

REVIEW

Bipedal animals, and their differences from humans

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Abstract

Humans, birds and (occasionally) apes walk bipedally. Humans, birds, many lizards and (at their highest speeds) cockroaches run bipedally. Kangaroos, some rodents and many birds hop bipedally, and jerboas and crows use a skipping gait. This paper deals only with walking and running bipeds. Chimpanzees walk with their knees bent and their backs sloping forward. Most birds walk and run with their backs and femurs sloping at small angles to the horizontal, and with their knees bent. These differences from humans make meaningful comparisons of stride length, duty factor, etc., difficult, even with the aid of dimensionless parameters that would take account of size differences, if dynamic similarity were preserved. Lizards and cockroaches use wide trackways. Humans exert a two-peaked pattern of force on the ground when walking, and an essentially single-peaked pattern when running. The patterns of force exerted by apes and birds are never as markedly two-peaked as in fast human walking. Comparisons with quadrupedal mammals of the same body mass show that human walking is relatively economical of metabolic energy, and human running is expensive. Bipedal locomotion is remarkably economical for wading birds, and expensive for geese and penguins.

Key words bipedal locomotion; running bipeds; walking bipeds.

Introduction

Bipedal walking and running are the normal human gaits. Apes and a population of Japanese macaques sometimes walk bipedally (Napier & Napier, 1967). Kangaroos and a few rodents hop bipedally. Birds on the ground walk, run or hop. Some lizards run bipedally, and cockroaches have been filmed running bipedally at their highest speeds (Full & Tu, 1991).

In bipedal walking and running, the feet move alternately, half a cycle out of phase with each other. Such gaits are generally classed as walking if the duty factor (the fraction of the time for which each foot is on the ground) is greater than 0.5, and running if it is less than 0.5. In hopping, the feet generally move more or less simultaneously. Jerboas and crows, however, use a peculiar out-of-phase hopping gait, in which the phase difference between the feet is neither zero nor half a

cycle (Hayes & Alexander, 1983). Gaits like this are sometimes described as skipping (Minetti, 1998).

In the remainder of this paper I consider only walking and running, the gaits normally used by humans. Apes on the ground usually travel quadrupedally. They make only occasional use of bipedalism, often in the context of display. Bipedal walking is the normal slow gait of birds, and running is the fast terrestrial gait of many of them. There seems to be a tendency for birds that spend a lot of their time in trees to use hopping as their fast gait, and for other birds to run. Lizards vary in the use they make of bipedalism. Many species are exclusively quadrupedal. Some such as *Uma* are bipedal for only a small proportion of their strides, but others such as *Callisaurus* are frequently bipedal for many successive strides (Irschick & Jayne, 1998, 1999a). *Basiliscus* is well known for its ability to run bipedally for short distances over the surface of water (Glasheen & McMahon, 1996). The cockroach *Periplaneta* runs on all six legs at low speeds, but at high speeds (1.0–1.5 m s⁻¹) it makes about half its runs on four legs (the middle and hind legs) and half on the hind legs only (Full & Tu, 1991).

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Dynamic similarity

Patterns of bipedal locomotion change with speed. For example, humans walk at low speeds and run to go fast, and within each gait quantities such as stride length change as speed increases. I will be making quantitative comparisons between animals of very different sizes, from 1-g cockroaches to 70-kg humans.

The concept of dynamic similarity will be useful. Geometrically similar forms could be made identical by multiplying all lengths by the same factor. Dynamically similar movements could be made identical by multiplying all lengths by one factor, all times by another and all forces by a third. For example, two pendulums of different lengths, swinging through the same angle, would be dynamically similar. If gravitational forces are important, as they are in the swinging of pendulums and in terrestrial locomotion, dynamic similarity is possible only between systems moving at equal Froude numbers, $(\text{speed})^2/(\text{length} \times \text{gravitational acceleration})$. In this expression, any speed and any length characteristic of the motion can be used.

Alexander (1976) and Alexander & Jayes (1983) formulated the hypothesis that similar animals of different sizes, travelling over land at equal Froude numbers, would tend to move in dynamically similar fashion. Strict dynamic similarity would not be possible, because animals of different sizes are generally not geometrically similar; for example, a buffalo is not geometrically similar to a gazelle, still less is an elephant geometrically similar to a mouse. Consequently, tests of our dynamic similarity hypothesis depend on appropriate choices of the characteristic speed and length used to calculate the Froude number. For our characteristic speed, we used the mean forward speed averaged over a complete stride; this choice is so obvious that it is unlikely to be challenged. For our characteristic length, we used the height of the hip joint from the ground in normal standing, or while the foot is on the ground in locomotion. Equally appropriately, Aerts et al. (2000) used lower leg length, measured from knee to heel.

Stride lengths and duty factors

Relative stride length is the distance travelled in a complete cycle of leg movement (i.e. between successive footfalls of the same foot), divided by the chosen characteristic length. Duty factor, as already noted, is the fraction of the duration of a stride for which a particular

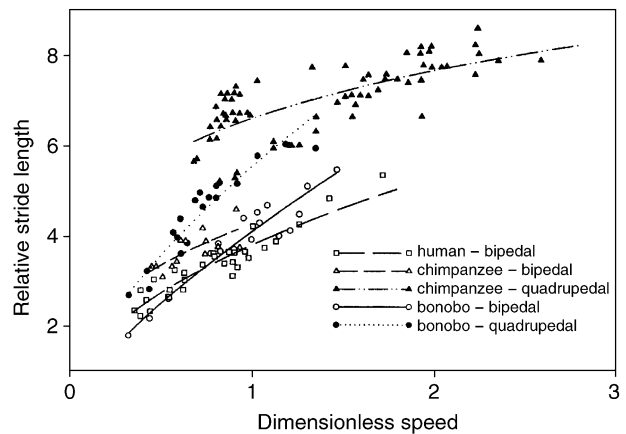


Fig. 1 A graph of relative stride length against dimensionless speed for humans, chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) moving bipedally and quadrupedally. From Aerts et al. (2000) Spatio-temporal gait characteristics of the hind-limb cycles during voluntary bipedal and quadrupedal walking in bonobos (*Pan paniscus*) *Am. J. Phys. Anthropol.* III, 503–517. Reprinted by permission of Wiley-Liss Inc., a subsidiary of John Wiley & Sons Inc.

foot is on the ground. Two animals making dynamically similar movements would have equal relative stride lengths and equal duty factors.

In Fig. 1, relative stride length is plotted against dimensionless speed (the square root of Froude number). These quantities have been calculated using lower leg length as the characteristic length. On this basis, the relationships between relative stride length and dimensionless speed for bipedal walking of humans, common chimpanzees (*Pan troglodytes*) and bonobos (pygmy chimpanzees, *P. paniscus*) are little different. Both species of chimpanzee take longer strides in quadrupedal locomotion.

The graph would have given a different impression if it had been based on hip height rather than lower leg length. For humans, lower leg length is about 0.54 (hip height) (Aerts et al. 2000), so relative stride lengths based on hip height are 0.54 times and dimensionless speeds $\sqrt{0.54} = 0.73$ times the values shown on the graph. The positions of points for bipedal apes would be almost unchanged, because for them hip height and lower leg length are approximately equal (see the estimates of 'functional leg length' in Aerts et al. 2000). Thus comparisons based on hip height would show the apes using larger relative stride lengths than the humans, at the same dimensionless speed.

Humans use duty factors of about 0.7 in very slow walking, falling to about 0.55 in fast walking (for example, see Alexander, 1989). For bonobos walking

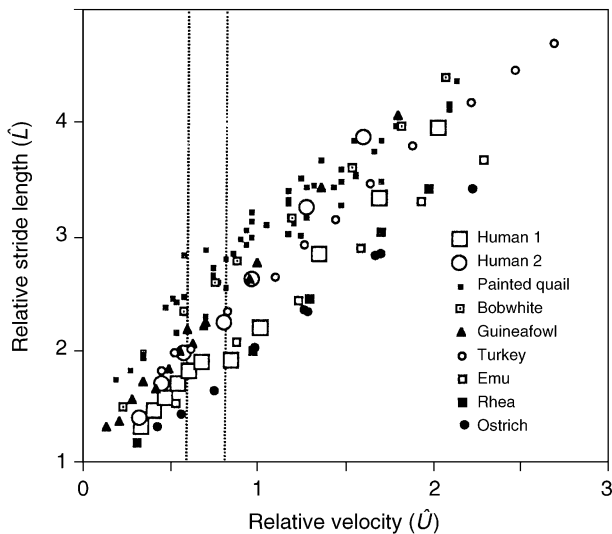


Fig. 2 A graph of relative stride length against dimensionless speed for humans and various birds. Dotted lines mark the range of speeds in which the transition from walking to running is made. From Gatesy SM, Biewener AA (1991) Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool. Lond.* **224**, 127–147. Cambridge University Press.

bipedally, the range is very similar, from about 0.75 at the lowest speeds observed to 0.58 at the highest (Aerts et al. 2000).

Figure 2 compares relative stride lengths of birds with those of humans. The horizontal axis is dimensionless speed. Hip height has been used as the characteristic length. On this basis of comparison, quail (*Excalfactoria*) take longer strides than humans, and large ratites (*Rhea*, *Dromaius* and *Struthio*) take shorter ones, at any given dimensionless speed. The differences between birds and humans are not very marked; indeed, there are differences of similar magnitude between the two individual humans featured in the graph. The differences between birds and humans would be even less if the lower leg were chosen as the characteristic length. The lengths of the tibiotarsi (roughly equivalent to the lower leg length used in the discussion of apes above) were 0.60(hip height) for the quail and 0.39–0.46(hip height) for the ratites. We have already seen that human lower leg length is intermediate between these values.

Duty factors of birds are similar to or a little smaller than those of humans at walking speeds, but larger than those of humans in running (Gatesy & Biewener, 1991). The lowest duty factor I can find recorded for a bird is 0.29 for an ostrich running fast in the wild (Alexander et al. 1979). Nigg et al. (1987) report peak

vertical forces of 3.16(body weight) on the feet of humans running at 6 m s^{-1} , from which I estimate that the duty factor was about 0.25.

Step length is the distance travelled while a foot is on the ground. Step lengths both of humans and of ratites are in the range 0.8–1.2(hip height) throughout the range of walking and running speeds (Gatesy & Biewener, 1991). Galliform birds take relatively longer steps, rising in the extreme case of quail running fast to 2.2(hip height) (Fig. 3). Such long steps are possible because the total of the lengths of the leg bones is much greater than hip height.

Irschick & Jayne (1999b) filmed five species of lizard running at near-maximal sprinting speeds on a treadmill. For *Callisaurus* and *Dipsosaurus*, about half the analysed strides were bipedal. *Uma* and *Cnemidophorus* made fewer bipedal runs, and *Phrynosoma* made none. In no case was there a significant difference in maximum speed between bipedal and quadrupedal running. Neither stride length nor duty factor differed significantly between bipedal and quadrupedal strides, for any species.

The mean speeds of the analysed bipedal runs, of the four species that ran bipedally, were $3.2\text{--}4.5 \text{ m s}^{-1}$. The corresponding dimensionless speeds were 7.2–8.9 based on mid-stance hip height, or 8.3–9.9 based on tibia length. The relative stride lengths were 10.6–15.6 based on mid-stance hip height, or 15.0–20.7 based on tibia length. The duty factors were 0.25 or 0.26 for three of the species, and 0.16 for *Uma*. These stride lengths and duty factors cannot be compared directly with data for humans, because the dimensionless speeds of the fastest human sprinters, in the fastest section of a 100-m race, is only about 4.

Full & Tu (1991) reported stride lengths for cockroaches (*Periplaneta*), without distinguishing between gaits using different numbers of legs. In their graph of stride length against speed, all the points lie close to a single line, suggesting that the number of legs in use has little effect on stride length. Stride length was about 42 mm at 1.0 m s^{-1} and about 58 mm at the highest recorded speed of 1.5 m s^{-1} . A drawing of bipedal running at 1.5 m s^{-1} shows the 'hip' joints of the hind legs 0.45 body lengths above the ground, implying a hip height of about 16 mm. Taking this as the reference length, the speed of 1.5 m s^{-1} corresponds to a dimensionless speed of 3.8, and relative stride length at that speed was 3.6. A force record of running at 1.5 m s^{-1} shows a duty factor of about 0.46, giving a step length (for a 58-mm stride) of 26 mm. This duty factor is much

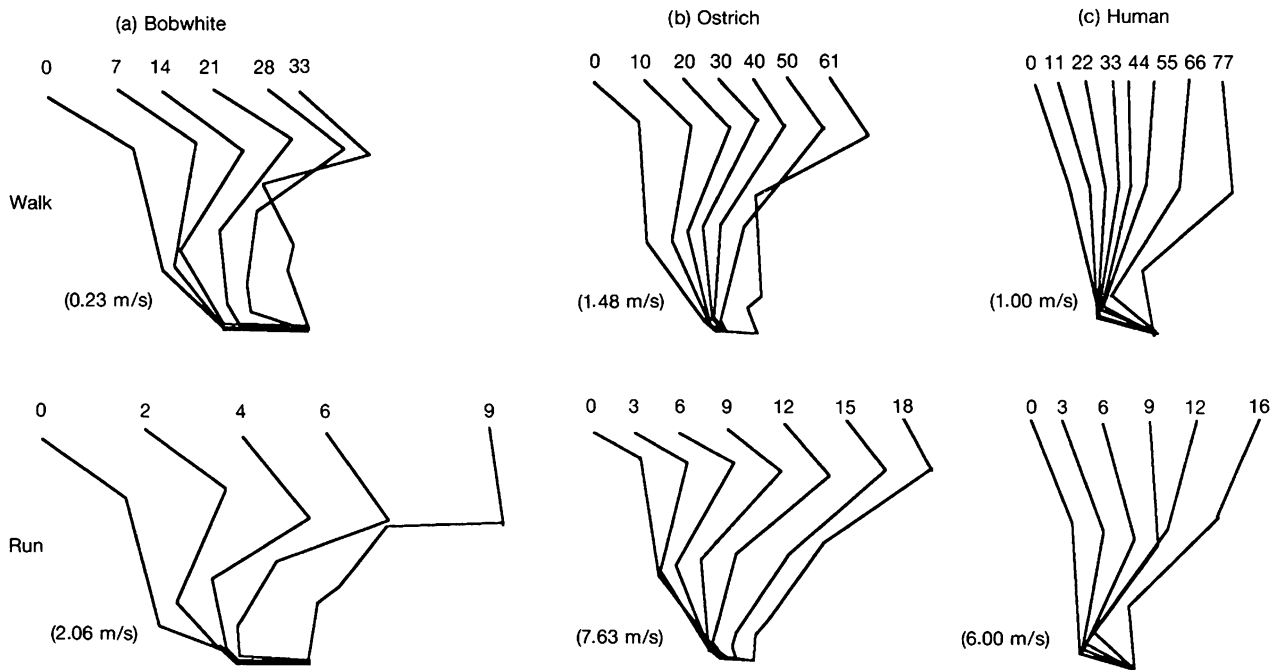


Fig. 3 Limb positions during the stance phase of slow walking and fast running of bobwhite quail (*Colinus*), ostrich and human. From Gatesy SM, Biewener AA (1991) Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool. Lond.* 224, 127–147. Cambridge University Press.

higher than in human sprinting, or in fast running by lizards and some birds.

Posture and joint angles

The bipedal gait of apes is often described as bent-hip bent-knee walking. The trunk slopes forward from the hip at an angle (in the case of bonobos) of about 70° to the horizontal (D'Août et al. 2002). This is much more erect than in quadrupedal walking, in which the bonobo trunk slopes at about 30° , but much less erect than in the vertical trunk of walking humans. The knee is strongly bent at mid-stance, to about 100° in bonobos walking bipedally and 90° in quadrupedal bonobos. By contrast, in walking humans the mid-stance knee angle is about 170° . D'Août et al. (2002) also showed differences in the phase relationship between knee and ankle movements, between bonobo (bipedal or quadrupedal) and human walking. When walking bipedally, orang utans (*Pongo*) keep the hip and knee of the supporting leg more extended than do chimpanzees.

The slope of the chimpanzee trunk presumably places the centre of mass of the body forward of the hips. In steady (unaccelerated) bipedal walking, the mean force on the foot must be vertical and in line with the centre of mass. For this reason, we may expect to

find that the mean position of each foot, while on the ground, is vertically below the centre of mass. Chimpanzees walking bipedally achieve this by keeping the knee forward of the hip throughout the stance phase. For example, in bonobos the thigh is at an angle of about 150° to the ground when the foot is set down in bipedal walking, falling to about 98° just before the toes leave the ground (D'Août et al. 2002). The corresponding angles for human walking are about 116° and 78° (Winter et al. 1974). Like humans, apes are plantigrade, placing the whole length of the foot, from heel to toe, on the ground. In human walking, the heel hits the ground before any other part of the foot, but chimpanzees place the lateral midfoot on the ground at the same time as the heel (Vereecke et al. 2003).

Penguins walk with the trunk vertical, but other birds keep it much more horizontal. For example, Gatesy's (1999) cineradiographs of guineafowl (*Numida*) show the sacrum tilted anterior-end-up at angles of about 25° to the horizontal in slow walking at 0.2 m s^{-1} , falling to 11° in fast running at 3 m s^{-1} . As in apes, the centre of mass is forward of the hip. Also as in apes, the knee remains forward of the hip throughout the stance phase (Fig. 3), but the angle of the thigh to the ground remains much more constant at low speeds than in apes. For example, in guineafowl it is about 155°

throughout the stance phase of slow walking, though it falls from about 140° to about 100° in the course of the stance phase of fast running (Gatesy, 1999). Another major difference from humans is that birds are digitigrade. Their long tarsometatarsals keep the ankle well clear of the ground.

The four species of lizard studied by Irschick & Jayne (1999b), which sometimes ran bipedally, had their trunks tilted (head up) at mean angles of $1\text{--}6^\circ$ in fast quadrupedal running and $8\text{--}15^\circ$ in fast bipedal running. Much larger trunk angles may be used in the first few strides of a sprint starting from rest (Irschick & Jayne, 1998). The long tails of most lizards presumably ensure that the centre of mass is much closer to the hips than to the shoulder joints. In contrast to apes and birds, the knee passes behind the transverse plane of the hips, in the later part of the contact phase of bipedal running. In Irschick & Jayne's (1999b) study, 55% of all strides (bipedal or quadrupedal) had digitigrade posture at footfall, and the rest were plantigrade.

The most striking difference between the bipedal locomotion of lizards, and of mammals, is that lizards place their feet much further from the median plane. Trackway width is the distance between the line of left footprints left by an animal and the line of right footprints. In the data that follow, it is measured between lines drawn through the centroids of the footprints. In bipedal running of the species studied by Irschick & Jayne (1999b), mean trackway width was 2.0–2.8 times tibia length. It was not significantly different in quadrupedal locomotion. Trackway width for normal adult human walking is about 0.12(leg length) or 0.25(tibia length) (Donelan

et al. 2001). Drawings in Murie (1974) show a trackway width of about 150 mm (about equal to tibiotarsus length) for a walking Canada goose, and less for other birds.

Cockroaches running bipedally tilt their bodies head up at angles around 25° to the horizontal. Consequently, aerodynamic lift as well as drag acts on the body. Even at the maximum speed of 1.5 m s^{-1} , these aerodynamic forces are small compared with the weight of the body (Full & Koehl, 1993), so cannot have much importance for the insect's equilibrium. Bipedal trackway width does not seem to have been measured, but is presumably large as in slow (six-legged) running.

Forces and mechanical energy

The forces that an animal's feet exert on the ground must balance its weight, but these forces are never constant in locomotion. The vertical component of the force on the ground always fluctuates about a mean value equal to body weight. Figure 4 shows some of the possibilities. Each of these schematic graphs shows vertical force plotted against time. Continuous lines show the forces exerted by the left and right feet, and broken lines show the total vertical force when both feet are on the ground simultaneously. In cases (i) and (ii), the force exerted by a foot shows two maxima in each step, as in human walking. In cases (iii) and (iv), however, there is a single maximum for each foot, in each step.

Consider a foot that is on the ground from time $t = -\tau/2$ to $t = +\tau/2$. The pattern of vertical force F_{vert} that it exerts in this interval can be represented with complete generality by the Fourier series

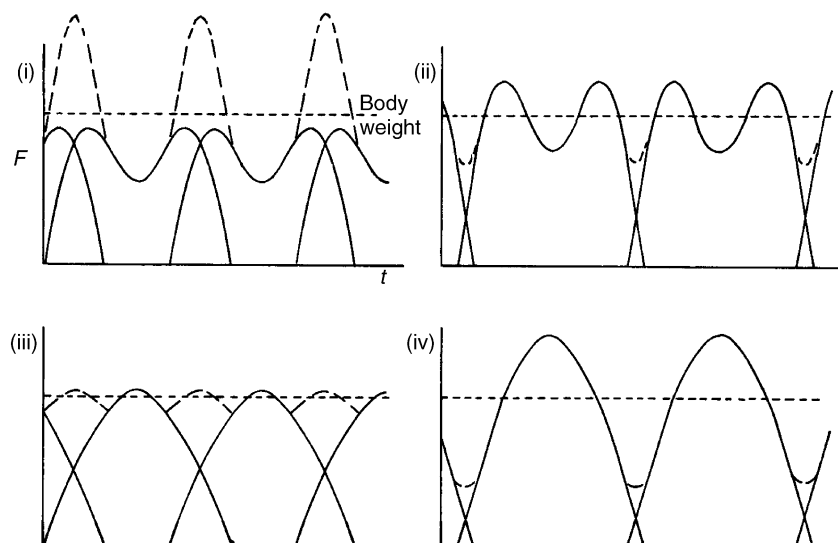


Fig. 4 Schematic graphs of the vertical force F exerted on the ground, against time t , for examples of four types of walking. Each graph shows the forces exerted individually by the left and right feet in several successive steps and, by a broken line, the total force when both feet are on the ground. Shape factors are 0.4 in (i) and (ii), 0 in (iii) and (iv). Duty factors are 0.75 in (i) and (iii), 0.55 in (ii) and (iv). From Alexander & Jayes (1978), by permission.

$$F_{\text{vert}} = a_1 \cos(\pi t/\tau) + b_2 \sin(2\pi t/\tau) + a_3 \cos(3\pi t/\tau) + b_4 \sin(4\pi t/\tau) + a_5 \cos(5\pi t/\tau) + \dots \quad (1)$$

where a_n and b_n are constants (Alexander & Jayes, 1980). There are no even-numbered cosine terms or odd-numbered sine terms in the series, because the force must be zero at the instants when the foot is set down and lifted, at times $-\tau/2$ and $+\tau/2$. In the cases we will be considering, the force exerted by a foot in a step is generally fairly nearly symmetrical in time, so we can ignore the sine terms, which describe asymmetry. We will not be concerned with the (generally small) high-frequency components of the force, so we can ignore high-numbered terms in the series. For these reasons, we can replace Eq. (1) with a truncated series

$$F_{\text{vert}} \approx a_1 [\cos(\pi t/\tau) - q \cos(3\pi t/\tau)] \quad (2)$$

(Alexander & Jayes, 1978). The coefficient q ($= -a_3/a_1$) is known as the shape factor, because it describes the shape of the graph of force against time. Because feet cannot exert negative vertical forces, it must lie in the range -0.33 to $+1.00$. When the shape factor is zero, as in Fig. 4(iii,iv), the graph of force against time is a half cycle of a cosine curve. As the shape factor increases, the force curve becomes flatter-topped and eventually, for values above 0.15, two-peaked. In Fig. 4(i,ii) it has been given the value 0.4. Negative shape factors describe bell-shaped force curves.

In human walking, the shape factor generally increases from about 0.2 in very slow walking to about 0.7 at the fastest walking speeds; and in running it generally lies between 0 and -0.2 (Alexander, 1989). Only a few force records of bipedal walking by chimpanzees and other non-human primates have been published (Kimura, 1985; Li et al. 1996). None of them shows shape factors greater than 0.3. The lower shape factors of bipedally walking chimpanzees, in comparison with humans, may be a direct consequence of their walking posture. Men and women whose shape factors had mean values of 0.50 and 0.40, respectively, when they walked normally at comfortable speeds, had shape factors of 0.24 and 0.26 when they walked with bent knees and hips, imitating chimpanzees (Li et al. 1996).

Like humans, chickens exert two-peaked vertical forces on the ground when walking, and single-peaked forces when running. Muir et al. (1996) published composite force records from which I estimate that the shape factor was about 0.2 and 0.3, respectively, for

1–2-day-old and 14-day-old chicks at a dimensionless speed of 0.38, and 0 (for both ages) at a dimensionless speed of 0.9. Force records by Cavagna et al. (1977) of turkeys and a rhea running show shape factors close to zero. Full & Tu's (1991) force record of a cockroach running bipedally shows slightly bell-shaped curves, implying small negative shape factors as in human running.

The fluctuations of the total force on the ground (the sum of the forces exerted by the left and right feet) depend on the duty factor and the shape factor. Figure 4 illustrates the possibilities. In Fig. 4(i), both the duty factor and the shape factor have relatively high values. The total force has maxima when both feet are on the ground, twice in each stride. In Fig. 4(iv), both factors are lower and the total force has maxima when there is only one foot on the ground, as the centre of mass of the body passes over the supporting foot. Again there are two maxima in each stride, but they are shifted one-quarter of a cycle from the positions of the maxima in case (i). Figure 4(ii,iii) show combinations of duty factor and shape factor that result in four force maxima in each stride. The maxima occur at different stages of the stride in these two cases.

In oscillatory motion, forces are half a cycle out of phase with displacements. This is as true of the vertical movements of walking and running as of the oscillations of a spring-mounted mass. The animal's centre of mass must generally be lowest when the force its feet exert on the ground is highest, and highest when the ground force is lowest. Figure 5(a) shows how the height of the centre of mass fluctuates in the course of a stride, in the four cases represented in Fig. 4. In case (i) the vertical force has maxima as the centre of

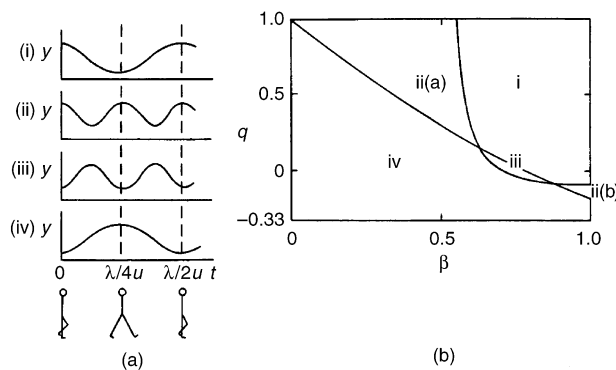


Fig. 5 (a) Schematic graphs of the height y of the centre of mass against time t for the four patterns of force illustrated in fig. 4. (b) A graph of shape factor q against duty factor β divided into the areas that give rise to each of the four styles of locomotion. From Alexander & Jayes (1978), by permission.

mass passes over the supporting foot. In case (iv) it has maxima during the dual-support phases, when both feet are on the ground. In cases (ii) and (iii) it has two maxima, during the half stride illustrated in the diagram.

Figure 5(b) shows shape factor on the vertical axis and duty factor on the horizontal axis. Lines separate the regions of the graph corresponding to the four possibilities shown in Fig. 4. Possibility (ii) occurs in two separate regions of the graph. Notice that possibility (i) is restricted to walking gaits, with duty factors greater than 0.5. Possibility (iv), however, occurs if the shape factor is low enough throughout the range of duty factors. Alexander & Jayes (1978) described walks of type (iv) as compliant walks, because the legs bend more while the foot is on the ground than in type (i) (stiff) walks.

Humans practise stiff walking; points for human walking would lie in zone (i) of Fig. 5(b), close to the left edge of the zone. Points for human running lie in zone (iv), very well separated from the points for walking. Data for quail also show walking in zone (i) and running in zone (iv), but the walking and running points are much less sharply separated (Alexander & Jayes, 1978). Chickens also walk in zone (i) and run in zone (iv) (Muir et al. 1996).

So far we have considered only the vertical component of the force on the ground. Longitudinal components of force also act, in such a way as to keep the resultant force on a human foot more or less in line with the centre of mass of the body. While a foot is in front of the body, it pushes forward as well as down, decelerating the body as well as supporting it. Later in the step it is behind the body and pushes backward and down, re-accelerating the body. Thus the forward velocity of the centre of mass passes through a minimum as it passes over the supporting foot. This is true both of walking and of running (Margaria, 1976). It is as true of other bipeds as it is of humans (see for example Kimura, 1985, on chimpanzees; Cavagna et al. 1977, on turkeys and rheas; and Muir et al. 1996, on chicks).

Whether a biped is walking or running, its body is always moving most slowly, and has minimum kinetic energy, as the centre of mass passes over the supporting foot. At this stage of the stride in type (iv) gaits its height is also minimal, giving it minimum gravitational potential energy (Fig. 5). Its height and potential energy have maximum values at this stage, however, in type (i) gaits. Thus kinetic and potential energy fluctuate in phase with each other in type (iv) gaits, and out of phase in type (i) gaits. Cavagna et al. (1977) showed that

they fluctuate in phase in running and out of phase in walking, in humans, rheas and turkeys. They stressed the energy-saving potential of the out-of-phase fluctuations in walking; energy is saved by swapping energy back and forth between the kinetic and potential forms, on the principle of the pendulum. Once set in motion, a frictionless pendulum in a perfect vacuum would continue swinging forever, without any fresh input of energy.

The kinetic energy calculated by Cavagna et al. (1977) from their force records is the external kinetic energy, the energy associated with the velocity of the centre of mass. The internal kinetic energy (due to movements of parts of the body relative to the centre of mass) cannot be obtained from force plate records. Cavagna and colleagues used the kinetic and potential energy changes to calculate the work required for locomotion. In any interval of time in which (kinetic plus potential energy) increases, the animal's muscles must do (positive) work to supply the extra energy. In any interval in which it decreases, muscles must do negative work; that is to say, they must function like brakes, degrading mechanical energy to heat. If the animal is walking or running steadily over level ground, its potential and kinetic energies are the same at the end of each stride as at the beginning, so numerically equal quantities of positive and negative work must be done during the stride.

Let an animal's external kinetic energy and potential energy increase by $\delta E_{k_{ext}}$ and δE_p , respectively, during a short increment of time. During a complete stride, the external kinetic energy shows increases totalling $1/2 \sum |\delta E_{k_{ext}}|$ and decreases also totalling $1/2 \sum |\delta E_{k_{ext}}|$. The vertical lines in this expression indicate that the absolute value of $\delta E_{k_{ext}}$ is meant (i.e. positive and negative values are both treated as positive). The summation sign \sum indicates that values are to be summed over a complete stride. The potential energy similarly increases and decreases by amounts totalling $1/2 \sum |\delta E_p|$. The positive and negative work required in a complete stride can each be estimated as $1/2 \sum |\delta E_{k_{ext}} + \delta E_p|$. Cavagna et al. (1977) assessed the effectiveness of pendulum-like energy savings by calculating the percentage recovery:

$$100 \{ \sum |\delta E_{k_{ext}}| + \sum |\delta E_p| - \sum |\delta E_{k_{ext}} + \delta E_p| \} / \{ \sum |\delta E_{k_{ext}}| + \sum |\delta E_p| \}.$$

If the external kinetic and potential energy fluctuate in phase with each other, both increasing or both decreasing in any interval of time, the percentage

recovery is zero. If, by contrast, whenever one of these energies increases the other decreases by an equal amount (as in a perfect pendulum), the percentage recovery is 100.

Cavagna et al. (1976) had found percentage recoveries of about 60% in human walking at moderate speeds, less in faster and slower walking, and less than 5% in running. Cavagna et al. (1977) similarly obtained values of about 70% for turkeys and rheas at normal walking speeds, 20% or less for very fast walking and 0–5% for running. Muir et al. (1996) obtained values up to 80% for walking chickens, falling to zero in fast running. Percentage recovery in fast running by cockroaches was around 5% (Full & Tu, 1991; who do not show which runs were quadrupedal and which bipedal).

Although the pendulum principle cannot save energy in running, elastic mechanisms can. Much of the (kinetic plus potential) energy lost by a human runner, in the first half of a step, is stored as elastic strain energy in stretched tendons and ligaments, and returned by elastic recoil in the second half (Ker et al. 1987). Similarly, in running ostriches, turkeys and guinea fowl, energy is saved by elastic storage in the digital flexor tendons (Alexander et al. 1979; Daley & Biewener, 2003). I am not aware of any demonstrations of energy saving by elastic mechanisms in running lizards or cockroaches.

Adult humans and most birds have narrow trackways, as we have seen. The transverse components of the forces they exert on the ground are much smaller than the longitudinal components (Clark & Alexander, 1975; Donelan et al. 2001). Lizards and cockroaches have wide trackways. Farley & Ko (1997) have shown for quadrupedal locomotion of lizards, and Full et al. (1991) have shown for hexapedal locomotion of cockroaches, that the transverse forces are similar in magnitude to the longitudinal forces. It seems likely that the same is true for bipedal running, in both taxa.

In walking and in the majority of cases also in running, humans strike the ground first with the heel. The centre of pressure moves forward from the heel to the ball of the foot, in the course of the step, and the toes are the last part of the foot to leave the ground (see for example Debrunner, 1985). Both in bipedal and in quadrupedal locomotion, bonobos typically set down the heel and the lateral part of the midfoot simultaneously. As in humans, the centre of pressure moves forward along the sole of the foot, and the toes are the last part of the foot to leave the ground (Vereecke et al. 2003).

Metabolic energy costs

The metabolic energy used in bipedal walking or running has been measured for humans, chimpanzees and various birds, but apparently not for lizards or cockroaches. Many of the data are given in a classic paper by Taylor et al. (1982), which also reports energy costs for bipedal hopping mammals and for numerous quadrupedal mammals. Taylor and colleagues found as a general rule that the metabolic rate increased linearly with speed:

$$\text{metabolic rate/body mass} = A + B (\text{speed}) \quad (3)$$

where A and B are constants for each individual species. This equation predicts that an animal will have a metabolic rate A per unit body mass when stationary, and will use additional energy B per unit mass per unit distance travelled. B is known as the metabolic cost of transport. Taylor et al. (1982) found that it was smaller for larger species, and was generally close to the value given by the equation:

$$\begin{aligned} \text{metabolic cost of transport (J/kg m)} \\ = 10.7 \times (\text{body mass, kg})^{-0.32}. \end{aligned} \quad (4)$$

This equation gave a reasonable fit for the data set as a whole, but some species deviated markedly from its predictions. Table 1 shows costs of transport for various bipeds. Human walking is more economical, and human running more costly, than the equation predicts. The very high costs of transport for geese and penguins are generally attributed to their waddling (wide trackway)

Table 1 Metabolic costs of transport for bipedal locomotion divided by the values predicted by Eq. (4). The data for human running are from Taylor et al. (1982). For data for human walking have been calculated from the difference between the metabolic rates given by Margaria (1976) for standing and for walking at the most economical speed. The data for chimpanzees are from Taylor & Rowntree (1973), and for birds from Bruinzeel et al. (1999)

	Mean \pm SD	No. of species
Human run	1.45	
Human walk	0.73	
Chimpanzee bipedal walk	1.07	
Game birds (Galliformes)	0.95 \pm 0.26	7
Waders (Charadriiformes)	0.68 \pm 0.03	6
Geese (Anseriformes)	1.70 \pm 0.29	3
Penguins (Sphenisciformes)	2.11 \pm 0.07	5

gaits. Humans walking with a very wide trackway of 0.45(leg length) used 40% more metabolic energy than when using their preferred trackway width (Donelan et al. 2001).

Minetti & Alexander (1997) showed how the metabolic cost of walking and running could be expected to depend on duty factor, shape factor and stride length. For any given speed, our model predicted an optimum combination of values for these three variables. The predicted duty factors were lower and the predicted shape factors higher than people generally use at the same speed, but the predicted changes with speed paralleled the observed ones. Close quantitative agreement could not be expected with so simple a model, and it seems quite likely that human duty factors, shape factors and stride lengths are adjusted to minimize energy costs. The model suggests that other bipeds, like humans, should use high shape factors when walking fast, but they are not observed to do so. We may speculate about the possibility that the gaits of at least some bipeds may be suboptimal, in terms of energy cost, but our understanding of the energetics of bipedal locomotion is not good enough to justify a firm conclusion.

Conclusion

In this paper, I have compared the gaits of animals that walk or run bipedally, with human gaits. The general conclusion is that no animal walks or runs as we do. We keep the trunk erect; in walking, our knees are almost straight at mid-stance; the forces our feet exert on the ground are very markedly two-peaked when we walk fast; and in walking and usually in running we strike the ground initially with the heel alone. No animal walks or runs like that.

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