

Stability and Manoeuvrability of Terrestrial Vertebrates¹

R. McNEILL ALEXANDER²

School of Biology, University of Leeds, Leeds LS2 9JT, UK

SYNOPSIS. For a standing animal to be statically stable, a vertical line through its centre of mass must pass through the polygon of support defined by its feet. Statically stable gaits are possible for quadrupeds but do not seem to be used. Physical and mathematical models have shown that bipedal gaits can be dynamically stable. Accelerations and decelerations of animals may be limited by muscle strength, by the coefficient of friction with the ground or by considerations of stability. Cornering ability similarly may be limited by strength or by the coefficient of friction. It may be faster to use a longer route involving corners of larger radius than a shorter one with sharper corners.

STATIC STABILITY

A body is in equilibrium if the forces acting on it are balanced, in which case it will be stationary or move with constant velocity and angular velocity. The equilibrium is stable if it returns to its initial condition after a small displacement. For example, if I tilt and release a table it falls back to its initial position on the floor. A condition for stability of a structure resting on the ground is that a vertical line through its centre of mass must fall within the polygon formed by the points of support on the ground. In the case of a table, this is the rectangle (or triangle, in the case of a three-legged table) of which the corners are the table's feet. Three is the minimum number of point supports required for stability, but a biped can be stable standing on two or even on one foot because each foot contacts the ground over a finite area, equivalent to a distribution of points of support.

If a table is placed on too steep a slope, the vertical line through its centre of mass will be moved outside the polygon of support, and it will topple over. A wide table can be tilted through a larger angle than a narrow one of the same height, before this happens. Thus the angle of displacement that can be tolerated depends on the ratio of the dimensions of the triangle of support, to the height of the centre of mass from the ground. A mammal such as a horse, that stands with its left and right feet close together, has to control transverse movements of its centre of mass much more precisely than a reptile such as a tortoise, that stands with its feet far apart. Bipedal animals with small feet also need to keep displacements within narrow limits. The slight movements made by standing people, due to involuntary sway of the body, have been monitored by experiments in which subjects stood on force plates. Harris *et al.* (1982) found that the point of intersection with the ground, of the vertical line through the centre of mass of a standing human adult, usually remains within a circle of diameter about 25 mm (or a little more for elderly subjects). Thus we have no difficulty in keep-

ing it within the polygon of support, between the feet. Alexander (1971) argued that very small animals are more susceptible than large ones, to displacement by gusts of wind, so that animals of the size range of insects may need to stand with their feet well apart (though the problem could be overcome by adhesive feet). Also, submerged walkers such as crabs may need to place their feet well apart because of the danger of being overturned by water movements (Martinez, 2001).

Nashner and Woollacott (1979) investigated the response of human subjects to unexpected displacements by standing them on a pair of force plates, one foot on each plate, and moving one plate suddenly up or down. Two possible effective responses would have been to flex the knee on the side of the higher foot, or to have adducted one leg and abducted the other. The results of the experiment showed that the former response was generally used. Papantoniou *et al.* (1999) point out that for animals that stand with their left and right feet close together, with their knees not too straight, this is the option that requires less angular movement of the joints. However, humans stand with their knees straighter than any animal.

A quadruped can be stable with only three feet on the ground. By moving its feet one at a time, it can maintain static stability throughout the gait cycle. However, the order of movement of the feet must be chosen in such a way as to ensure that the vertical line through the centre of mass is always kept within the triangle of support. The options depend on the duty factor, the fraction of the duration of the stride for which each foot is on the ground. The condition that there must always be at least three feet on the ground implies that a statically stable walk requires a duty factor of at least 0.75. McGhee and Frank (1968) showed that for duty factors in the range 0.75 to 0.83 only one sequence of leg movements is consistent with static stability. They called the statically stable gait that uses this sequence a regular crawl. The sequence is left fore, right hind, right fore, left hind etc. This is the sequence generally used by walking mammals (Hildebrand, 1976). Duty factors above 0.83 allow two other sequences, but even at these high duty factors

¹ From the Symposium *Stability and Maneuverability* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 3–7 January 2001, at Chicago, Illinois.

² E-mail: r.m.alexander@leeds.ac.uk

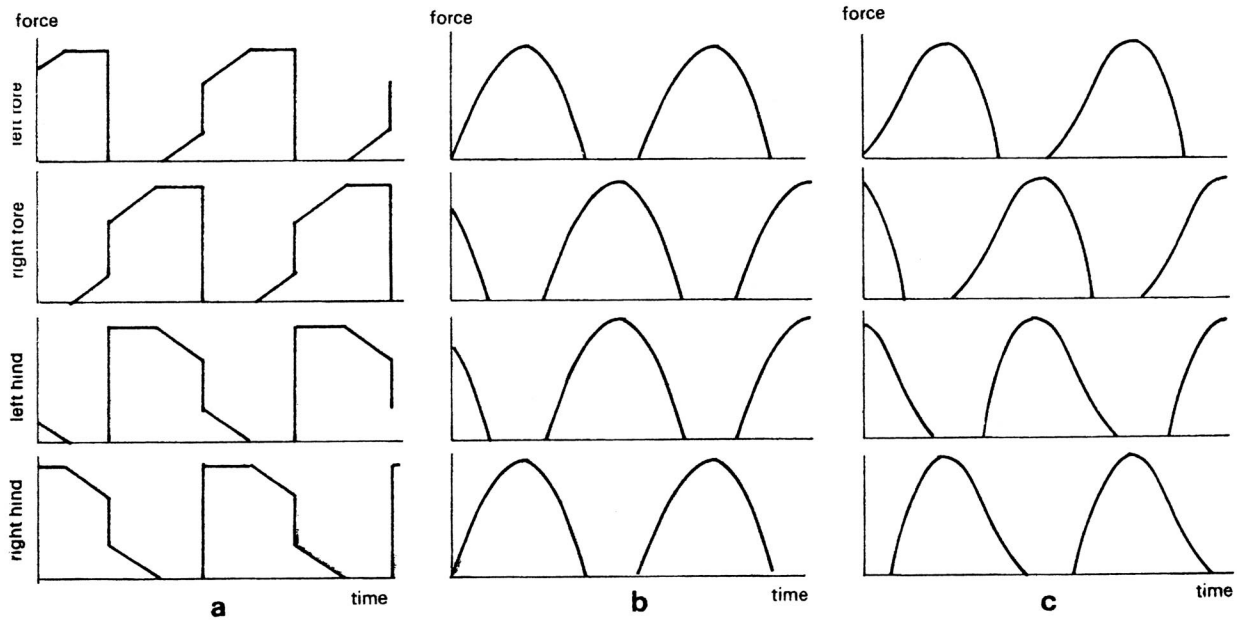


FIG. 1. Graphs of the vertical components of the forces on the feet of a quadruped, against time, for three gaits. (a) maintains equilibrium throughout the stride, (b) minimizes unwanted displacements for an animal with very slow muscles, and (c) minimizes unwanted displacements for an animal with slightly faster muscles. From Alexander (1982).

the regular crawl gives a larger margin of stability (that is to say, it allows the centre of mass to be kept further from the edges of the triangle of support).

Despite this theoretical advantage, animals use the regular crawl rarely, if at all. Duty factors of 0.75 or more have been recorded for toads, turtles and (at very low speeds) hippopotamus, but are not generally used by other animals (Barclay, 1946; Walker, 1971; Hildebrand, 1976). Both toads and turtles have more than one foot off the ground, at some stage in the stride.

Alexander (1981) considered an animal walking with stride frequency f , so that the duration of each stride was $1/f$. If the animal fell freely for this time, starting from rest, it would fall a distance $g/2f^2$. If its legs had length h , the distance it could fall before hitting the ground would be a little less than h . Thus the dimensionless parameter $g/2f^2h$ can be used as a measure of the need for an animal to maintain equilibrium as it walks. This parameter is high for animals with short legs, moving slowly. It is 1 or less for a dog galloping, about 5 for a dog walking very slowly, and about 200 for turtles such as *Geoemyda* walking at their normal (very slow) speed. This implies that dogs and other mammals can tolerate much larger departures from equilibrium than turtles can.

Jayes and Alexander (1980) asked why, despite their apparent need to keep departures from equilibrium small, turtles and tortoises use gaits in which there are, at times, only two feet on the ground. They pointed out that an animal using the regular crawl, preserving equilibrium throughout the stride, would have to exert forces on the ground as shown in Figure 1a. Notice that large, instantaneous changes of force would be required whenever a foot was lifted or set down. These

animals have very slow muscles, incapable of changing force abruptly, which (apparently as a concomitant of their slowness) work very efficiently (Woledge, 1968). Alexander and Jayes (1980) presented a mathematical model of turtle walking in which the slowness of the muscles was represented by requiring the feet to exert forces that rose and fell like a half cycle of a cosine curve. They varied the times at which feet were set down and calculated the amplitudes of unwanted displacements (pitch, roll and vertical movements). They found that unwanted displacements were minimized by using the gait represented in Figure 1b, in which diagonally opposite feet move together and there are, at times, only two feet on the ground. They then allowed for slightly faster muscles by adding a sine term to the cosine one, allowing force patterns to be skewed. Unwanted displacements were then minimized by the gait shown in Figure 1c, in which diagonally opposite feet move slightly out of phase with each other and there are again times when only two feet are on the ground. Figure 1c is very like records of turtles walking, both in the relative phases of the feet and in the skewed shapes of the graphs of force against time.

DYNAMIC STABILITY

In statically stable gaits, the forces on the walker are in equilibrium at all stages of the stride. A gait of which this is not true may nevertheless be dynamically stable, in the sense that the walker returns automatically to its normal pattern of movement, following a disturbance. Dynamic stability can be conferred by feedback control, that is by a control system that detects unwanted movements and takes action to correct

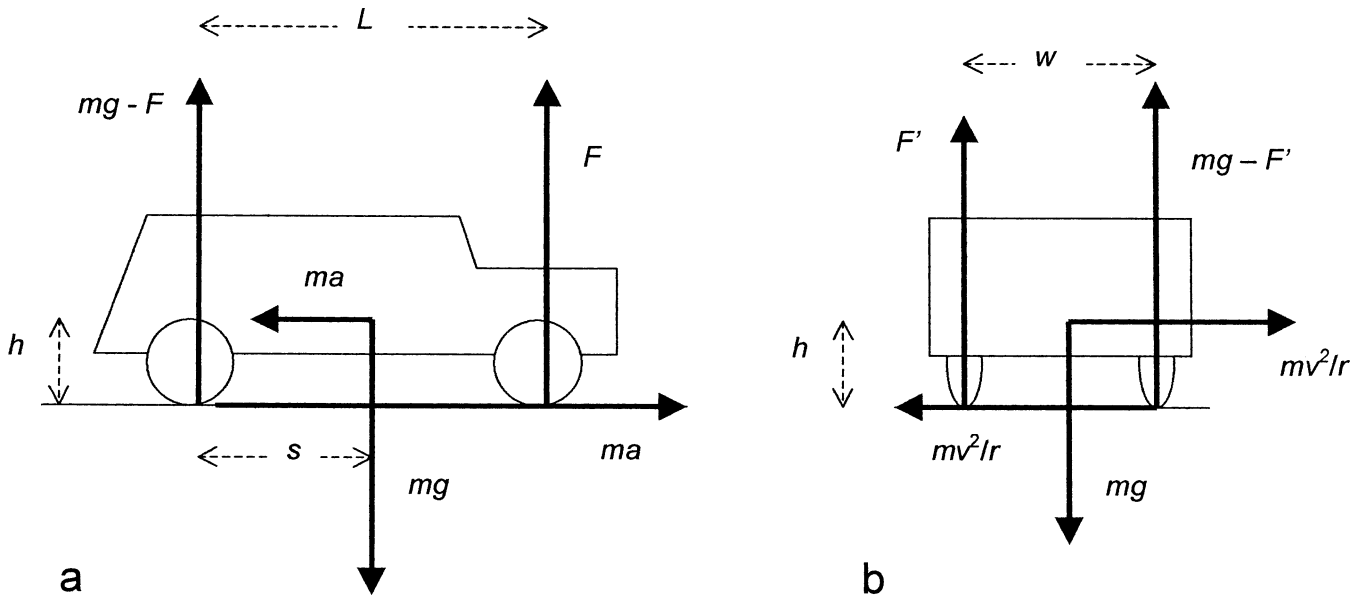


FIG. 2. Diagrams showing the forces on a vehicle (a) accelerating and (b) turning towards the left of the diagram.

them. For example, Raibert's one-legged hopping robot was stabilized by feedback control. Raibert (1986) reproduced records of this robot being disturbed by a sharp push, while hopping in place. It returned to its desired position within a few seconds.

McGeer (1990a, 1993) examined the interesting possibility that a passive walking system may be dynamically stable. He started by considering a traditional wooden toy that walks passively down slopes, rocking from side to side as it goes. He designed and built a planar, non-rocking version of this toy. He performed experiments with it and analyzed its motion mathematically, and showed that its motion was stable throughout its speed range. Kuo (1999) extended the analysis to the three-dimensional case in which roll is possible. He showed that the model was unstable in roll, but could be stabilized by several alternative feedback control systems. He argued that control of lateral foot placement (step width) would be a particularly favourable mechanism. Bauby and Kuo (2000) confirmed by experiment that walking humans control roll in this way.

McGeer (1990b) presented a mathematical model of running by a biped with telescoping legs containing springs. The model would run passively downhill and could be stabilized by making the stride frequency sufficiently high, but McGeer argued that active stabilization was desirable.

ACCELERATION AND DECELERATION

Acceleration and deceleration are important components of manoeuvrability, but very few data are available for walking or running. Human sprinters leave the starting blocks with accelerations of about 10 m/sec^2 (Ballreich and Kuhlow, 1986). Elliott *et al.* (1977) filmed lions hunting in East Africa, and calculated equations describing the movements both of

the lions and of their prey. These equations imply, as would be expected, that acceleration fell in the course of a run, as speed increased. It can be calculated from them that the initial accelerations of the animals, starting from rest, were 9.5 m/sec^2 for the lions, but only 5.0 , 5.6 and 4.5 m/sec^2 , respectively, for zebra, wildebeest and Thomson's gazelle.

High accelerations and decelerations require large forces, so may be limited by the strengths of muscles. Alternatively, they may be limited by friction with the ground, or by a problem of stability. The vertical force exerted on the ground by an animal of mass m , averaged over a complete stride, must average mg , where g is the gravitational acceleration. If the animal is accelerating with acceleration a , the horizontal component of the force on the ground must average ma . Thus, for the acceleration to be possible, the effective coefficient of friction of the feet with the ground must be at least a/g . I use the adjective "effective" to indicate the possibility that the foot's purchase on the ground may be augmented by means that are not strictly frictional such as spiked running shoes, claws or irregularities in the ground. Nigg (1986) reports measurements of the coefficients of friction of sport shoes with artificial surfaces. The coefficients ranged from around 0.3 for a surface covered with loose granules to around 1.5 for artificial grass. Cartmill (1979) measured the coefficients of friction of prosimian primates' feet with a board by tilting the board and observing the angle at which they started to slide. Most of the coefficients lay between 1 and 2 . When bare footed humans were tested in the same way, most of the coefficients lay between 0.5 and 1.0 .

The problem of stability that may limit acceleration and deceleration is illustrated by Figure 2a. The vehicle has mass m and acceleration a , so its weight is mg (g is the gravitational acceleration) and the hori-

zontal component of the force exerted by the wheels on the ground is ma . The wheelbase length is L and the centre of mass is a distance s in front of the points of contact of the rear wheels with the ground, at a height h from the ground. The vertical components of the forces on the wheels are F for the front wheels and $(mg - F)$ for the rear wheels. By taking moments about the points of contact of the rear wheels with the ground

$$FL + mah - mgs = 0 \quad (1)$$

Thus F must fall as a increases. The condition for F to be positive is

$$a < gs/h \quad (2)$$

The force F cannot be negative, because the tires do not adhere to the road. If an acceleration greater than the limit set by condition 2 is attempted, the front wheels will leave the road and the vehicle will perform a back somersault. A similar condition applies to deceleration. If the absolute value of the deceleration is greater than $g(L - s)/h$, the rear wheels will leave the road. It is well known that a cyclist who brakes too hard will be thrown over the handlebars. Automobiles are designed with the centre of mass sufficiently low to avoid this danger.

The same principle applies to legged animals. Lee *et al.* (1999) showed that the fraction of body weight supported by the fore feet of trotting dogs increases when they decelerate and falls when they accelerate. However, the conditions for stable acceleration and deceleration are more complicated for a quadruped than for a wheeled vehicle. If we ignore the small movements allowed by a vehicle's suspension, the point of contact of a wheel with the ground is in a fixed position, relative to the centre of mass. In contrast, an animal's feet move posteriorly, relative to the centre of mass, while they are on the ground. Thus s and $(L - s)$ change in the course of a step. A quadruped might increase the effective value of s for acceleration by delaying the exertion of peak force until late in the step, when the hind foot is well behind the hip joint. It might increase the effective value of $(L - s)$ during deceleration by exerting peak force early in the step, when the fore foot is in front of the shoulder. In the experiments on dogs, such adjustments were found to be less important than the redistribution of weight between the fore and hind feet.

Humans and other bipeds must lean forward while accelerating and backward while decelerating.

CORNERING

An animal running along a curved path has an acceleration towards the centre of curvature, at right angles to its path. More specifically, an animal running with speed v along a path of radius r has a transverse acceleration v^2/r . If its mass is m , a transverse force mv^2/r is required to give it this acceleration. Figure 2b represents a vehicle seen in front view, turning towards the left of the diagram. The centre of mass is midway

between the left and right wheels, which are a distance w apart. Vertical components of force F' and $(mg - F')$ act on the wheels on the inside and outside of the bend, respectively. By taking moments about the point of contact of the outer feet with the ground

$$F'w + mv^2h/r - mgw/2 = 0 \quad (3)$$

and for F' to be positive

$$v^2/r < gw/2h \quad (4)$$

If a turn involving a greater transverse acceleration v^2/r than this is attempted, the vehicle will roll over. Automobiles are designed with low centres of mass to ensure that this does not happen.

Animals can eliminate the danger of rolling over in a curve, by leaning into the curve. Animals that have a low ratio of trackway width to centre of mass height (the equivalent of the ratio w/h) must lean even on quite gentle curves. This is the case for most large mammals. For example, footprints of horses show that the trackway width is only 10–20% of the estimated height of the centre of mass. In an extreme case, if the trackway width were zero (the left and right feet were set down along a single line), the animal would have to lean in at an angle $\arctan(v^2/rg)$ to the vertical. Turning cyclists must also lean at this angle.

Alexander (1982) suggested that the cornering ability of running animals might be limited by the danger of skidding. An animal running at speed v round a curve of radius r will be able to exert the necessary transverse force only if the coefficient of friction μ of its feet with the ground is at least v^2/rg .

$$\mu \geq v^2/rg \quad (5)$$

Greene (1985), who investigated the ability of human runners to run in circles, made the alternative suggestion that cornering might be limited by the ability of the musculoskeletal system to generate the required forces. Consider an athlete of mass m running as fast as possible (at speed v) round a curve of radius r . Let the duration of a half stride be T (this is the time from setting down one foot to setting down the other). Let the step length be l (this is the distance travelled while a foot is on the ground). Make the plausible but uncertain assumptions that T and l are both constant. Let the mean vertical and horizontal components of force **while a foot is on the ground** be F_v , F_h respectively. The mean values of these components of force over a complete half stride are mg , mv^2/r . The foot is on the ground for time l/v out of the half stride duration T . Hence

$$F_v = mgTv/l \quad (6)$$

$$F_h = mv^3T/rl \quad (7)$$

The athlete's maximum speed when running in a straight line is v_0 , and at this speed the force on his or her feet is $mgTv_0/l$. The resultant force on the ground in cornering cannot exceed this, according to Greene's

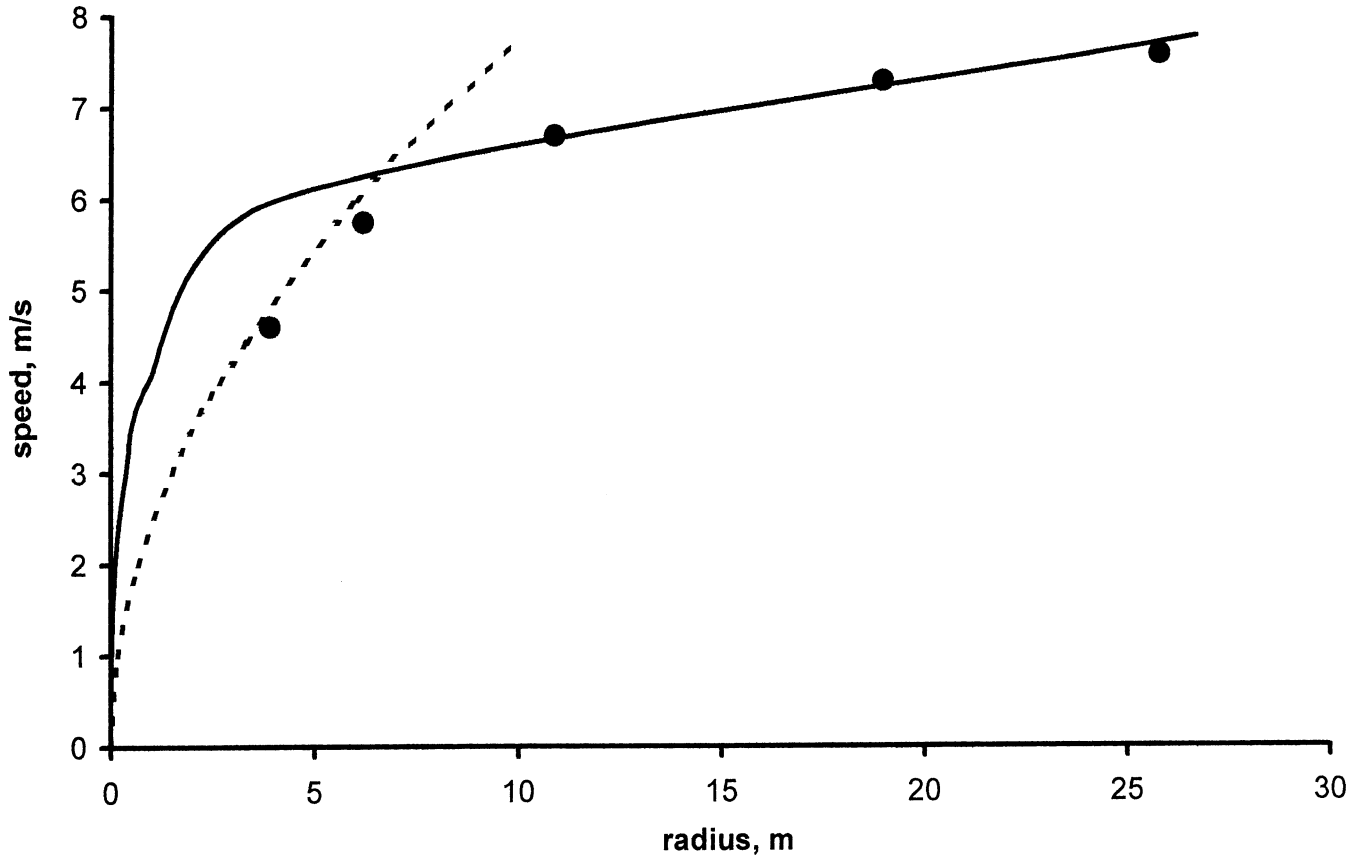


FIG. 3. The maximum speeds at which adult humans can run on curves of different radii. The broken line shows predictions from equation 5, taking $\mu = 0.6$; the continuous line shows predictions from equation 9 for a subject for whom $v_0 = 8$ m/sec; and the points show observed speeds, from McMahon (1984), for the same subject.

hypothesis, so when the athlete runs as fast as possible in a curve of radius r

$$F_v^2 + F_h^2 = (mgTv_0/l)^2 \tag{8}$$

By substituting 6 and 7 in 8 and rearranging so that both sides of the equation are dimensionless

$$rg/v_0^2 = (v/v_0)^3/[1 - (v/v_0)^2]^{0.5} \tag{9}$$

Figure 3 shows graphs of maximum speed against radius calculated both from equation 9 (taking $v_0 = 8$ m/sec) and from equation 5 (taking $\mu = 0.6$). It also shows empirical points for a man running in spiked shoes on grass. Equation 9 fits the data for large radii well, but when the radius is small equation 5 gives the better fit. The same is true for runners on concrete

(Fig. 2b of Greene, 1985). One possible hypothesis is that speed on curves may be limited by ability to exert the required forces, if the radius is large; and by friction if the radius is small. Experiments on surfaces giving different coefficients of friction would be needed to test this hypothesis.

Barrel racing is a sport that tests the cornering ability of horses. Competitors are required to ride as fast as possible round a course that loops around oil barrels placed about 30 m apart. Photographs show horses leaning at about 45° to the vertical as they round the barrels, suggesting that their transverse accelerations must be approximately equal to the gravitational acceleration, and that the coefficient of friction with the ground must be at least 1.0.

A simple model suggested by barrel racing will help to clarify the principles of fast manoeuvring. Suppose that it is required to ride repeatedly, as fast as possible, around a circuit marked by two barrels a distance $2s$ apart (Fig. 4). We will assume that the path chosen consists of two semicircles of radius ps joined by two straight segments of length $2s(1 - p)$. Speed on the curves is constant and as high as possible for a curve of that radius. On the straights, the contestant accelerates with acceleration a for the first half of the distance, and decelerates with acceleration $-a$ for the sec-

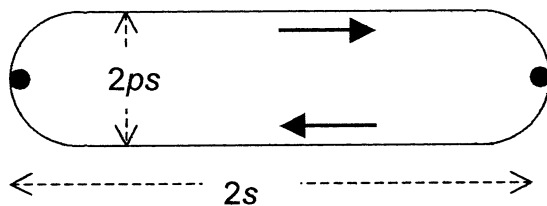


FIG. 4. A circuit around two obstacles (filled circles). A model presented in the text predicts the radius for the circular segments, that minimizes the running time.

ond half. The assumption of constant acceleration implies that the course is too short for the contestant to approach the maximum speed that would be attainable in a longer straight sprint. What radius should be used on the curves, to minimize the time required for a circuit of the course?

We will assume that the transverse acceleration has the same value in fast cornering on any radius. As we have seen, this would be consistent with cornering being limited by the coefficient of friction with the ground. Further, we will make what appears to be a reasonably realistic assumption, that this transverse acceleration is equal to the maximum forward acceleration a . An animal running with speed v on a curve of radius r has transverse acceleration v^2/r , so the speed on the curves is $(aps)^{1/2}$. The total length of the two semicircles is $2\pi ps$, so the total time spent on the two curves is

$$t_{\text{curves}} = 2\pi(ps/a)^{1/2} \quad (10)$$

The animal enters each straight at speed $(aps)^{1/2}$, and accelerates with acceleration a over the first half of the straight, a distance $s(1-p)$. The time required to cover this distance, t_{accel} , can be calculated from the standard equation for constant acceleration

$$s(1-p) = (aps)^{1/2}t_{\text{accel}} + (1/2)at_{\text{accel}}^2.$$

The solution of this quadratic equation is

$$t_{\text{accel}} = (1/a)\{- (aps)^{1/2} \pm [aps + 2as(1-p)]^{1/2}\} \quad (11)$$

The ambiguous sign must be made positive, to make the time positive. An equal time is needed for the second half of each straight, when the animal is decelerating.

The total time T required for one circuit of the course is given by

$$\begin{aligned} T &= t_{\text{curves}} + 4t_{\text{accel}} \\ &= 2\pi(ps/a)^{1/2} \\ &\quad + (4/a)\{- (aps)^{1/2} + [aps + 2as(1-p)]^{1/2}\} \\ &= 2(s/a)^{1/2}\{(\pi - 2)p^{1/2} + 2(2-p)^{1/2}\} \quad (12) \end{aligned}$$

We wish to find the value of p that minimizes T .

$$dT/dp = 2(s/a)^{1/2}\{0.5(\pi - 2)p^{-1/2} - (2-p)^{-1/2}\} \quad (13)$$

This is zero when $p = 0.49$; the optimum radius for the turns is expected to be almost one quarter of the distance between the posts. It must be stressed that one of the assumptions, on which this conclusion depends, is that the distance between the posts is short.

A transverse force applied at the centre of mass is sufficient to make a moving vehicle or animal travel along a curve, but a moment about the centre of mass is needed when turning is initiated, to give it the angular velocity needed to keep it facing in the direction of travel. In automobiles, this is done by steering the front wheels so that they are no longer aligned with the initial direction of travel; the resulting transverse force on the front wheels provides the required moment.

Stability of cornering is an important issue in vehicle design (see for example Ellis, 1994). The crucial concepts are oversteer and understeer. As speed is increased on a turn of constant radius, the steering angle must be reduced on an oversteering vehicle, and increased on an understeering vehicle. These steering adjustments are needed because a lateral force on a wheel makes it slip sideways over the ground as it rolls forward. Understeering vehicles are stable in cornering at all speeds; that is to say, the vehicle tends to return to its original radius of turn after disturbance by (for example) a gust of wind or an irregularity in the road surface. Oversteering vehicles, however, become unstable above a critical speed. We do not seem to know enough about animal turning to establish whether any analogous phenomenon can make the steering of animals unstable. However, it may be worth noting that a vehicle steered by its front wheels is less likely to oversteer if its centre of mass is well forward, so that most of the weight of the body is carried by the front wheels. The front legs of quadrupedal mammals typically support about 60% of body weight (Alexander and Jayes, 1983).

Our understanding of the stability and manoeuvrability of land vertebrates is disappointing, compared to our knowledge of other aspects of their locomotion. There is a particular need for more research on dynamic stability in walking and running. Some superb work has been done in this field, but it has focused on bipedal robots that move (more or less) like people, and has paid little attention to quadrupedal gaits.

REFERENCES

- Alexander, R. McN. 1971. *Size and shape*. Arnold, London.
 Alexander, R. McN. 1981. The gaits of tetrapods: Adaptations for stability and economy. *Symp. Zool. Soc. London*. 48:269–287.
 Alexander, R. McN. 1982. *Locomotion of animals*. Blackie, Glasgow.
 Alexander, R. McN. and A. S. Jayes. 1983. A dynamic stability hypothesis for the gaits of quadrupedal mammals. *J. Zool.* 201: 135–152.
 Ballreich, R. and A. Kuhlow. 1986. *Biomechanik der Leichtathletik*. Enke, Stuttgart.
 Barclay, O. R. 1946. The mechanics of amphibian locomotion. *J. Exp. Biol.* 23:177–203.
 Bauby, C. E. and A. D. Kuo. 2000. Active control of lateral balance in human walking. *J. Biomechan.* 33:1,433–1,440.
 Cartmill, M. 1979. The volar skin of primates: Its frictional characteristics and their functional significance. *Am. J. Phys. Anthropol.* 50:497–510.
 Elliott, J. P., I. McT. Cowan, and C. S. Holling. 1977. Prey capture by the African lion. *Can. J. Zool.* 55:1,811–1,828.
 Ellis, J. R. 1994. *Vehicle handling dynamics*. Mechanical Engineering Publications, London.
 Greene, P. R. 1985. Running on flat turns: Experiments, theory, and applications. *J. Biomech. Eng.* 107:96–103.
 Harris, G. F., T. A. Knox, S. J. Larson, A. Sances, and E. A. Millar. 1982. A method for the display of balance platform centre of pressure data. *J. Biomechan.* 15:741–745.
 Hildebrand, M. 1976. Analysis of tetrapod gaits: General considerations and symmetrical gaits. In R. M. Herman, S. Grillner, P. S. G. Stein, and D. G. Stuart (eds.), *Neural control of locomotion*, pp. 203–236. Plenum, New York.
 Jayes, A. S. and R. McN. Alexander. 1980. The gaits of chelonians: Walking techniques for very low speeds. *J. Zool.* 191:353–378.
 Kuo, A. D. 1999. Stabilization of lateral motion in passive dynamic walking. *Int. J. Robotics Res.* 18:917–930.

- Lee, D. V., J. E. A. Bertram, and R. J. Todhunter. 1999. Acceleration and balance in trotting dogs. *J. Exp. Biol.* 202:3,565–3,573.
- Martinez, M. M. 2001. Running in the surf: Hydrodynamics of the shore crab *Grapsus tenuicrustatus*. *J. Exp. Biol.* 204:3,097–3,112.
- McGeer, T. 1990a. Passive dynamic walking. *Int. J. Robotics Res.* 9(2):62–82.
- McGeer, T. 1990b. Passive bipedal running. *Proc. Roy. Soc. B* 240:107–134.
- McGeer, T. 1993. Dynamics and control of bipedal locomotion. *J. Theor. Biol.* 163:277–314.
- McGhee, R. B. 1968. On the stability properties of quadruped creeping gaits. *Math. Biosci.* 3:331–351.
- McMahon, T. A. 1984. *Muscles, reflexes and locomotion*. Princeton University Press, Princeton, New Jersey.
- Nashner, L. M. and M. Woollacott. 1979. The organisation of rapid postural adjustments of standing humans: An experimental-conceptual model. In R. E. Talbot and D. R. Humphrey (eds.), *Posture and movement*, pp. 243–257. Raven Press, New York.
- Nigg, B. M. 1986. *Biomechanics of running shoes*. Human Kinetics, Champaign, Illinois.
- Papantoniou, V., P. Avlaktiotis, and R. McN. Alexander. 1999. Control of a robot dinosaur. *Phil. Trans. Roy. Soc. B* 354:863–868.
- Raibert, M. H. 1986. *Legged robots that balance*. MIT Press, Cambridge, Massachusetts.
- Walker, W. F. 1971. A structural and functional analysis of walking in the turtle *Chrysemys picta marginata*. *J. Morph.* 134:195–214.
- Woledge, R. C. 1968. The energetics of tortoise muscle. *J. Physiol.* 197:685–707.