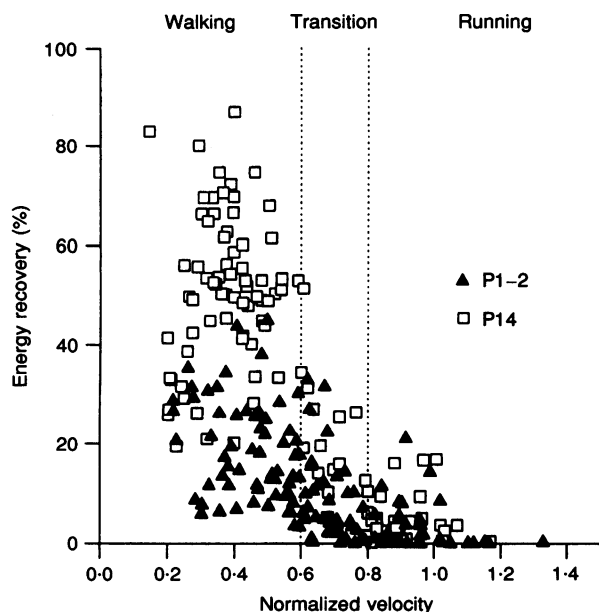


Figure 7. Percentage energy recovery as a function of normalized velocity for 3–5 steps from twelve chicks at P1 and 3–5 steps from eight chicks at P14

Percentage recovery is a measure of the total body energy recovered through exchange between potential and kinetic energy. Percentage recovery is highest during walking by P14 chicks (\square), lower during walking by P1 chicks (\blacktriangle) and lowest during running by both groups of animals. Vertical dotted lines indicate the range of velocity over which the transition between running and walking occurs.

velocity, 0.9), there were no differences between P1–2 and P14 chicks (Fig. 8). Stride length determines, in part, the degree to which the centre of mass is lowered between the two legs, so that shorter stride lengths in P1–2 chicks may contribute to a reduction in the sinking of the centre of mass between the legs.

Examination of the joint angle changes during walking at both ages showed that P1–2 chicks did not extend their knees and ankles at the beginning of the stance phase as much as P14 chicks (Fig. 9). As extension of the knee is primarily responsible for the forward movement of the foot in birds (Jacobson & Hollyday, 1982), young birds did not move the foot as far forward during the swing phase. This naturally resulted in a shortened walking stride length. Differences in knee and ankle movement between P1–2 and P14 animals might also be expected to be accompanied by differences in hip movement. The body centre of mass is positioned over the knee and in front of the hip joint in birds, unlike in humans where both the hip and knee are

beneath the centre of mass during stance (Jacobson & Hollyday, 1982). Small changes in hip angle in birds will alter the position of the knee joint under the centre of mass and therefore may have significant effects on balance. However, we found no statistically significant differences in the action of the hip between P1–2 and P14 animals. In addition, examination of joint angle changes during running by P1–2 and P14 chicks (data not shown) revealed no significant differences for hip, knee or ankle at any stage of the stride.

One remaining question was why young birds took shorter steps than older birds while walking, but not while running. A possible explanation may be that young birds have not acquired sufficient control of balance to support the body on one leg while moving the opposite leg fully through the swing phase. Lack of muscular strength might also be considered as a cause for shorter strides, except for the fact that running, which young chicks do well, requires more muscular output than walking. Young birds appear to

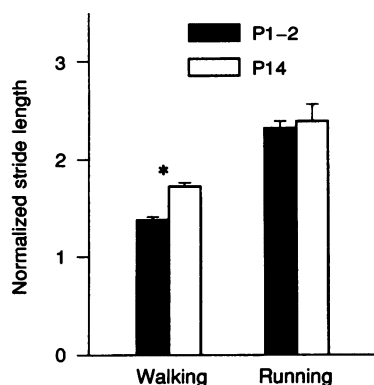


Figure 8. Mean stride length during walking and running for P1 and P14 chicks

Walking: P1–2, $n = 7$; P14, $n = 5$. Running: P1–2, $n = 5$; P14, $n = 6$. * Indicates that the walking stride length of P1–2 chicks is significantly shorter than P14 animals, $P < 0.001$.

shorten the swing phase during walking by placing the leg on the ground sooner, prior to full knee and ankle extension. Examination of the duration of foot contact with the ground during walking and running supported this suggestion. The duty factor (ratio of the stance phase to total stride duration) in P1 and P3 chicks was significantly more dependent on velocity than in P14 chicks (Fig. 10). At lower velocities, each limb maintained contact with the ground for a longer proportion of the stride duration when compared with older animals. For example, at a relative velocity of 0.2, the duty factor for a P1 chick was approximately 0.7 (i.e. 70% of the stride duration), whereas that for a P14 chick was 0.6 (60% of the stride duration). Figure 10 also shows that there was a gradual change within the first week of life before attaining the P14 pattern. Thus the relationship between duty factor and velocity for P5 chicks was intermediate between that for P1 and P14. The relationship between duty factor and velocity for P9 chicks (data not shown) showed no difference from that for P14 chicks.

A more detailed examination of the characteristics of the stance phase of each limb revealed that walking birds less than 5 days old spend significantly less time supported by a single leg than do older birds. When the duration of single leg support as a proportion of the stance phase of each leg

was plotted against velocity, P1 and P3 birds had much shorter durations of single leg support during walking (Fig. 11). For example, at a normalized velocity of 0.2, P1 chicks spent approximately 125 ms (40% of the stance duration) supported by a single leg, whereas P14 animals maintained single leg support for 200–300 ms (60% of the stance duration). The relationship between single leg support duration and velocity for P5 (and for P9, data not shown) chicks does not differ significantly from that for P14 birds. Single leg support durations at a run are similar for all age groups (approximately 100 ms, or 90–100% of the stance duration).

DISCUSSION

In summary, the data suggest that young birds (\leq P5) are less competent than older birds in maintaining single leg support while walking and take shorter steps to compensate. Young birds also walk with smaller vertical oscillations of the centre of mass and consequently undergo smaller potential energy changes within each step. P14 chicks are able to conserve energy within each walking stride by exploiting the exchange between potential and kinetic energy, but younger chicks are unable to conserve energy in this manner and thus walk less efficiently.

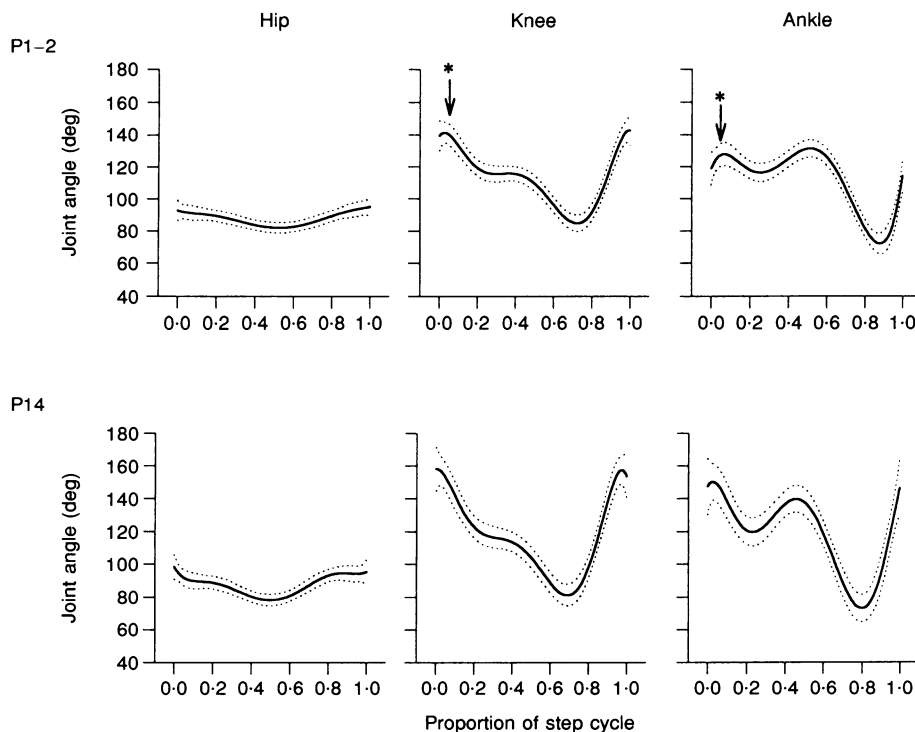


Figure 9. Joint angles of the left leg during walking (normalized velocity, 0.27) versus the proportion of the step cycle for P1 chicks ($n = 9$) and P14 chicks ($n = 7$)

Onset of stance phase occurs at 0.0. End of stance phase for P1 chicks occurs at approximately 0.62, for P14 chicks at 0.57. Continuous lines represent a 6th order regression through data for all animals. Dotted lines represent 99% confidence limits. * Indicate that knee and ankle angles are significantly smaller, at the onset of the stance phase, for P1–2 chicks when compared with P14 ($P < 0.01$).

The fact that young chicks can run in an adult-like manner, but walk inefficiently, may be due to different actions of the limb in these two behaviours. During walking in adult animals, the leg is used as a rigid strut and the body rises and falls over each leg in succession (Heglund *et al.* 1982). However, young chicks do not appear to effectively use the leg in this manner. We have shown that P1–2 chicks walk with shorter stride lengths than P14 chicks. If the leg was acting as a rigid strut in young animals, shorter stride lengths would cause a reduction in the vertical oscillations of the centre of mass and also a proportionate reduction in kinetic energy oscillations in the fore-aft direction. Thus, the magnitude of potential and kinetic energy oscillations within each step would be reduced but efficient exchange between the two forms of energy would be maintained. For example, a plot of potential energy as a function of kinetic energy (Fig. 4) would show a slope comparable to that of walking P14 animals, although the line would be shorter.

In contrast, the measured data from P1–2 animals display an entirely different slope in Fig. 4, because young chicks walk in a manner that causes potential energy oscillations to be disproportionately small compared with oscillations in fore-aft kinetic energy. Therefore, we suggest that young chicks do not innately use their leg as a rigid strut, but learn to do so during the first week after hatching.

In contrast to walking, chicks appear to have an innate ability to run in an adult-like manner. The leg acts like a spring during running, storing elastic energy in the first half of stance and releasing the elastic energy as kinetic energy in the latter half of stance (Cavagna *et al.* 1977). The rapid loading of the leg upon foot contact increases muscle tone by activating stretch reflexes, including mono-synaptic stretch reflexes (Griffiths, 1991). This stiffens the leg spring and allows efficient storage of kinetic energy as elastic energy in tendons and muscle. Monosynaptic stretch reflexes are thought to play less of a role during walking, in

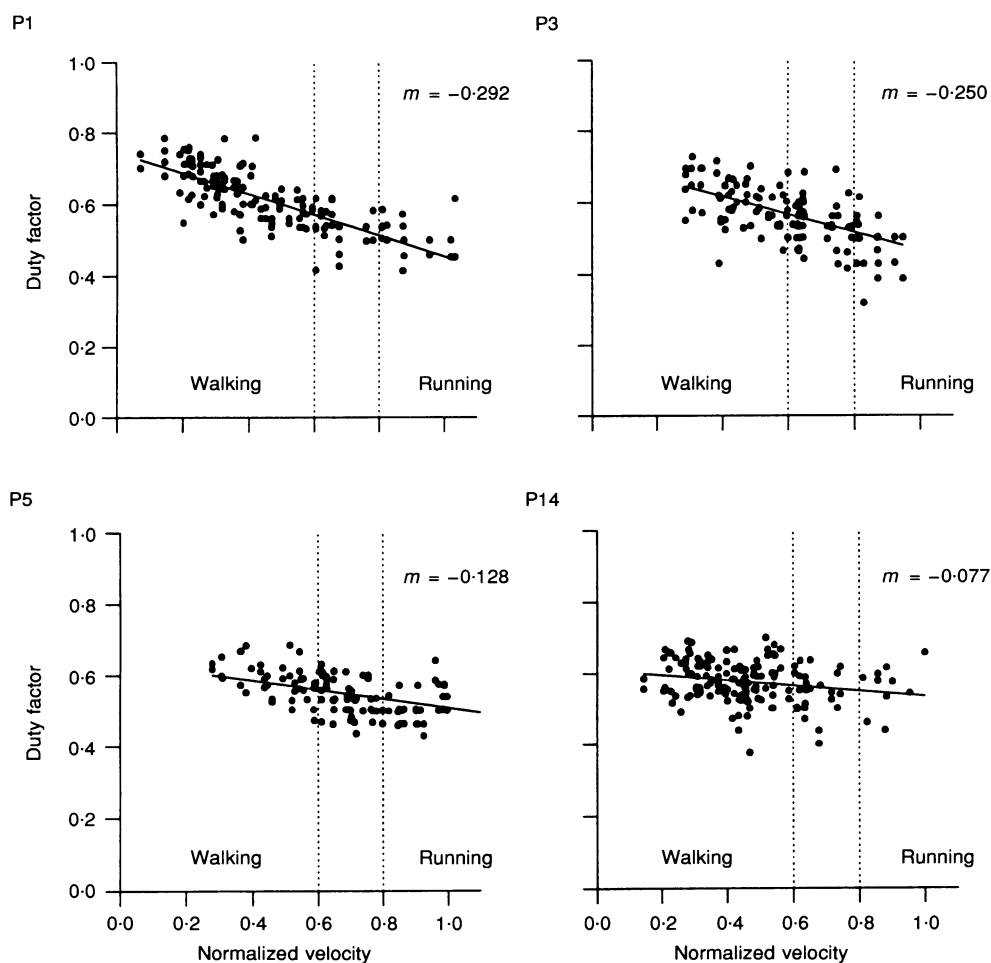


Figure 10. Duty factor (duration of the stance phase divided by stride duration) as a function of normalized velocity for chicks at P1, P3, P5 and P14

Continuous line represents a 1st order regression. Note that regression slopes for P1 and P3 chicks are significantly greater than for P5 and P14 (ANOVA of slopes: $F = 7.57$, $P < 0.001$). This indicates that duty factors of walking P1 and P3 chicks are greater than those of P5 and P14 walking chicks, but duty factor values do not differ with age during running. For all regressions, $P < 0.05$.

part because the time course of the walking stance phase is much longer than the duration of the monosynaptic reflex. Instead, polysynaptic reflexes, involving type Ib, II and cutaneous afferents, may contribute to maintaining appropriate muscle stiffness during stance (Aniss, Gandevia & Burke, 1992; Duysens, Tax, Trippel & Dietz, 1993; Pearson & Collins, 1993; Gossard, Brownstone, Barajon & Hultborn, 1994; Muir & Steeves, 1995). Interestingly, it has been shown that while polysynaptic reflexes are reduced or absent in young children, monosynaptic reflexes are present and may even be hyperactive compared with adult reflexes (Dietz, 1987; Evans, Harrison & Stephens, 1990; Vecchierini-Blineau & Guihneuc, 1981, 1982). Thus, the development of mature walking by chicks may depend, in part, upon the differential maturation of reflex pathways. Further studies will be required to examine developmental changes in reflex strength and/or timing and their potential effects during the ontogeny of bipedal locomotion.

The effect of size on bipedal locomotion

Gatesy & Biewener (1991) compared the locomotion of adult bipeds of varying sizes and found that small birds, such as the quail, walk with higher duty factors than humans and large birds, such as ostriches. Higher duty factors mean that small birds maintain contact with the ground for a longer proportion of the total stride duration. However, in contrast to the present developmental study, higher duty factors in small adult birds are the result of increased limb compliance. Small bipeds consistently have a crouched leg posture, where resting leg joint angles are smaller than those of large birds and humans. A similar effect can be imitated by humans walking or running with intentionally bent knees (referred to as 'Groucho running', McMahon *et al.* 1987). This increase in limb compliance results in a reduction of the vertical force when compared with a more normal upright gait at the same speed. Essentially, vertical movement of the centre of mass in

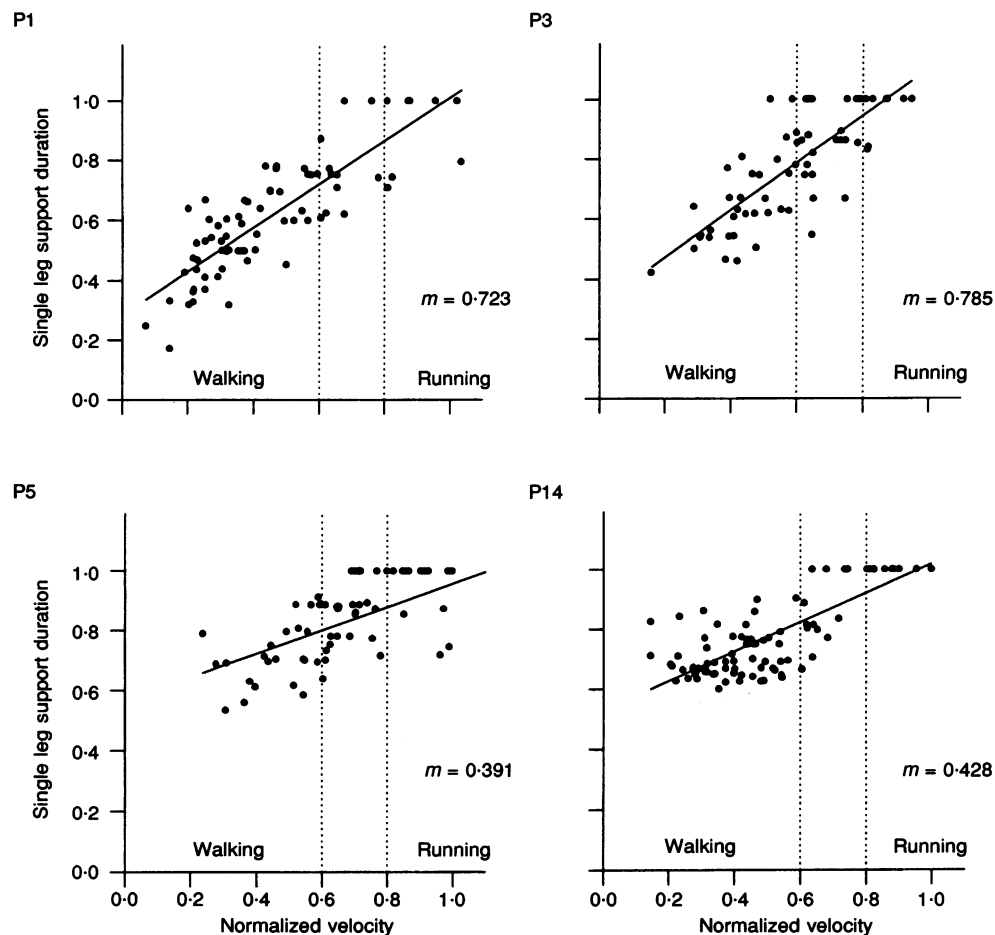


Figure 11. Single support proportion of stance duration as a function of normalized velocity for chicks at P1, P3, P5 and P14

Continuous line represents a 1st order regression. Note that slopes for P1 and P3 chicks are significantly greater than for P5 and P14 (ANOVA of slopes: $F = 4.55$, $P < 0.01$). This indicates that P1 and P3 chicks spend less time supported by one leg while walking when compared with P5 and P14 chicks. However, single leg support durations are similar during running at all ages. For all regressions, $P < 0.01$.

Groucho running is reduced by carrying the entire body closer to the ground throughout the stride. Importantly, Groucho running also results in longer relative stride lengths when compared with upright human locomotion.

The present study showed that, in contrast with the results of adult bipeds, young animals initially utilize a walking gait where increased duty factors and decreased vertical forces are accompanied by a decrease in stride length. Comparisons of joint angles (Fig. 9) also showed that P1–2 chicks do not maintain a more crouched limb posture throughout the stride than P14 birds. Instead of carrying the body closer to the ground and taking longer stride lengths, as would be expected if young chicks were increasing limb compliance, P1–2 chicks increase their stability by decreasing stride length.

Comparisons with the development of human locomotion

In children, independent locomotion begins to develop at approximately 1 year of age. The initial period of digitigrade walking is followed by a gradual transformation, over the following 1–2 years, to a more adult-like plantigrade pattern (Forssberg, 1985). Subsequent improvements in stability occur until at least 7 years of age (Sutherland, *et al.* 1988). Many of the changes seen during the first few weeks of a chicken's life are comparable to the locomotor changes in children from 1 to 7 years. Children show a decrease in duty factor from 0.67 to 0.62 during development from 1 to 7 years (Sutherland, Olshen, Biden & Wyatt, 1988). The proportion of the stride cycle occupied by single leg support increases from 0.32 to 0.38 over the same time period. More importantly, alterations in the vertical forces generated by children show similar changes during development to those observed in the present study. Young toddlers, 1–4 years, show smaller peaks and less of a trough in the vertical force traces than 6–7 year olds. As in the present study, the reduction in vertical movement of a young child's centre of mass results in a less efficient energy transfer during walking.

There are obviously some differences between avian and human locomotion which relate to differences in leg morphology and the production of plantigrade gait in humans. However, leg morphology does not influence the general characteristics of ground-reaction force patterns, as these are common to the patterns produced by a variety of terrestrial vertebrates (Cavagna *et al.* 1977). Furthermore, plantigrade gait development in humans is normally restricted to the first 2 years of life, whereas developmental changes in duty factor and single leg support durations occur over a period of 6–7 years. Hence comparisons in the development of bipedal locomotion between birds and humans may be insightful.

It appears, then, that many of the changes which occur during human locomotor development also occur, albeit over a much shorter time period, during the early post-

hatching development of chicks. These changes relate to common constraints inherent to bipedal locomotion, including the necessity for a period of stable single leg support. This constraint is most obvious during walking, where the action of the leg and the durations of single leg support differ from running gaits. Thus, contrary to conventional wisdom, perhaps we run before we walk!

- ALEXANDER, R. McN. & JAYES, A. S. (1983). A dynamic similarity hypothesis for the gaits of quadrupedal mammals. *Journal of Zoology* **201**, 135–152.
- ANISS, A. M., GANDEVIA, S. C. & BURKE, D. (1992). Reflex responses in active muscles elicited by stimulation of low-threshold afferents from the human foot. *Journal of Neurophysiology* **67**, 1375–1384.
- BEKOFF, A. (1976). Ontogeny of leg motor output in the chick embryo: a neural analysis. *Brain Research* **106**, 271–291.
- CAVAGNA, G. A. (1975). Force platforms as ergometers. *Journal of Applied Physiology* **39**, 174–179.
- CAVAGNA, G. A., HEGLUND, N. C. & TAYLOR, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *American Journal of Physiology* **233**, R243–261.
- DIETZ, V. (1987). Role of peripheral afferents and spinal reflexes in normal and impaired human locomotion. *Revue Neurologique* **143**, 241–254.
- DUYSENS, J., TAX, A. A., TRIPPEL, M. & DIETZ, V. (1993). Increased amplitude of cutaneous reflexes during human running as compared to standing. *Brain Research* **613**, 230–238.
- EVANS, A. L., HARRISON, L. M. & STEPHENS, J. A. (1990). Maturation of the cutaneomuscular reflex recorded from the first dorsal interosseus muscle in man. *Journal of Physiology* **428**, 425–440.
- FORSSBERG, H. (1985). Ontogeny of human locomotor control. I. Infant stepping, supported locomotion and transition to independent locomotion. *Experimental Brain Research* **57**, 480–493.
- FULL, R. J. & TU, M. S. (1990). Mechanics of six-legged runners. *Journal of Experimental Biology* **148**, 129–146.
- GATESY, S. M. & BIEWENER, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *Journal of Zoology* **224**, 127–147.
- GOSSARD, J.-P., BROWNSTONE, R. M., BARAJON, I. & HULTBORN, H. (1994). Transmission in a locomotor-related group 1b pathway from hindlimb extensor muscles in the cat. *Experimental Brain Research* **98**, 213–228.
- GRIFFITHS, R. I. (1991). Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: the role of tendon compliance. *Journal of Physiology* **436**, 219–236.
- HAMBURGER, V., BALABAN, M., OPPENHEIM, R. & WENGER, E. (1965). Periodic motility of normal and spinal chick embryos between 8 and 17 days of incubation. *Journal of Experimental Zoology* **159**, 1–14.
- HAMBURGER, V. & OPPENHEIM, R. (1967). Prehatching motility and hatching behaviour in the chick. *Journal of Experimental Zoology* **166**, 171–204.
- HEGLUND, N. C., CAVAGNA, G. A. & TAYLOR, C. R. (1982). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *Journal of Experimental Biology* **79**, 41–56.

- HEGLUND, N. C., WILLEMS, P. A., PENTA, M. & CAVAGNA, G. A. (1995). Energy-saving gait mechanics with head-supported loads. *Nature* **375**, 52–54.
- HOYT, D. F. & TAYLOR, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240.
- JACOBSON, R. D. & HOLLYDAY, M. (1982). A behavioural and electromyographic study of walking in the chick. *Journal of Neurophysiology* **48**, 238–256.
- LANDMESSER, L. T. & O'DONOVAN, M. J. (1984). Activation patterns of embryonic chick hindlimb muscles recorded *in ovo* and in an isolated spinal cord preparation. *Journal of Physiology* **347**, 189–204.
- McMAHON, T. A., VALIANT, G. & FREDERICK, E. C. (1987). Groucho running. *Journal of Applied Physiology* **62**, 2326–2337.
- MUIR, G. D. & STEEVES, J. D. (1995). Phasic cutaneous input facilitates locomotor recovery after incomplete spinal injury in the chick. *Journal of Neurophysiology* **74**, 358–368.
- PEARSON, K. G. & COLLINS, D. F. (1993). Reversal of the influence of group Ib afferents from plantaris on activity in medial gastrocnemius muscle during locomotor activity. *Journal of Neurophysiology* **70**, 1009–1017.
- SUTHERLAND, D. H., OLSHEN, R. A., BIDEN, E. N. & WYATT, M. P. (1988). *The Development of Mature Walking*. Clinics in Developmental Medicine, No. 104/105. MacKeith Press, London.
- VECCHIERINI-BLINEAU, M. F. & GUIHNEUC, P. (1981). Excitability of the monosynaptic reflex pathway in the child from birth to four years of age. *Journal of Neurology, Neurosurgery and Psychiatry* **44**, 309–314.
- VECCHIERINI-BLINEAU, M. F. & GUIHNEUC, P. (1982). Lower limb cutaneous polysynaptic reflexes in the child, according to age and state of waking or sleeping. *Journal of Neurology, Neurosurgery and Psychiatry* **45**, 531–538.
- WILLEMS, P. A., CAVAGNA, G. A. & HEGLUND, N. C. (1995). External, internal and total work in human locomotion. *Journal of Experimental Biology* **198**, 379–393.

Acknowledgements

We are grateful to Stephen Katz, Edward Lam, Farhana Nakhoda and Joshua Eades for their technical assistance. This study was supported by a grant to J.D.S. from the Natural Sciences and Engineering Research Council of Canada. G.D.M. was supported by a Fellowship from the Medical Research Council of Canada.

Received 23 August 1995; accepted 8 December 1995.