Gaits of Mammals and Turtles

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動物はその大きさや移動に使用する脚数にかかわらず、ほぼ同一のフルード数 v^2/gL (v : 歩行速度, L : 脚長) で歩容を変化させる。本解説ではこの歩容の変化をエネルギー消費の観点から説明している。まず人間の歩行から走行への歩容変化について考え、筋肉のバネ特性を考慮したモデルを用いて解析し、足底圧の変化については実験データとの対比を行っている。歩行においては、運動エネルギーと位置エネルギーの交換により消費エネルギーが節約され、また走行においては、運動エネルギーとバネに蓄えられるエネルギーの交換により消費エネルギーが節約されていることを強調している。かめを含む4足歩行動物についても同様の解析を行い、ウォーク、トロット、ギャロップについて論じている。

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1. Introduction

Legged animals are walking robots whose designs have been optimized by millions of years of evolution by natural selection. Theoretical analyses of walking and running by animals may be equally applicable to robots, and the study of animals may generate ideas that are useful to roboticists.

There are two large groups of legged animals, the arthropods (insects, crabs, spiders etc.) and the land vertebrates (amphibians, reptiles, birds and mammals). This review is concerned mainly with mammals, but also considers the turtles because the slowness of their walking raises a special problem. These relatively large animals seem more likely to present useful hints for robot design than the generally small arthropods.

Mammals such as dogs and horses walk to go slowly, trot at intermediate speeds and gallop to go fast. Measurements of the oxygen consumption of horses show that each gait is the most economical of energy in the range of speeds in which it is used¹⁾. This paper asks why.

An animal travelling steadily over level ground does very little net work, because frictional losses are small. However, its muscles do positive work

at some stages of the stride and negative work (degrading mechanical energy to heat) at others. We will adopt the hypothesis that gaits have evolved to minimize the positive work required of the muscles. This may be over simple, because muscles use metabolic energy wherever they exert tension, even if they do not shorten and so do no work. The relationship between muscle force, work and metabolic energy cost is not fully understood²⁾.

2. Description of gaits

When a horse changes from walking to trotting or from trotting to galloping, it obviously changes its pattern of movement. We need means of describing such changes quantitatively. Also if we are to make generalisations that will apply to animals of very different sizes (for example, both to cats and to camels) we must describe gaits in dimensionless terms.

Gravitational forces are important in walking and running. Therefore, geometrically similar systems of different sizes can walk or run in dynamically similar fashion, only if their speeds are such as to make their Froude numbers v^2/gL equal³⁾. Here v is the speed of travel, g is the acceleration of free fall and L is leg length. Animals of different sizes are not precisely geometrically similar, but observations of mammals ranging from small rodents to rhinoceros show that

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most change from walking to trotting at a Froude number of about 0.5 and from trotting to galloping at a Froude number of 2.5³⁾. Thus camels, with legs nine times as long as cats, make corresponding gait changes at about three times the speed of cats. It will be convenient to use Froude numbers to describe speed.

Different gaits involve the feet exerting different patterns of force on the ground. Consider a foot that is set down at time $-T/2$ and remains on the ground until time $T/2$. If the vertical component of the force that it exerts on the ground is symmetrical in time its value at time t in that interval can be approximated by the truncated Fourier series

$$F = A(\cos(\pi t/T) - q \cos(3\pi t/T)) \quad (1)$$

where A and q are constants. The factor q is known as the shape factor. Its values are restricted to the range -0.33 to $+1.00$, because F cannot be negative. Negative values of q describe bell-shaped graphs of force against time, as for human running (Fig. 1 (d)) and large positive values describe markedly two-humped graphs, as for fast walking (Fig. 1 (c)).

A stride is a complete cycle of leg movements, in which each foot moves forward once. Stride length is the distance travelled in a stride. The duty factor of each foot is the fraction of the stride duration for which it remains on the ground. The relative phase of each foot is the time at which it is set down, expressed as a fraction of a stride after the setting down of an arbitrarily chosen

reference foot. To avoid making mirror-image gaits seem very different from each other, the reference foot may be defined as whichever fore foot is set down less than half a stride before the other.

3. Bipeds

In walking and running the feet are set down alternately with relative phases 0, 0.5. When kangaroos hop the feet are set down together with relative phases 0, 0. Humans walk to go slowly and run to go fast. Similarly, kangaroos shuffle along at low speeds, using all four legs and the tail, but hop at higher speeds. In each case the gait change is made at a Froude number of about 0.5⁴⁾.

In walking, the duty factors of the feet are greater than 0.5 so there are double-support phases when both feet are on the ground. In running, however, the duty factors are less than 0.5 so there are aerial phases when both feet are off the ground. Another difference between human walking and running is that the shape factor q (equation (1)) has positive values in walking (higher values at higher speeds) and negative values in running (Fig. 1). A consequence of these differences in shape factor and duty factor is that in walking, the total ground force (exerted by both feet) is maximal in the double support phase and minimal as the centre of mass passes over the supporting foot: whereas in running the ground force is maximal as the centre of mass passes over the supporting

Fig. 1 Records of the vertical component of the force exerted on the ground by one foot of a 70 kg man (a), walking at 0.9 m/s; (b), walking at 1.5 m/s; (c), walking at 2.1 m/s; and (d), running at 3.6 m/s. Shape factors are (a) 0.22, (b) 0.36, (c) 0.55 and (d) -0.07 . From ref. 10.

foot. Therefore, the height of the centre of mass is maximal as it passes over the supporting foot in walking, but minimal at the corresponding stage in running.

Both in walking and running, and also in kangaroo hopping, the force on each foot is kept roughly aligned with the leg, while the foot is on the ground. Thus the horizontal component of this force tends first to decelerate the body, and then to accelerate it, during each footfall. Thus the speed of travel passes through a minimum as the centre of mass passes over the supporting foot.

The effect of these fluctuations of height and speeds is that in walking the body's potential energy rises as its kinetic energy falls and vice-versa. Some energy is inevitably lost at each impact of a foot with the ground⁵⁾, but little work is needed during the remainder of the stride as energy is swapped back and forth between the kinetic and potential forms. In running, however, kinetic and potential energy rise and fall together. In this case, the work required of the muscles can be reduced by springs which store (as elastic strain energy) the kinetic and potential energy lost at one stage of the stride and return it later by elastic recoil.

The leg's most important springs are tendons, especially those of the gastrocnemius and (in non-human mammals) plantaris muscles. In tests at physiologically relevant strains and strain rates, the elastic recoil of tendon returns about 93% of the energy used to stretch it⁶⁾. The arch of the human foot is another important spring, giving about 78% energy return⁷⁾.

In running humans and hopping kangaroos, stretching and recoil of the Achilles tendon accounts for about half of the length changes of the gastrocnemius while the foot is on the ground^{7,8)}. Because the muscle fibres need to lengthen and shorten only a little, they can be relatively short, for example about 5 cm in humans. This presumably saves energy because the metabolic cost of maintaining given tension in a short muscle fibre is less than for a long one. Much more striking adaptations of this kind are found in ungulate

mammals. For example, the plantaris muscle of the camel has muscle fibres only 1-3 mm long in a 1.3 m tendon⁹⁾. The length changes of this muscle-tendon complex must be due almost entirely to the elastic compliance of the tendon.

Fig. 2 shows energy costs of running for a mathematical model biped, using different gaits¹⁰⁾. The model has springs of realistic compliance in series with the actuators that represent its muscles. Each graph refers to a different speed. In each the horizontal axis shows duty factor, with low duty factors (as in running) on the left and high ones (as in walking) on the right. The vertical axis shows shape factor, with low values (as in running) at the bottom and high ones (as in fast walking) at the top. The contours on each graph show the positive work performed by the actuators, in travelling unit distance.

At low speeds (Fig. 2 (a)) the graph shows two work minima, one of them (left) for a very slow run and the other (right) for a walk. The optimal run involves a very low duty factor (implying very large ground forces) and would probably not be feasible, leaving the optimal walk as the best feasible gait for this low speed. As speed increases (Fig. 2(b)) the shape factor for the optimal walk increases: similarly, people walk with larger shape factors as they increase speed (Fig. 1). Eventually, as speed increases the walking optimum disappears and running is the best gait (Fig. 2(d)). At this speed, the optimal duty factor for running is higher than at lower speeds and may be attainable, but people actually run with larger duty factors than the theory predicts.

Humans, increase their stride length S as they increase speed, approximately according to the equation

$$S/L = 2.5(v^2/gL)^{0.3} \quad (2)$$

(ref. 10. L is leg length and v^2/gL is the Froude number, as before.) The graphs in Fig. 2 assumed this relationship between Froude number and stride length, but further investigation showed that the stride lengths predicted by equation (2) were close to optimal. Measurements of the oxygen consumption of people walking on a treadmill showed that

Fig. 2 Work done by the actuators of a model biped in different gaits. Each graph shows duty factor (horizontal axis) and shape factor (vertical axis) with contours showing work per unit distance (arbitrary units). Graph (a) corresponds to a speed (for a biped of adult human size) of 0.4 m/s, (b) to 0.8 m/s, (c) to 1.2 m/s, (d) to 1.6 m/s, (e) to 2.0 m/s and (f) to 2.4 m/s. From ref. 10.

their preferred stride length was the one that minimized metabolic costs, at each speed¹¹⁾.

4. Quadrupeds

A quadruped can be statically stable at all stages of its stride if it lifts only one foot at a time, and chooses the order in which the feet are lifted so as to keep the centre of gravity always over the triangle of support. Unless the duty factor is extremely high (over 0.83), only one sequence of foot movement is possible: left fore, right hind, right fore, left hind¹²⁾. This is the sequence in which horses, dogs etc. move their legs when they walk, but it seems doubtful whether static stability is important for them.

It would seem more likely to be important for turtles than for other quadrupeds. This is because they use very low stride frequencies, so unwanted displacements due to departures from equilibrium cannot be quickly corrected; and their bodies are low slung, so a small unwanted displacement is enough to make the carapace hit the ground. This point can be quantified by calculating the dimensionless number $n(2L/g)^{1/2}$ where n is stride fre-

quency, L is leg length and g is the acceleration of free fall. This number represents the number of stride periods required for the body to fall to the ground, if the legs suddenly ceased to support it. It is 0.05 for a turtle with 5 cm legs walking with a frequency of 0.5 Hz; 0.4 for a dog with 50 cm legs walking very slowly at 1.2 Hz; and higher for the dog travelling faster. It is much more necessary for the turtle to maintain near-equilibrium throughout the stride than for the dog.

This suggests that the turtle should move its legs in the sequence given above, not lifting the next foot until the previous one has been set down. Turtles do indeed move their feet in that sequence, but at unequal intervals, so that for parts of the stride the body is supported by only two diagonally opposite legs¹³⁾.

If the turtle were to maintain equilibrium throughout the stride it would have to move its feet one at a time, and the forces they exerted on the ground would have to make large, instantaneous changes whenever a foot was lifted or set down. No muscle can make a change of force instantaneously, and turtle leg muscles are particularly

slow. (Their slowness makes them unusually economical of energy). Because the leg muscles are slow, departures from equilibrium inevitably occur in the course of each stride: the animal must rise and fall, pitch and roll. Mathematical analysis showed that to minimize these unwanted displacements, the feet should be set down at unequal intervals. The optimum timing depends on how slow the muscles are, but it seems likely that the turtle's gait is near-optimal for its muscles¹³.

Quadrupedal mammals generally walk at Froude numbers below 0.5, using the footfall sequence given above. At Froude numbers between 0.5 and 2.5 most of them trot, setting down diagonally-opposite feet simultaneously (left fore with right hind, right fore with left hind). Duty factors and shape factors for trotting are similar to those used in human running, and a trotting quadruped resembles two bipeds running one behind the other. Galloping, however, used at Froude numbers above 2.5⁹, is a distinctively quadrupedal gait.

In galloping, the two hind feet are set down in rapid succession, and then the two fore feet. This footfall pattern makes it possible for bending and extension of the back to aid locomotion. As the fore feet move forward (with the hind feet on the ground) the back extends and as the hind feet move forward (with the fore feet on the ground) it bends. At the stage in the stride when the back is most strongly bent, the fore legs have swung back and are about to swing forwards, and the hind legs have swung forward and are about to swing back: both pairs of legs have to lose and regain kinetic energy. Much of this energy is stored briefly as elastic strain energy in a sheet of tendon, the aponeurosis of the principal extensor muscle of the back¹⁴.

The advantage of the gallop seems to be that it makes possible this energy-saving mechanism. It becomes preferable to symmetrical running gaits such as the trot only at high speeds because the kinetic energy fluctuations associated with leg movements become larger, relative to other kinetic and potential energy changes, as speed increases¹⁵.

5. Conclusion

This short review has shown how gait choice affects the energy cost of locomotion. Walking, taking advantage of the pendulum principle of exchange between kinetic and potential energy, is the most economical gait at low Froude numbers (dimensionless speeds). Trotting or bipedal running is better at intermediate Froude numbers and, for quadrupeds, galloping is the most economical gait at high Froude numbers. Both in trotting (or bipedal running) and galloping, energy is saved by exchanging energy back and forth between kinetic energy on the one hand and elastic strain energy on the other. Tendons are the most important energy-saving springs.

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