The Mechanics of Horse Legs
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The Mechanics of Horse Legs

Milton Hildebrand

Following two decades of growth and transition, functional morphology, the branch of biology that relates the form of animals to their manner of moving and eating, has emerged as a dynamic, experimental discipline. This field now integrates the study of structure at all levels with behavior, biomechanics, physiology, energetics (the transformation of energy), scaling (the relation between form and body size), paleontology, and evolution. Of the many locomotor and feeding mechanisms that could serve to illustrate the integrated nature of functional morphology, perhaps none is more dramatic than the legs of the horse (*Equus caballus*).

First, there is speed. Some horses can sprint at the gallop to nearly 70 km/hr, which is almost twice the speed of human athletes and probably faster than any other land animal of equal size. Harness pacers have run 0.8 km at 52.0 km/hr, and trotters the same distance at 49.7 km/hr. Horses and other equines also have great stamina: for example, a wild ass was chased in a car for 26 km at 48 km/hr, and one horse traversed 80 km at 18.2 km/hr. Maneuverability is another important skill of mounts used for dressage, polo, and herding cattle. Other breeds are trained to pull or carry great loads. How are their legs adapted to give horses such speed, endurance, agility, and strength?

The horse's great running ability coupled with its large size place unusual demands on its legs. They must be longer, relative to the body, than the legs of most slower animals, yet they must oscillate very fast. They must also be relatively light, yet strong enough to deliver enormous thrust and to sustain tremendous loads. All of this must be done with sufficient economy of effort to provide endurance. It is evident that nature places greater demands on the mechanical design of horse legs than on the legs of most other animals, even including those of the faster but smaller cheetah.

Design for long, fast strides

A racing horse completes about 2¼ strides per second, which, although indeed a rapid pace for such large legs to achieve, contributes less to the horse's speed than might be imagined. The limiting factor to the rate of stride appears to be the physiological constraints on the rate at which muscle fibers can shorten. Maximum rates

The coordinated functions of the legs as oscillating levers, powered struts, springs, and cushions provide remarkable speed, endurance, and maneuverability

vary among animals and muscles, and they vary among the several types of fibers found in differing proportions in each muscle. In general, the muscles of large animals, like horses, contract more slowly than those of small animals; a dashing rabbit, for example, often completes more than 4 strides per second.

It would appear, however, that even without causing muscles to shorten faster, nature could have evolved faster legs for the horse through a number of mechanical principles. One of these would be by gradually shifting the insertions of leg muscles closer to the joints turned. By way of analogy, you could pull shut a lightweight door faster if the knob were shifted closer to the hinge side of the door, because a short pull of the hand would then swing the door through a wider arc. Although nature has to a degree done just that for certain muscles, this has not significantly increased the rate of stride. The reason is that shifting the muscles in this way increases the load on them and thus tends to *slow* their rate of contraction. That is, if your door were heavy, it would be hard to swing it shut using a knob near the hinges, because you would have to pull too hard to move it.

Another possible way for the horse to increase the rate of its stride comes to mind. Muscles can shorten farther (or faster, or both) the longer their fibers are. Animals like anteaters and chameleons, which project their tongues far out of the mouth, have very long tongue muscles. However, muscles are most efficient when they shorten little in doing their work. Horse muscles have normal proportions.

Another method of increasing velocity at the hoof is used in the foreleg with good effect. If loads are moderate, two muscles cannot turn the same bone much faster than one, just as two athletes cannot run twice as fast as one alone. However, if two muscles turn different leg segments in the same direction at the same time, then the independent velocities *can* be summed—you can ascend faster by walking up the escalator than by walking up the stairs. The shoulder blade of the horse (unlike ours) is oriented vertically and, as there is no collar bone to anchor it, it is free to turn, adding its rotational velocity to those of other leg segments (though for want of a method, the arc of its travel has not yet been measured). However, even though this method of increasing velocity is effective, it does not go far to

explain the horse's impressive running speed.

Speed of travel is the product of rate of stride (defined as a full locomotor cycle) and length of stride. And it is in length of stride that the horse excels. As for most mammals adapted to running, rate of stride increases as the animal accelerates to moderate speed, but thereafter it is mostly an increase in the length of the stride that carries the animal to maximum velocity. The stride of a racing horse commonly measures 6.4 to 7.5 meters. How can the stride be so long?

To achieve a long stride an animal must have long legs. However, it would be counterproductive to gain long legs merely by increasing body size equally in all dimensions over those of the ancestor. For geometrically similar objects of different size, mass varies as the cube of the difference in linear dimensions. The large animal might even be slower than the small ancestor because its long legs would carry prohibitive loads. The legs must instead become long relative to the remainder of the body. Comparing leg length to chest-rump length, we

find that the legs of horses are proportionally longer than those of its closest relatives (rhinoceroses and tapirs), longer even than those of the cheetah, and similar to those of the greyhound. Perhaps their length is optimum; if they were even longer there would be interference between forelegs and hind legs. As it is, horses sometimes strike a forefoot with a hind at a fast trot and must straddle the fore with the hind at the gallop (giraffes are unable to trot at all because their legs are so long).

For reasons to be explained below, it was the anatomical equivalent of the human foot and toe that elongated the most as the horse family evolved longer legs. The foot increased not only in length relative to other leg segments, but also in functional length as a consequence of a change in foot posture, bringing wrist and heel high off the ground, as illustrated in Figure 2. We humans stand higher when we rise on the ball of the foot (the usual stance of dogs and of the first horses), and even higher if (with ballet slippers) we stand on the
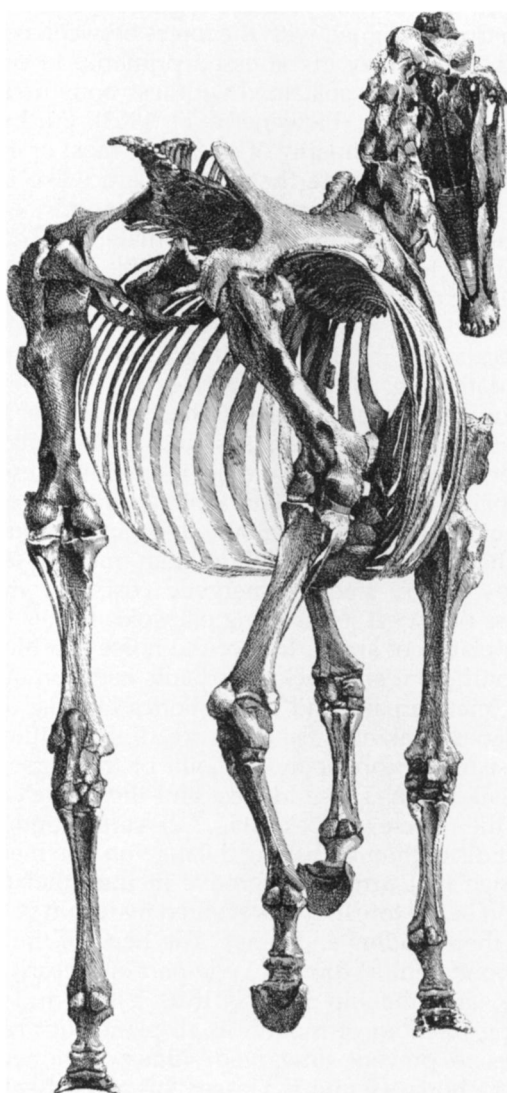

Figure 1. Although the horse has long been appreciated as a magnificent running machine, studies of its functional morphology have only recently begun to reveal the array of biomechanical adaptations for speed and endurance that have evolved in the horse's anatomy, particularly in its legs. (From *The Anatomical Works of George Stubbs*, reproduced courtesy of David R. Godine, publisher, Boston.)

ends of the toes, as modern horses do.

Horses increase stride length in another important way. The fast-trotting or pacing horse has two unsupported intervals in each cycle, totaling 35% to 43% of the duration of the stride. At a fast gallop the animal is off the ground once in each cycle, when the legs are gathered under the body, for 20% to 30% of the stride (Hildebrand 1959). In other words, horses lengthen their stride by jumping once or twice (according to gait) in each cycle.

Combining light weight with strength

Because it is costly in energy for an animal to maintain and transport itself, nature tends to limit the amount of each tissue and the size of each part to that which is actually needed. True, some tissues are relatively cheap; whale blubber, for example, has a low metabolic rate and, although it must be propelled, does not need to be supported in its buoyant environment. The most costly materials are those that have high metabolic rates (like active leg muscles), are heavy (like leg bones), or change velocity rapidly (like oscillating legs). Clearly, horse legs should be designed (and are designed) to be as light as possible, and to distribute their weight in an economical manner.

For muscle, tendon, and bone, "as light as possible" cannot represent only the amounts needed for usual activities, but instead must be those needed to sustain loads encountered in falls and jumps, and in sudden starts, stops, and turns. The largest bone of the forefoot, the metacarpal or cannon bone (Fig. 3), has a safety

thigh bone (femur)

stifle joint

shin bone (tibia)

hock joint

cannon bone
(metatarsal)

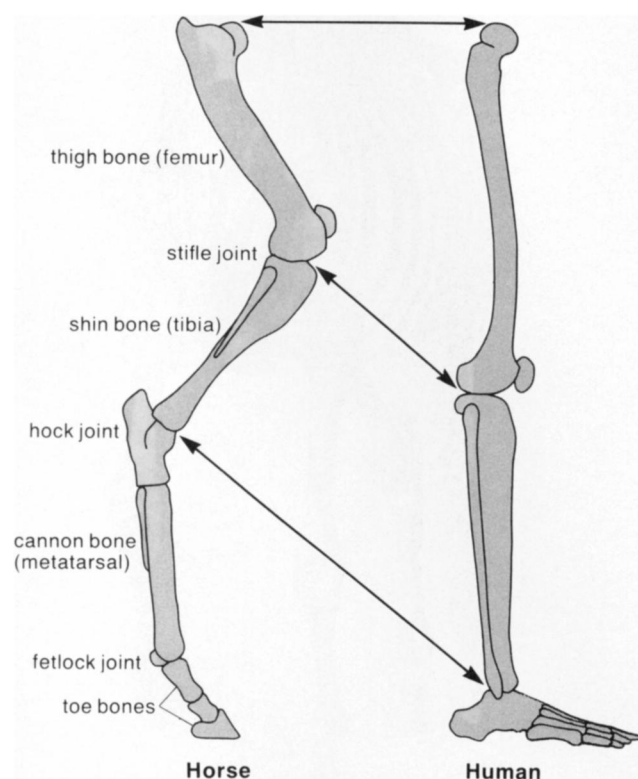fetlock joint

toe bones

Horse   Human

Figure 2. Horses and humans both have evolved a long stride with legs that are long relative to the body. In humans, this elongation has involved the lengthening of thigh and shin segments; in horses, the foot has lengthened and its posture altered so that the heel (or hock) is high above the ground.

factor of 3 to 4 for a steady gallop, and of 2 to 3 for a more demanding jump (Biewener et al. 1983). Nevertheless, when performing under unnatural conditions imposed by man, the lower leg, which is most at risk, does sometimes fail, either gradually or violently.

What structural adaptations bring the horse leg to its narrow balance between a light enough weight and adequate strength? Horse legs are adapted to swing primarily front and back—stand beside its hip and the animal cannot kick you. Muscles that we use to spread and close the legs have been reduced in the horse or turned to another purpose. The horse can scarcely toe in or out, and cannot rotate the lower leg (as we do in turning the palm up). It has but one digit on each foot, along with vestiges of two others (see Fig. 3); hence, there can be no manipulation. All muscles and bones associated with these actions have been lost, with a saving of much weight—particularly in the lower leg where, as we shall see, the saving is most beneficial.

The remaining digit is much larger than any of the five of the ancestrally remote foot. It can sustain loads that would have fractured several of the ancestral toes. When the legs are supporting weight, the cannon bones remain closely aligned with the forces between body and ground. Thus, they are stressed primarily in compression, which can be sustained with less bony tissue than tension or bending (Biewener et al. 1983). Furthermore, because stress is primarily of one kind, most of the bony spicules that constitute the porous, lattice-like interiors of the cannon bones can be oriented lengthwise to give adequate bracing with the least material (Thomason 1985). In order to withstand comparable bending forces it would be necessary to have more bracing spicules, and for these to arch in various directions.

Because of its large size, the running horse places more deflecting forces on its legs (in turning, or in stepping on angled surfaces) than do many smaller, slower animals. Yet its musculature, being adapted to function largely in one plane, is, if anything, less suited to stabilize the joints. This animal instead employs mechanisms that are better suited for speed and endurance, because they are lighter than muscles and are passive—hence, free of energetic cost. For example, whereas our wrist joint, being ellipsoid, allows motions in two planes of space, that of the horse is a hinge that turns only front and back. The joints between our palm bones (metacarpals) and finger bones likewise work in two planes (making a fist and spreading the fingers), in contrast to the corresponding joint of the horse, which again is a hinge. These hinges, and those at elbow and heel—the horse's hock (Fig. 2)—are strengthened against dislocation by having a flange on one member of the hinge that turns in a groove in the other (Fig. 3). Rotation of the forearm is prevented by fusion of the two bones there (radius and ulna). The head of the human thigh bone (femur) forms a large part of a nearly perfect sphere, and the hip joint is thus a ball and socket, allowing freedom of motion in all planes but requiring muscles to prevent unwanted sideways motions. The head of a horse's femur is a lesser part of a sphere, and is somewhat cylindrical on top (with axis transverse to the body), thus passively restricting motions that are not front and back.

Horses also have remarkable mechanisms for pos-

tural support that are passive and that therefore save both the weight and fuel cost of the muscles which would otherwise be required. The hock joint and stifle joint—corresponding to the human knee—are moderately flexed as a horse stands at rest. Accordingly, the leg tends to collapse under the animal's weight. This is prevented by a locking mechanism. As illustrated in Figure 4, the shin bone (tibia) on one side, and a tendon that evolved from a flexor muscle on the other side, form the long arms of a parallelogram that is completed by the width of the knuckle of the femur and by the heel bone. The four angles of the parallelogram must change simultaneously so that if one cannot move, none can move. The patella, or kneecap, which is anchored to the tibia by several strong ligaments, and which normally slides in its patellar groove as the stifle flexes, can be pulled by a special slip of muscle behind an eminence above the inner border of the patellar groove when the joint is extended. The patellar ligaments then hold the joint against collapse, effectively locking the stifle and hock joints in place. (It is noteworthy that cloven-footed mammals also have this mechanism—seemingly as the result of convergent evolution.)

Another lightweight, passive support mechanism is provided by the lateral ligaments of the hock and elbow joints. These are positioned so as to be shortest when the joints are in the open and closed positions, thus making these positions stable. The ligaments are stretched when the joints are in intermediate positions, making them unstable. When in the open position, such a joint (called a snap joint) will not collapse without the application of force. Unfortunately, the turning force (or torque) needed has not yet been measured, so we do not know the importance of the mechanism for maintaining posture. The angled fetlock joint near the hoof is also prevented from collapsing by a system of suspensory ligaments, as will be described in another context below.

Inertia, energetics, and endurance

The effort required for an animal to run increases rapidly with its mass and thus its inertial resistance to acceleration and deceleration. The energetic cost of the motion of an animal, or of its parts, relates to the mass and square of the velocity (linear for the whole body, or angular for oscillating parts). Furthermore, if body size is doubled without change of proportions, the strength of muscles and tendons increases four times (the square of the degree of difference), whereas the masses loading them increase eight times (the cube). These considerations make it clear why various small animals, such as foxes, can run fast and far without marked structural modifications for speed and endurance, whereas the massive horse requires just the right form and function to achieve the same ends. Horses must be as economical as possible in the expenditure of energy.

A first way to conserve is to reduce or eliminate nonessential oscillations. For example, passive mechanisms resulting from joint configurations and constraining ligaments hold the spine of a running horse relatively rigid. In contrast, cheetahs, greyhounds, and rabbits flex and extend their backs as they gallop, which benefits their speed in several ways, but which is costly—these animals are not endurance runners. Likewise, the small-

er speedsters lift their legs high during the unweighted phase of their cycles: the hind foot of the cheetah rises (on its follow-through) higher than the knee, and the wrist (before coming down) nearly as high as the elbow. Horse legs have more conservative trajectories.

We have seen that to achieve a long stride the galloping horse is unsupported for about one quarter of each cycle and so must accelerate its mass upward for each jump in order to avoid falling. This is costly, but smaller runners are more extravagant: the dashing cheetah is off the ground half the time. Horses have relatively much less vertical displacement of the body than cheetahs (Hildebrand 1959).

Even when there is no unsupported interval, as at the walk or easy trot, a horse must raise part of its weight four times in each cycle, as the forequarters and hindquarters vault up and over the supporting legs in sequence. (Our hips also rise and fall when we walk.) A mathematical model that relates speed and gait to the cost of repeatedly lifting the body has been developed by R. McNeill Alexander at the University of Leeds and was summarized by him in *American Scientist* (1984). A team at Harvard quantified the cost to horses (Heglund et al. 1982). The cost is less than predicted by the model (as Alexander also explained), because the fetlock joints are most flexed when the respective legs are about vertical, as illustrated in Figure 5, thus shortening the legs just when needed to reduce the lifting. (This is like the pole being shortened at the top of the vault.)

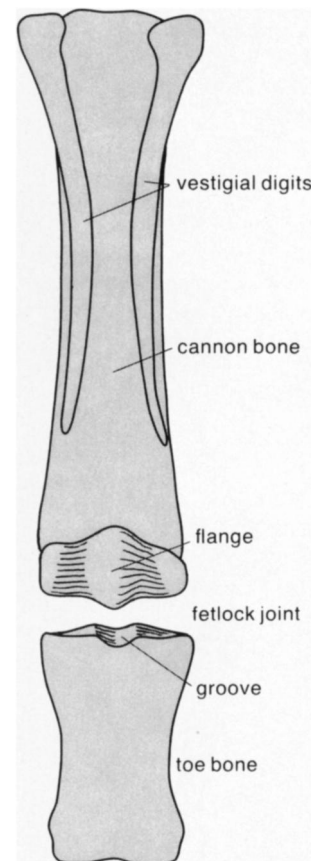Furthermore, and more important, horses recycle

Figure 3. The fetlock joint is functionally a hinge between the cannon bone (evolved from the ancestral palm bone of the third digit) and the uppermost toe bone. This hinge is strengthened by a flange on the cannon bone that turns in a groove in the toe bone.

much mechanical energy instead of dissipating it as heat. There are three principal mechanisms for doing this: one stores and releases spring energy, and functions at faster rates of travel. The other two cycle between kinetic energy and potential energy, and both function at slower rates of travel, with one applying to the weighted and the other to the unweighted phase of the leg cycle. We start with the last, when the leg is swinging forward.

A simple pendulum is a ball that is suspended by a virtually weightless cord and swings to and fro under the pull of gravity. The potential energy it has at the top of its swing is converted to kinetic energy at the bottom of the swing, and back to potential energy as it rises again. It would oscillate forever if friction and air resistance could be eliminated. The period, or duration of its cycle, depends only on the length of the cord, not on the weight of the ball.

A leg can also be a pendulum, though not a simple one because it has an irregular shape and its mass is not concentrated in one place. Its radius of gyration becomes the distance from pivot at hip or shoulder to the center of oscillation, which is the imaginary place where the mass of a simple pendulum would be located to have the same period as the leg. Because of the serious practical difficulties in measuring the period of a leg-pendulum directly, I instead approximated the natural periods of legs of various proportions by calculating their centers of oscillation using geometric models, as illustrated in Figure 6 (Hildebrand 1985). Comparing the results with the walking cycles of a range of mammals as recorded on film

Figure 5. The fetlock joint, shown here in three successive positions, flexes sharply when the leg of the running animal is vertical (position 2), thus reducing the effective length of the leg. The suspensory, or springing, ligament behind the joint cushions impact and recycles spring energy.
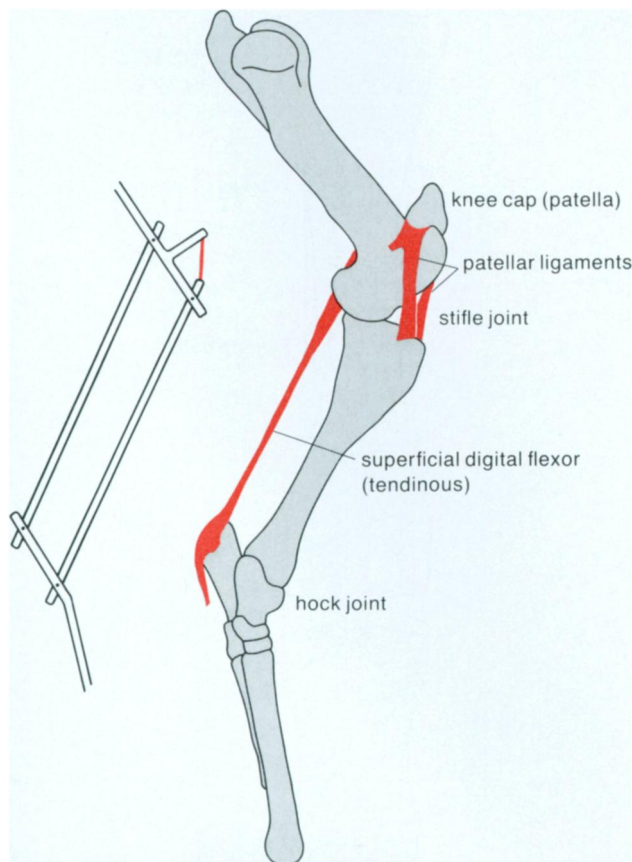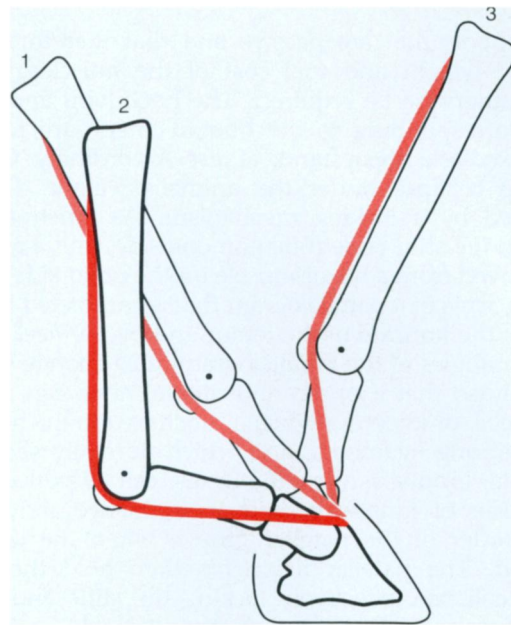

Figure 4. When a horse is at rest, the stifle and hock joints are passively supported against collapse by locking one of four angles of a parallelogram. The stifle cannot flex because the knee cap, anchored by ligaments to the shin bone, holds the joint open.

showed that, as expected, mammals tend to walk at close to the natural periods of their legs. Although no animal always walks at exactly the natural period of its legs, it can still recycle energy; if the actual period of the leg is between $\frac{2}{3}$ and $1\frac{1}{4}$ times the natural period, which includes most walks, easy trots, and slow gallops, the saving should be substantial ("should," because the saving was not measured directly).

Turn now to the support phase of the leg cycle. When a foot touches down, the leg is angled forward from hip or shoulder (Fig. 7). As the body advances until the leg is vertical, it slows, losing kinetic energy but also vaulting upward and gaining potential energy. Then, as the stride continues, the body arcs downward again, reconverting to kinetic energy. Cavagna and his associates (1977) showed experimentally that the phasing of all events is as required, and that at intermediate walking speeds the recovery of energy reaches 35% to 50% for dogs, sheep, and monkeys. Horses probably have corresponding benefit, although this has not been demonstrated. (Vertical displacement, and hence conversion between potential and kinetic energy, is reduced by flexing of the fetlock at midstride.)

Now, the springing device. As Figure 8 shows, a strong ligament arises from the back of the upper end of the cannon bone, divides near the lower end of that bone, passes around both sides of the fetlock joint, and attaches to the front of the last toe bone. A study of scars on the bones of fossil horses has shown that this ligament, called the suspensory or springing ligament, evolved from an ancestral foot muscle (Camp and Smith 1942). The tendons of two powerful muscles that flex the toe also run behind the foot: the tendon of the deep flexor has a strong tie (the check ligament) to the upper end of the cannon bone; and the tendon of the superficial flexor is in part continuous with ligamentous bands that go without interruption to bones higher in

the leg (radius for foreleg, femur for hind leg).

All of these ligaments and tendons stretch under load, and all are highly elastic, snapping all the way back to the original length when the load is removed. All of them pass behind the pivot of the fetlock hinge and hence must stretch when the impact of the body weight on the supporting foot bends the fetlock—nearly to the ground in fast travel (Fig. 5). During the second half of the support phase (the impact having been checked) these powerful elastics shorten, thus straightening the fetlock and giving the body forward and upward impetus. Alexander and Dimery (1985) have shown that for donkeys, the recovery of energy at a trot is close to optimum. This extraordinary mechanism cushions impact, enabling leg bones to be lighter, supports the angled fetlocks on resilient stirrups, and recycles energy during fast locomotion.

In the hind leg there appears to be a remarkable adjunct to this mechanism (Wentink 1979). A muscle in front of the shin (peroneus tertius, Fig. 8) has a tendinous core, which is stretched as the hock is extended just before the hoof lifts off the ground, only to snap back, like an echo, at the start of the foreswing, thus passively giving the hock the flexion needed as the hoof starts to move forward.

Another mechanism, not reported heretofore for horses, conserves angular momentum by exchanging it between segments of the foreleg. Since the oscillating legs constantly start and stop the direction of their rotation, reducing or saving angular momentum is important: angular momentum equals the mass of the rotating object, times its angular velocity, times the radius of gyration (see Fig. 6). If one variable decreases, another increases, as when the human diver tucks, decreasing the radius of gyration, and thereby increasing the spin of the body. For a series of linked segments, angular momentum is conserved between segments. The heavy handle of a cracking bullwhip imparts its momentum to successively lighter and lighter segments of the whip, which rotate ever faster, reaching the speed of sound at the tip. Similarly, at the trot and gallop, the heavy upper arm of the horse, pivoting at the shoulder, accelerates forward at the start of the swing phase of the leg (see Fig. 9). At midswing, however, it decelerates—sometimes, at an easy trot, even coming to a momentary stop—thus imparting its rotation to the lighter forearm, which then rapidly advances to its highest point. When that point is reached, and the "knee" (anatomical wrist) starts to descend, the upper arm accelerates again to complete its foreswing.

Horse legs are designed to economize on energy in yet another way. As noted above, in the evolution of long legs, it was the lower segments that lengthened. They are relatively light because they consist only of minimal bone, tendon, and hoof. The fleshy, heavy parts of the leg are close to the body. In that position they oscillate over shorter arcs; hence they move more slowly and need not be accelerated and decelerated as fast. The cost of moving the leg is low if the mass is concentrated close to the pivot at hip or shoulder, and high if the weight is shifted closer to the foot, as for a bear (Fig. 6). By way of analogy, if you grasp a mallet by its head, then, using the wrist, you can swing the handle end through a given arc quickly with relatively little
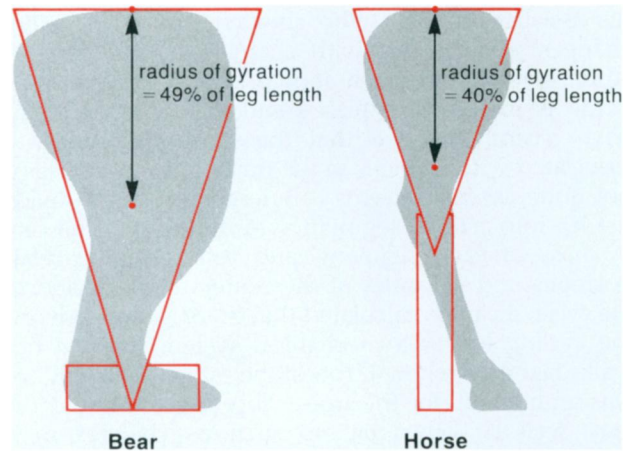

Figure 6. The weight of the hind leg of a horse is concentrated much higher on the leg than, for contrast, the weight of a bear's hind leg. This concentration reduces the horse leg's radius of gyration (approximated here), which is the distance from the pivot at the hip to the center of oscillation, and thus reduces its resistance to rapid acceleration and deceleration in running.

effort. If you turn the mallet over, hold it by the end of the handle, and swing the heavy head through the same arc, it is slower and more difficult. The weight distribution of the horse leg approaches that of the mallet turned head uppermost. Studies on other animals have shown that at high speed, leg conformation makes a big difference in the energy of the cycling system (Hildebrand and Hurley 1985).

Finally, another factor relates to the energetics of horses. In a short but important paper, researchers at Harvard (Hoyt and Taylor 1981) showed that ponies have, for each gait, a speed that is most economical for moving a given distance. When forced by an accelerating treadmill to move gradually faster, the animals come to a narrow range of speeds at which they can walk or trot, but prefer to trot, if not trained otherwise, because they use less energy at the trot. The same occurs (though to a lesser degree) at the trot-gallop transition. Why this is so is not entirely clear, but a clue is offered by Dušek and
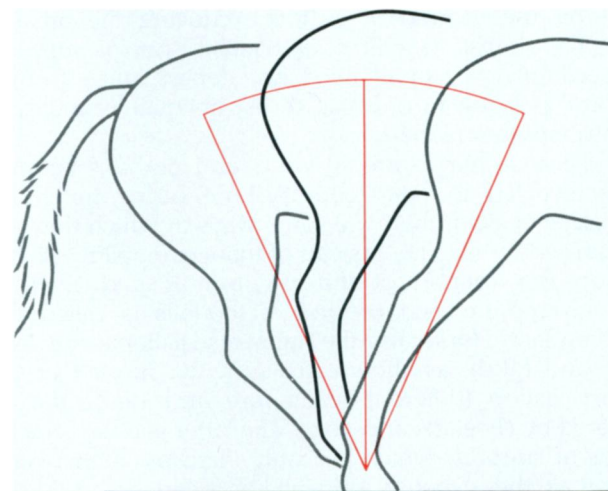

Figure 7. Walking horses recycle between potential energy, which is maximum when the supporting leg is about vertical, and kinetic energy, which is maximum when the leg is extended front and back. (The vertical displacement of the body is somewhat exaggerated here.)

his associates (1970), who showed that when a horse changes gait upward with changing speed, length of stride is reduced, which should save energy, as rate of stride is increased, which should use more energy. I have recently learned that these changes (which are associated with changes in the trajectories of the legs) do not quite cancel in terms of energetic cost: by dividing the leg into a three-segment system, locating the center of mass of each segment, and recording the relative positions and velocities of the centers at all positions of the cycle, it can be calculated that there is more energy in the cycling leg as a mechanical system when a horse walks fast than when it trots at the same speed. My work was ambiguous for the trot-gallop transition, and there may well be other factors such as changes in the recycling of energy, in the vertical displacement of the body, or in the thrusts required. In any event, horses (like humans) sense when it is best to change gaits.

Maneuverability and stability

Maneuverability is the capacity for rapid and controlled change in speed and direction. It is favored by small body size, because inertia increases with mass. Horses cannot be as agile as mice, monkeys, or dogs. Nevertheless, horses do well for such large animals.

Maneuverability and stability are both important for runners, yet they have opposed requirements. To be highly stable, an animal's center of mass should be low (as a short ladder is more secure than a tall one) and should be positioned over a large area enclosed by the supporting feet. Short or crouched legs, large feet, and a wide stance contribute. In order to maneuver, in contrast, it is necessary that the feet, as they come down, can thrust obliquely against the center of mass, pushing it away from a small area of support, and thus altering the speed or direction of the body. In this the horse is favored by its long legs, which keep its center of mass high, and by its small footprints, which reduce the area of support. Furthermore, walking and trotting horses place the feet so that the track along the line of travel is narrow, and fast-running horses have only one or two feet on the ground at a time, reducing the area of support almost to a line, or even a spot of support. Accordingly, a footfall need not depart much from a neutral position in order to thrust obliquely enough to contribute to a maneuver.

Because horses are so large, and perhaps because they evolved in open country, not caring much for dressage or polo, there are some ways in which they are optimized for stability instead of maneuverability. At the gallop, the second foot of a pair, fore or hind, to strike the ground in each couplet of footfalls is called the leading foot. Horses use the transverse gallop (same lead fore and hind), as shown in Figure 10, instead of the rotary gallop (different leads fore and hind) that is favored by cheetahs and dogs. The latter gait has smaller areas of support, which probably increases maneuverability at the expense of stability (Hildebrand 1980). Furthermore, in order to maintain support on a turn, a galloping animal must lead with its inside forefoot. This enables the successive footprints of the pair of feet to be closer to the curving line of travel than if the opposite lead were used. Dodging requires frequent and rapid
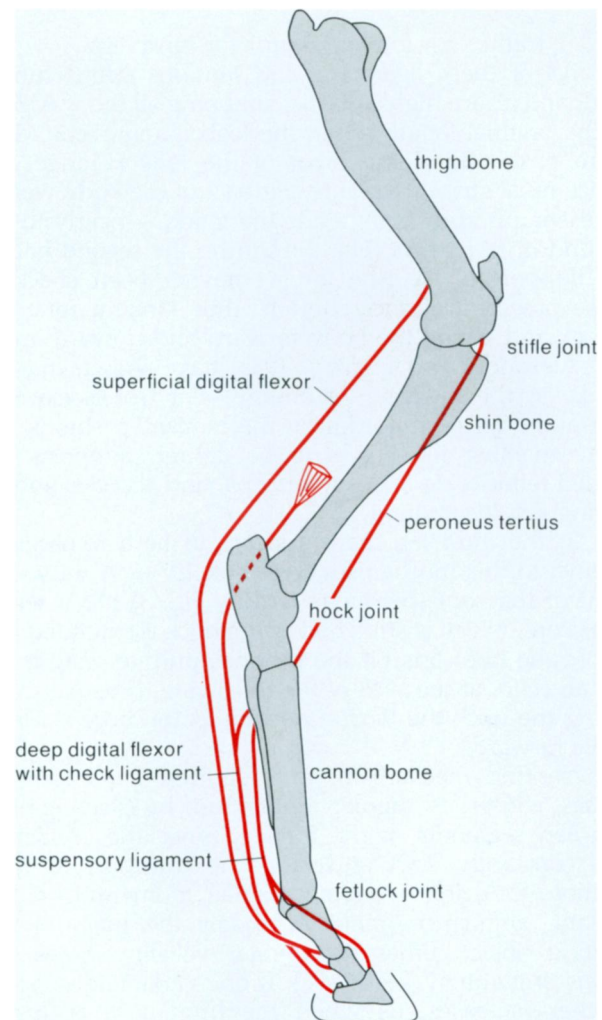

Figure 8. Ligaments of the hind leg form four integrated systems of elastic bands. They recycle energy by stretching when heavily loaded on impact in running, and then snapping back with great force. A similar mechanism functions in the foreleg.
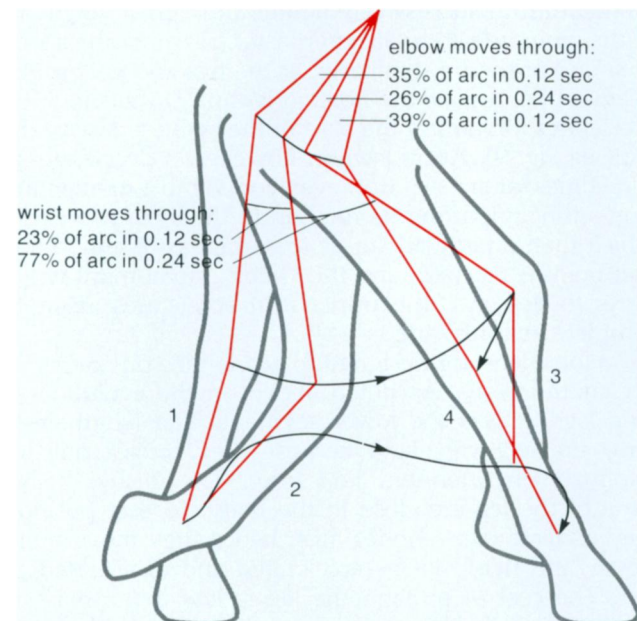

Figure 9. In the unweighted phase of its cycle, the upper arm of the trotting or galloping horse decelerates at midswing, and then accelerates again. While the upper arm is reducing its angular velocity, the lighter forearm accelerates to reach the high point of its trajectory, thus conserving angular momentum.
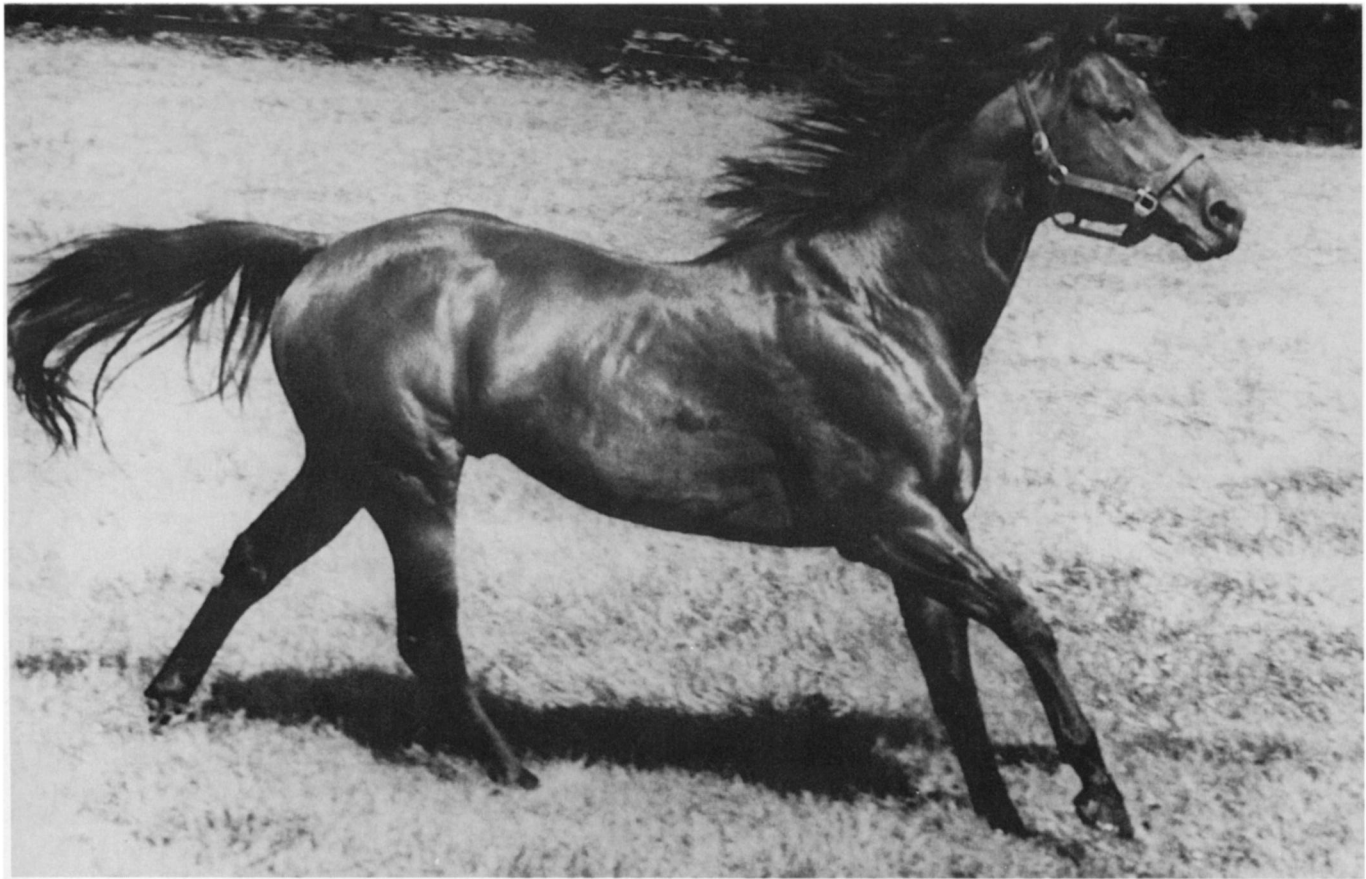
Figure 10. Horses use a transverse gallop, in which the leading foot is the same for the fore and hind pairs.

change of lead. Lead is changed by repositioning the feet when all feet are off the ground. The horse has one unsupported interval per stride, whereas fast carnivores have two. Foxes, wolves, and the big cats can dodge on shorter notice.

Virtually all of the analysis of the mechanics of horse legs reported in this article was unknown 20 years ago, and most was learned in the last 8 years. The tools necessary for the analysis have included high-speed cinephotography, stop-motion film analyzers, large treadmills, force plates, strain gauges, accelerometers, computers, digitizers, and the instrumentation of the physiology lab. We have learned much, but horses are still far ahead of us. We must test our guesses and refine our estimates, and surely there are many factors yet to be discovered. It is fascinating to study the functional morphology of any animal, and the more so for one so large, beautiful, and masterful as the horse.

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