

example, consider two conducting spheres of radius a in contact and exposed to an electric field E_0 oriented parallel to the axis joining them. The free static charge Q induced on each sphere can be shown to be

$$Q = \frac{\pi^2}{6} E_0 a^3 \quad (10)$$

Upon separation, one of the spheres will be positively charged and the other negatively. This mechanism is important in rain areas if collisions occur as frequently as our present estimates suggest.

On the cover of this issue a special case is shown in which one drop overtaking another accelerates it downward but is itself retarded. Such a specialized collision and recoil taking place in an impressed electric field induce free charges of opposite signs on the drops that later contribute to an increase in the magnitude of the impressed field. This special mechanism may be important in describing certain aspects of thunderstorm electricity.

The outstanding observed charac-

teristic of thunderstorm rain is the fact that nearly equal amounts of positive and negative free charge are brought down on the raindrops and, moreover, about half of the drops carry large positive charges whereas the other half carry large negative charges (4). We have shown further that on the ground below thunderstorms the charges brought down on the drops are related to their radii by an expression of the form of Eq. 10, but with a different coefficient (5). We are persuaded that this outstanding parallelism implies that raindrop collisions resulting in disruption play an important role in thunderstorm electricity.

Summary and Conclusions

The development of a practical method for serially and reproducibly dispensing pairs of medium or large water drops and arranging for their collision during free fall in synchronism with an electronic flash stroboscope has permitted a visual study of

the basic collision processes. The main collision types which are controlled by the relative kinetic energies include (i) elastic collisions resulting in drop recoil, (ii) collisions resulting in drop coalescence, (iii) collisions resulting in drop disruption, (iv) collisions producing drop spatter, and (v) hailstone collisions. In typical heavy rain, it is estimated that seven collisions occur for every kilometer of free fall. This is frequent enough to influence the drop size distribution and through inductive effects the electrical properties of the entire rain cloud.

Surface tension plays an important role in determining whether drops associate during collision, and its influence has been quantitatively estimated. Drop disjections by hail are of special importance.

References and Notes

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Symmetrical Gaits of Horses

Gaits can be expressed numerically and analyzed graphically to reveal their nature and relationships.

Milton Hildebrand

A gait is a manner of moving the legs in walking or running. The objectives of my research are to devise precise methods for describing and contrasting quadrupedal gaits, to survey the gaits of vertebrates, and to interpret the gaits used by particular species in relation to speed, body conformation, body size, maneuverability, and ancestry. This article presents results for the best-documented species, the horse. This master cursor has received particular attention because it is readily

available, its locomotion is more controllable than that of other animals, and at the hand of man it has learned to be versatile in the selection of gaits and also to use gaits (termed artificial) that are unnatural to the species and unique to itself.

In symmetrical gaits the footfalls of a pair of feet (fore or hind) are evenly spaced in time. The walk, trot, and pace are symmetrical. In asymmetrical gaits the footfalls of a pair of feet are unevenly spaced in time. The gallop is an example. All gaits are under study, but asymmetrical gaits, having

more variables, are more difficult to describe briefly and are not treated here.

In the 1880's, Muybridge triggered a battery of still cameras to take sequential photographs of the motions of 25 kinds of mammals (1). He noted that for each manner of moving, combinations of support by the several legs follow one another in a given sequence. Thus, for a walking horse, support by both hind legs and the right foreleg is followed by the left hind and right fore, which is followed by the left hind and both fore, and so on for five other support patterns before the cycle is repeated. I call any given sequence of this nature a *support sequence*. Muybridge recognized four principal support sequences for symmetrical gaits of horses. He represented each by a group of stylized diagrams (2) which, however, did not show the relative durations of the support provided by the various combinations of legs and did not assess variation.

Applications of this method have been somewhat extended (3), and one investigator attempted other correlations among the gaits (4). It is remarkable, however, that in spite of the advent of the motion picture camera

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and the appearance of scholarly papers on locomotion of arthropods (5), the study by Muybridge remained for 70 years the only significant contribution to the analysis of quadrupedal gaits.

From Film to Gait Formula

The raw material of this study is 368 meters of 16-millimeter motion-picture film. Twenty-six meters was taken under the auspices of the Horse Association of America and was exposed at 128 frames per second (normal speed is 16 frames per second). The remainder was taken by myself and was exposed at 64 frames per second. Sixty-eight different horses are recorded, including examples of the Belgian, Clydesdale, Arabian, Peruvian Paso, Thoroughbred, Quarter Horse, Morgan, Standardbred (pacers and trotters), American Saddle Horse (three- and five-gaited), Tennessee Walking Horse, Roadster, Hackney Pony, and Harness Pony. Elsewhere I have commented on the nature of suitable motion pictures and means of taking such pictures (6).

Since successive frames of motion pictures are virtually instantaneous records separated by known and equal intervals of time, the film can reveal the durations of the various events it portrays. Frame counts must be made as the film is examined one frame at a time. The notation I have adopted for recording the data has been illustrated (7, 8).

Verbal descriptions of gaits, even when complete and accurate (as most are not), are too cumbersome to lend themselves to analysis. A first step in developing a concise description of a gait is to identify independent variables that include all essential information with maximum economy. For the hind legs, one variable is the duration of the stride (a stride is one cycle of motion) and another is the duration of the contact that each foot makes with the ground in each stride. Symmetrical gaits have no other variables that relate to placing the hind feet down and lifting them again. The two variables identified are conveniently combined by expressing one in terms of the other. All the desired information about the hind legs can be expressed as the *percent of the stride interval that each hind foot is on the ground*. This parameter correlates with rate of

travel and is influenced by "animation" as explained below.

The duration of the stride for a foreleg equals that for a hind leg, and assuming for the moment the simplest case (usual for pleasure horses but not show horses), the duration of contacts of the forefeet with the ground in each stride is virtually equal to the duration of contacts of the hind feet. In short, all desired information about the forelegs is nearly identical with the corresponding information about the hind legs. No separate statement is needed for the forelegs.

It remains to relate the motions of the forelegs as a pair to the motions of the hind legs as a pair. The relationship is expressed as the *percent of the stride interval that the footfall of a forefoot lags behind the footfall of the hind foot on the same side of the body*.

The two percentage figures described, written in the order presented, constitute the *gait formula*. From the formula one can read out precise information regarding the sequence of footfalls, support sequence, and also (as explained in 8) the relative durations of the various combinations of support that make up the support sequence. These elements constitute a reasonably complete analysis of the gaits of most animals. The gaits of show horses are also characterized by the degree of elevation of the feet, reduction in relative duration of contact of forefeet with the ground, and high carriage of head and neck (these constitute "animation"), and by other matters of style.

From Gait Formula to Named Gait

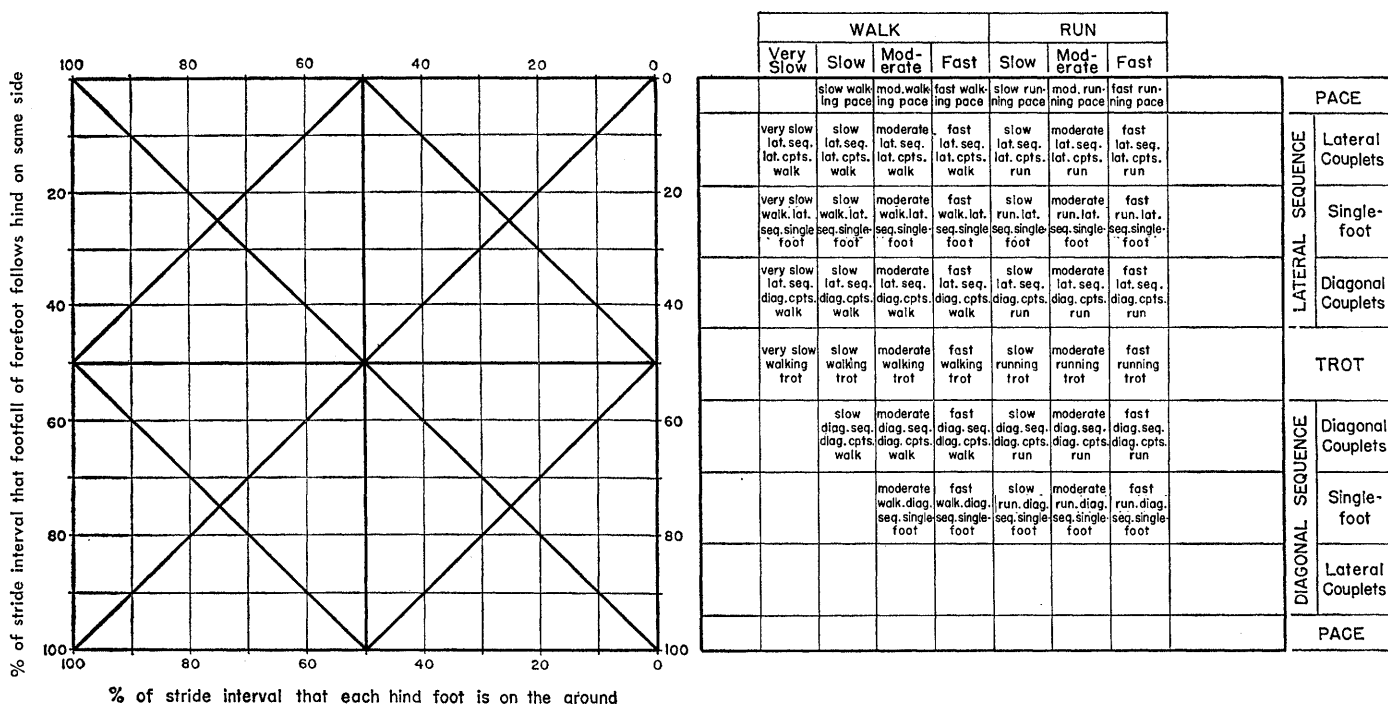
It was implied above that for symmetrical gaits consecutive strides are identical and, further, that the duration of a stride and the duration of the contact of a foot with the ground are equal on right and left sides of the body. In practice these conditions do not quite obtain; the idiosyncrasies of one stride tend to be compensated by those of preceding and following strides. Two precautions are taken to secure gait formulas that are as representative as possible of a general manner of moving. First, the film records used show only sound animals moving smoothly at constant rates of travel on level, unobstructed ground.

Second, each gait formula is calculated from at least two, and usually three or four, consecutive strides.

Gait formulas for repeated performances of a single horse, moving each time under the same conditions, usually vary by 3 to 5 percentage points for each parameter. Numerous records of different horses, performing as nearly the same as riders can make them, vary by about 5 points for the first parameter and by at least 10 points for the second (to 15 points for artificial gaits). It follows that gait formulas should be expressed only as whole integers and that any single formula accurately represents a particular sequence of several strides but never a general manner of moving of either a species or an individual.

Gait formulas are compared and analyzed by plotting them on a graph having the variables and scales arranged as shown in Fig. 1. Plots representing similar gaits fall near one another: the various support sequences—those actually observed and others that are only theoretically possible—are distributed over the graph in a geometrical pattern. If fore and hind feet have equal contacts with the ground, then the pattern consists of 16 triangles (Fig. 1). All gait formulas that fall in one triangle represent performances having the same support sequence but differing in the relative durations of the support provided by the various combinations of legs. Other support sequences are represented on the graph by the lines that delineate the triangles and still others by the single gait formulas that lie at the intersects of such lines. By counting the triangular areas, lines, and intersects, it is found that 44 support sequences are theoretically possible. (Left and right borders of the graph are not counted because they represent two improbable gaits—having all feet always on the ground and never on the ground. The bottom border duplicates the top border.)

If the duration of contacts made with the ground by the forefeet is shorter than that of the hind feet (the usual circumstance for show horses), then only the duration of the contacts of the hind feet (selected for several reasons as the independent variable) is used in calculating the gait formula. In this circumstance, support sequences are distributed over the graph in a more intricate pattern of triangles and



quadrangles (not illustrated), and 60 additional sequences become theoretically possible. (The anterior contacts are commonly a little longer than the posterior contacts for some kinds of animals, but only rarely and insignificantly so for horses.)

Of the 104 support sequences thus found to be theoretically possible for quadrupeds doing symmetrical gaits and having contacts of forefeet equal to or shorter than contacts of hind feet, about 55 might be used by horses. It was noted above, however, that variability is of such magnitude that only those areas on the graph having diameters of about 10 points can be considered to represent modes of moving that are characteristic of either individuals or species. Of the 55 or so support sequences of which the horse is capable, only about seven are distributed on the graph over areas of that size or larger. These support sequences, and some others that are less frequently used, are identified and related to named gaits in Fig. 3.

The support sequence was used by Muybridge as a basis for naming gaits. Unfortunately, as he himself realized, some support sequences can rarely be identified (those represented on the graph by lines and intersects), whereas

range of variation of like animals moving similarly. In running gaits each foot is on the ground less than half the time. Lateral-sequence gaits have the footfall of a given hind foot followed by the footfall of the forefoot on the same side of the body. Diagonal-sequence gaits have the footfall of a given hind foot followed by the footfall of the forefoot on the opposite side of the body. Lateral-couplets gaits have footfalls of the fore and hind feet on the same side of the body related in time as a pair. Diagonal-couplets gaits have footfalls of the fore and hind feet on the opposite sides of the body related in time as a pair.

One thousand and eight gait formulas have thus far been calculated for 158 genera of quadrupeds, including eight genera of amphibians, nine genera of reptiles, and representatives of 15 orders of mammals. The horse is represented by 167 formulas. When plotted, 98.8 percent of all the formulas lie within the irregular area (bordered peripherally by both solid and dotted lines) illustrated on Fig. 4.

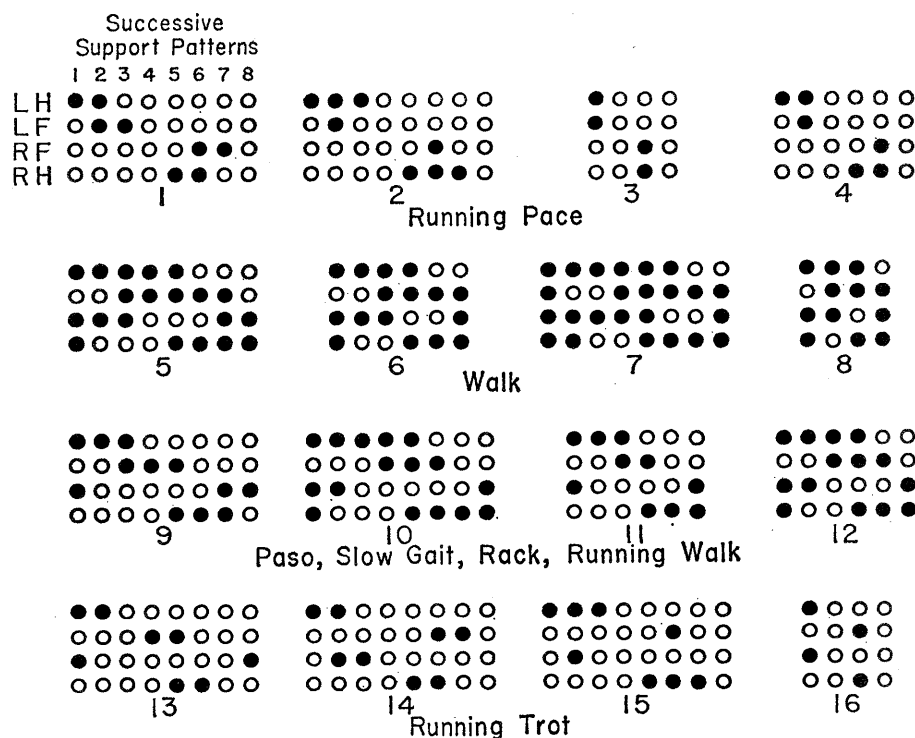


Fig. 3. Sixteen of the many support sequences that might be used by horses doing the gaits indicated. The initials L, R, F, and H stand for left, right, fore, and hind feet. Black circles indicate feet supporting weight; open circles, unweighted feet. Within each diagram, a vertical row of four circles shows a particular pattern of support. Thus, in the fifth support pattern of support sequence No. 1, only the RH foot is on the ground. Each sequence starts with the footfall of the LH foot. Sequences 1, 5, 9, 10, 13, 14, and 15 are relatively common for horses.

The remaining 13 plots are scattered elsewhere as shown. Additional data will surely enlarge the area somewhat, yet the border figured is a close fit for the data at hand; were it reduced all around by a distance equal to only one percentage point on the scale of the graph, 70 additional plots would be excluded.

The dotted line on Fig. 4 encompasses the records for horses, except, however, that all but the lowest of the scattered individual plots shown on the right of the graph are also for horses. The solid line (and remaining scattered plots) indicates the positions of the records for all other animals. Note the extent of the areas that are unique to the horse.

The total area representing horses is repeated in the background of Fig. 6, where 20 specific gait formulas are identified (small circles) and tracings of horses made from films show the particular performances from which the 20 formulas were calculated. Each sketch was drawn from the first moving-picture frame of a cycle that shows the left hind foot on the ground. Advancing across the figure from left to right, the right hind leg is more and more elevated and the supporting fore-

leg is ever more advanced in its travel under the body. This follows from the fact that to the right are gaits in which each foot is off the ground for a relatively large percentage of its cycle. Advancing across the figure from top to bottom, the footfall of the left forefoot lags longer and longer behind the footfall of the left hind foot; hence the forelegs move successively counterclockwise for slightly more than half a cycle.

The Pace and Related Gaits

In Fig. 5 the principal named symmetrical gaits of horses are related to one another and to the parameters of gait formulas. The pace, represented in this study by 22 formulas, is primarily a running gait of Standardbred horses trained to race in harness. It is an uncomfortable gait to ride because the mount sways from side to side. It is not performed in the show ring and therefore is not done with animation. The legs on the same side of the body swing more or less together, but few plots fall on the upper border of the graph (horse 1, Fig. 6) where the ordinate is zero and fore

and hind hoofs strike the ground in unison. Pacers usually place the hind foot down before the forefoot by 3 to 10 percent of the duration of the stride (horses 3 and 4, Fig. 6, and Fig. 7 at left). It is unusual (and probably less efficient) for a pacer to place the forefoot after the hind foot by as much as 12 percent of the duration of the stride (horse 5).

Neither horses nor other vertebrates place a forefoot on the ground just *before* the hind foot on the same side of the body (see the vacant lower quarter of the graph, Fig. 4). The reasons for this have not been analyzed and may be subtle and complex. I suggest one reason why such gaits might be inefficient and jarring. Running diagonal-sequence, lateral-couplets gaits would have a forefoot strike the ground while all other feet were lifted. One may infer that this would cause the hindquarters to rotate downward around the supporting forequarters. Muscles that swing the foreleg to the rear would accentuate the rotation, and such rotation would increase the initial loading of the hind leg next to strike. When a hind foot strikes the ground while all other feet are lifted (as is usual for the pace), it is the forequarters that tend to rotate downward around the supporting hindquarters. However, the powerful muscles that swing the hind leg to the rear this time counter the rotation and thus reduce the initial loading of the foreleg. Running lateral-sequence, diagonal-couplets gaits may be avoided partly for the same reason.

The duration of the contacts that the forefeet of pacers make with the ground is 85 to 100 percent (usually about 95 percent) as long as the duration of contacts of the hind feet—a relatively small discrepancy. Twelve records of horses pacing at various speeds show 2.4 to 3.0 strides completed per second.

Pacers use one principal support sequence (No. 1, Fig. 3). Sequence 2 is not unusual, but support patterns 3 and 7 would be of fleeting duration. Sequence 4 is unusual. Sequence 3, and two others not shown, are more unusual, yet 3 is the stereotype of the pace. Sequence 9 might be used at the slow run, patterns 3 and 7 being predominant.

Speed records for pacing horses indicate that at all distances they are faster by a narrow margin than are trotters. Pacers have run $\frac{1}{2}$ mile (0.80 km) at 32.3 miles (52.0 km) per

hour and 4 miles at 23.6 miles per hour. My data suggest (but are insufficient to establish) that pacers tend to keep each foot on the ground for a slightly larger fraction of the stride interval than do trotters at the same rate of travel. The pacer has the advantage that it cannot strike a forefoot with a hind hoof—a fault which most trotters experience sooner or later.

Few animals pace. Members of the camel family use the slow running pace and perhaps also the moderate running pace. An occasional dog uses the fast walking and slow running pace. Most horses must be trained to pace, but foals of pacers sometimes adopt the gait without training. Pacers are prevented or discouraged from trotting. It is not known if ancestral wild horses paced. The gait has probably always been restricted to cursorial mammals having long legs and occasion to sustain a slow run.

Horses may do the fast walking pace while slowing from the running pace to the normal walk, or while being led a little too fast for the walk. However, horses rarely use gaits for which the first parameter of the gait formula is more than 45 and the second less than 20; my single record (sketch 2, Fig. 6) shows a ranch horse. Walking gaits related to the pace fall on the graph where the geometric pat-

tern of support sequences is complex—particularly if the gaits are done with animation. Sequences 5, 10, 11, 12 (Fig. 3), and any of 10 others are at least theoretically possible. No common name is assigned to these gaits; “amble,” “stepping pace,” and “pacing walk” have been used, but they have also been applied to other gaits.

Animals that use walking lateral-sequence, lateral-couplets gaits are the elite cursors (many canids, large cats, slender antelopes), the natural pacers (camels), and the giraffe. All animals avoid the slow and very slow walking pace and the very slow lateral-sequence, lateral-couplets walk because, unlike the very slow gaits actually used (Fig. 4), these gaits have periods of support by the two legs on the same side of the body—an unstable combination at slow rates of travel.

Walk, Running Walk, and Related Gaits

Across the center of Fig. 5 is a jumble of related gaits which, with their synonyms, are often described in confusing terms. They have in common a sequence of footfalls (left hind, left fore, right hind, right fore) and about equal spacing of footfalls in time (but with some tendency to diagonal couplets). Hence these gaits are collec-

tively called four-beat gaits. I use “single-foot” as the noun. Only the slowest of these gaits, the walk, is natural to the species. The walk of show horses may be called “flat walk” to distinguish it from other four-beat gaits performed by the same animals.

I have 27 gait formulas for the walk. Horse 6 (Fig. 6) is a Belgian walking at 1.8 miles (2.9 km) per hour; horses 7 and 11 are Quarter Horses walking 3.5 and 3.1 miles per hour. From 0.6 to 1.0 stride is commonly completed per second. The duration of contacts made with the ground by forefeet is usually about equal to the duration of contacts by hind feet (the range of 19 records was 95 to 104 percent), but may be less (± 92 percent) for show horses.

The principal support sequence for the walk is No. 5 (Fig. 3). Sequences 6 and 7 may be used momentarily when the second parameter of the gait formula is relatively large. When the first parameter is relatively large, sequence 8 and five others might be identified.

The extreme variation of the second parameter of gait formulas for the walk (vertical range, Fig. 5) results from the fact that the walk may merge into the trot, pace, and artificial gaits. The right-hand and upper boundaries of the area assigned to the walk on Fig. 5 are, therefore, somewhat arbi-

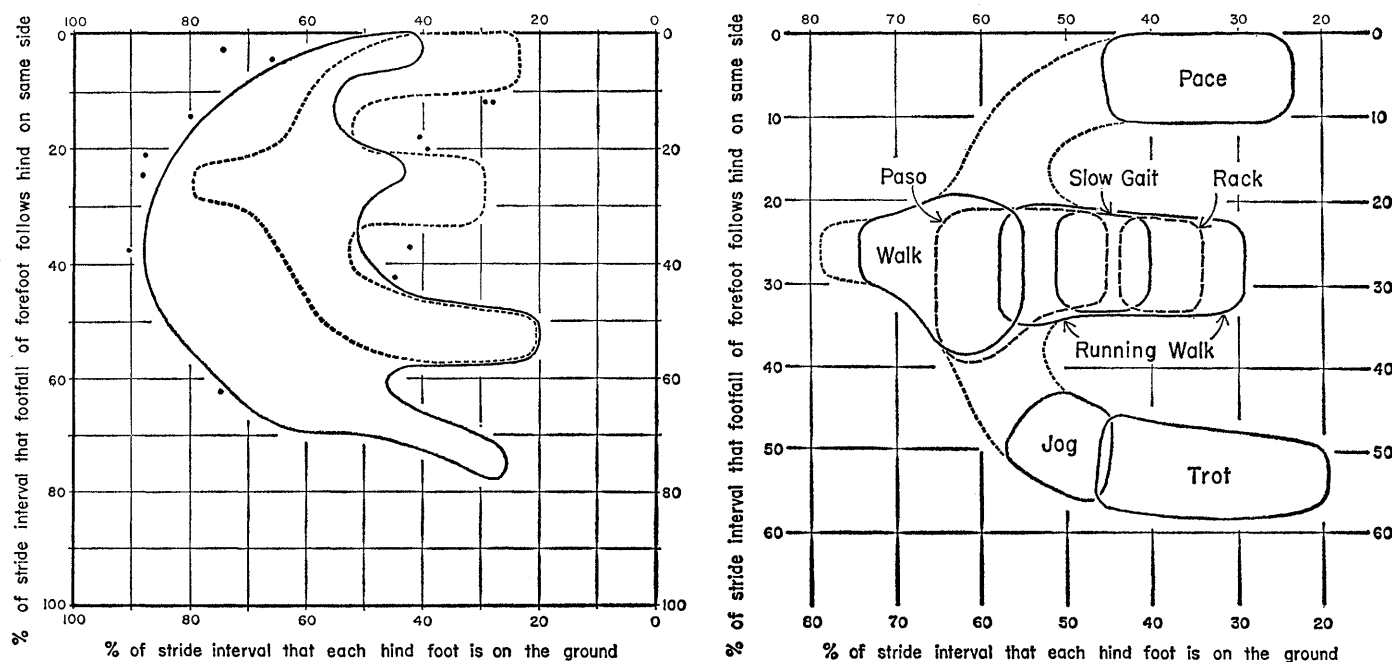


Fig. 4 (left). One hundred sixty-two gait formulas for horses fall within the area indicated by a dotted margin; 833 formulas for other animals belonging to 158 genera fall within the area indicated by the solid margin. Thirteen peripheral plots (including five for horses) are shown. Fig. 5 (right). A portion of the basic graph on which is shown the relation between the principal named symmetrical gaits of horses, and their relation to the parameters of gait formulas. (Gaits for which formulas would fall within the dotted areas are unusual and have no common names.)

trary. Most performances fall in the left, middle, or lower parts of the area shown. Variation for individual animals is normal.

The manner of walking used by horses is also used by cattle and some other animals. Plots for smaller cursors fall higher on the graph; plots for noncursors fall lower.

The remaining four-beat gaits are artificial, although paso and walking horses have come to perform their

special gaits with minimum training. The range of individual variation in the second figure of the gait formula is greater for these gaits than for any others: up to 15 points for seven plots of a champion paso horse and up to nine points for 12 plots of a fine five-gaited horse. The areas assigned to the artificial gaits on Fig. 5 will be somewhat modified when additional data become available. These are the smoothest of gaits to ride. At moderate

and fast walking speeds they have been considered ideal by plantation owners wishing to ride quickly and comfortably; hence the term "plantation gait."

The Peruvian Paso Horse is only now becoming known in North America. It is a small horse with deep chest, slender legs, flexible joints, and a tractable disposition. The paso horse uses the flat walk, trot, canter, and paso gait. The paso may be done slowly or fast: some owners dis-

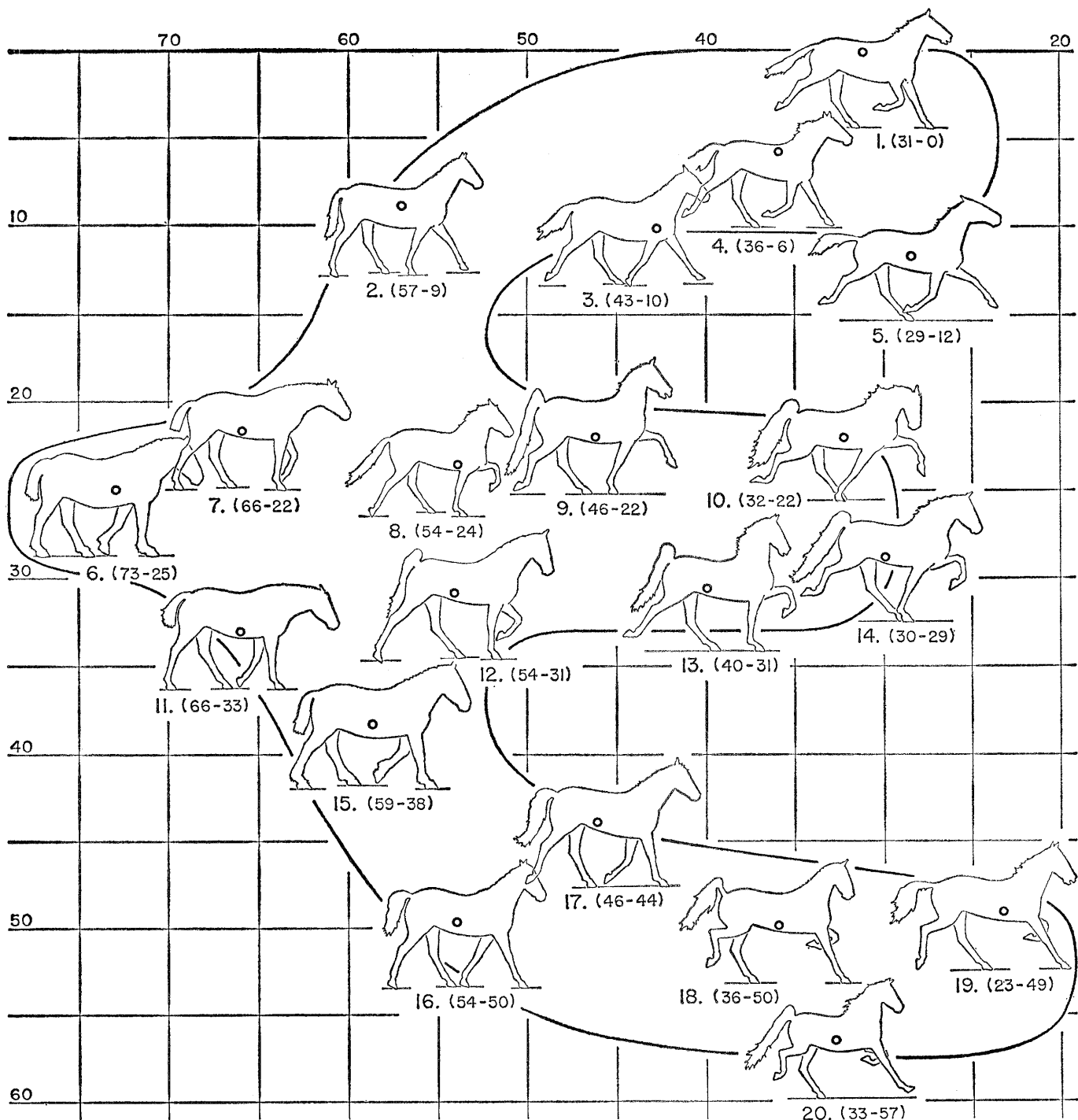


Fig. 6. In the background is shown the area of the basic graph within which fall nearly all gait formulas for symmetrical gaits of horses. Twenty specific formulas are located (small circles), and around each is drawn a silhouette of the horse moving as represented by the formula. In every sketch the left hind foot has just touched the ground.

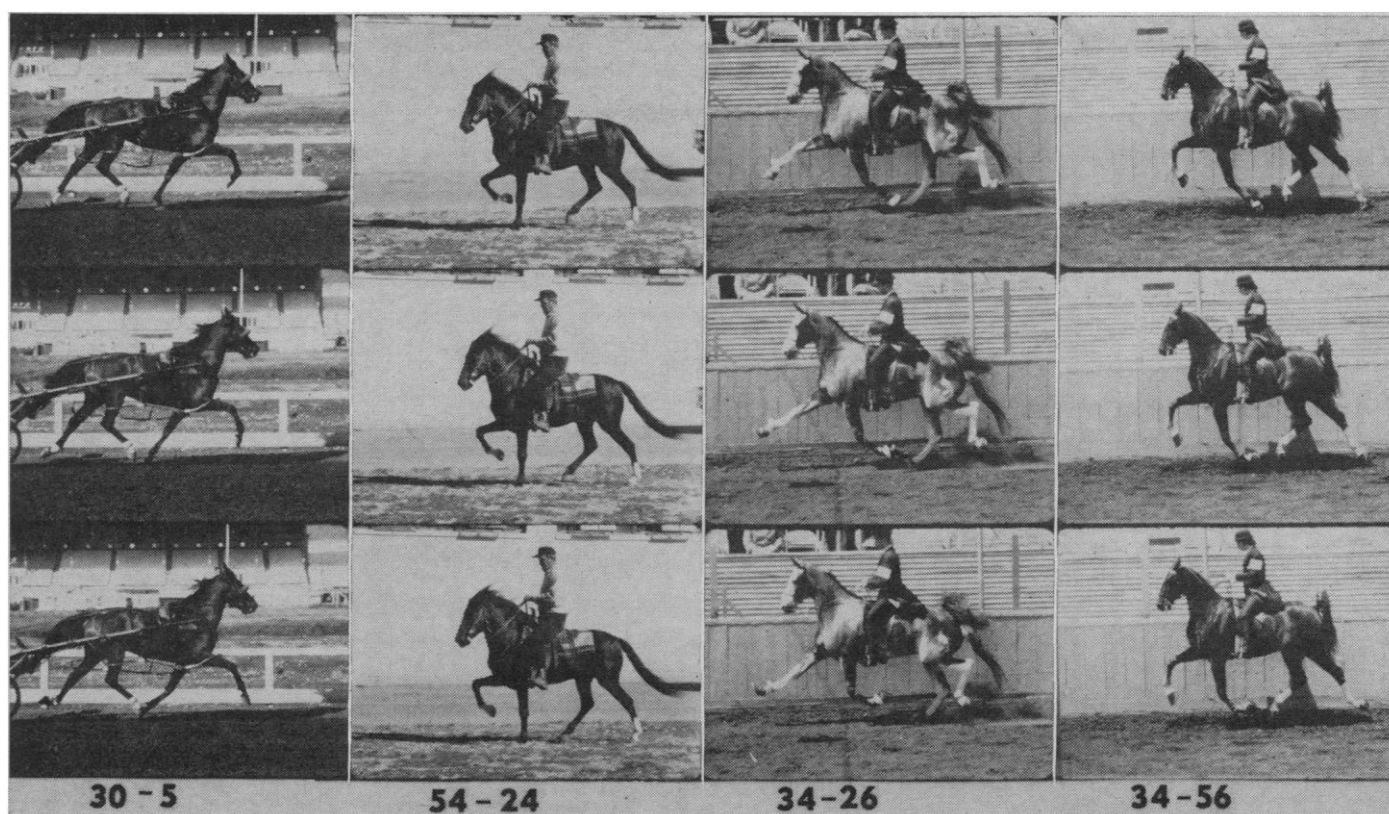


Fig. 7. Moving-picture sequences of representative gaits of horses. At left, a Standardbred harness pacer runs at racing speed; the middle frame shows that the hind foot is slightly more advanced in its cycle than is the forefoot on the same side. At left center a champion Peruvian Paso stallion demonstrates the paso gait. At right center, a Tennessee Walking Horse does the running walk. At right, a three-gaited American Saddle Horse shows the trot. The pictures were exposed at 64 frames per second. Figures below the pictures are descriptive of the respective gaits.

tinguish a paso and running paso, or pacing walk and paso. At shows, events are often designed to demonstrate control and smooth riding qualities. I have 15 plots for two horses and a filly doing the paso gait (horse 8, Fig. 6, and Fig. 7, left center). These records show a single-foot or (less frequently) a lateral-sequence, diagonal-couplets gait done at the moderate or fast walk. The paso gait is performed with animation and a marked lateral motion of the forehoof as it is advanced. (Horsemen call this "winging.") Support sequences 5, 10, and (at speed) 9 are usual. The transitional sequences 11 and 12 might be identified.

The slow gait and rack are two gaits of the five-gaited American Saddle Horse. They are represented in this study by 16 and 17 plots, respectively. "Stepping pace" has been used as a synonym for slow gait and "single-foot" as a synonym for rack. The term "rack" has also been applied to the pace. "Amble" has been used for certain four-beat gaits, but its meaning is vague. Animation is paramount for the slow gait (horse 9 is a champion). The step is quick and not long; the legs are carried well under the body. Animation

also characterizes the faster rack (horse 13). For each gait the forefeet are on the ground only 62 to 78 percent as long as the hind feet (33 records for five horses). By reducing the part of the stride that each hind foot is on the ground, high stepping tends to shift gait formulas to the right on the graph, where they fall with formulas of animals moving with less animation but somewhat greater speed. One horse took 1.6 to 1.8 strides per second at the slow gait, and 2.0 to 2.1 at the rack. Each gait, but particularly the rack, is tiring for the horse. In each, support sequence 9 is used almost exclusively; sequences 10 and 11 might be used in a slow, slow gait. Horse-show premium lists may state that the slow gait should be "true" and "not a slow rack." Nevertheless, my records, which, though few, include performances of champions, indicate that the differences between the gaits are related to speed. Speed is correlated with the first parameter of the gait formula, and, as Fig. 4 illustrates, the value of this figure overlaps markedly for the two gaits. Even for a single horse, plots for the gaits may fall as a continuum, not as two populations. The two gaits

are more nearly alike than any others performed in competition by the same horse.

The running walk is the distinctive gait of the Tennessee Walking Horse. It was initially a plantation gait and was formerly performed at shows at the fast walk (6.5 to 13 km/hr)—horse 12 was a champion in 1948. Now the gait is shown at the slow or (usually) moderate run (horses 10 and 14 in Fig. 6, and Fig. 7, right center). As performed by the best horses, it is the fastest of four-beat gaits (to more than 32 km/hr). Walking horses also exhibit the flat walk and canter; they are not allowed to trot. My data on the running walk consist of 24 plots for 11 horses. Demands of style are less restrictive than for the similar rack and slow gait: the feet are lifted high but the head is held forward and nodded gently up and down as the forelegs are advanced. Forefeet are on the ground longer (79 to 92 percent as long as hind feet in 14 records for 9 horses). Motion is less tight, more flowing. Most characteristic, walking horses take enormous steps. Overstriding (the placing of the hind foot in advance of

the preceding footprint of the forefoot on the same side of the body) of $\frac{1}{2}$ to 1 meter is common. Twenty records show 1.5 to 2.2 strides completed per second. The principal support sequence of the running walk is also No. 9. At the fast walk, sequence 10 or (rarely) 11 might be used; at maximum speed, sequences 1, 13, and three others might be briefly identified.

The faster four-beat gaits are used only by horses. Charging elephants (and their more agile calves) manage the slow running single-foot. They select it to the exclusion of alternatives (trot, gallop) because it provides the greatest continuity of support and is achieved from the walk merely by increasing the rate and length of the step—advantages for an animal of great bulk.

The Trot and Related Gaits

Diagonally opposite legs (for example, right hind and left fore) swing more or less together in the trot: this gait, like the pace, is therefore called a two-beat gait. It is natural to all horses except breeds developed for the pace and running walk (and some of those horses revert to the ancestral gait). Pleasure horses and Standardbred harness racers (horse 19) trot freely without restraint of style. Three-gaited (horse 18, Fig. 6, and Fig. 7, at right) and five-gaited American Saddle Horses, Roadsters, and Hackney and Harness Ponies (horse 20) must display animation. I have 31 gait formulas for 22 horses.

Length and rate of stride and relative duration of contacts by fore and hind feet may be slightly different for racing trotters and racing pacers, but if so, sufficiently numerous and precise data to establish the differences are not yet available. A gaited horse trots in a collected manner, with feet well under the body.

If the forefoot strikes just before the hind, then the support sequence (at the run) is No. 13. If the forefoot strikes just after the hind foot—which is somewhat more usual—the support sequence is No. 15 (rarely one other) if the gait is done with animation, and No. 14 if the duration of contacts with the ground is the same by

all feet. The two feet do not often strike the ground in exact unison, but neither do they often depart much from this desired relationship. Such a trot is said to be “square.” The support sequence of an exactly square trot is No. 16 (the stereotype of the trot) or (with animation) one other.

A slow, easy, relaxed trot is called a jog or dogtrot. I have 5 plots for 3 horses (horses 16 and 17 are Arabians). Three records indicate 1.2 to 1.4 strides, completed per second. A slow, animated, prancing trot is called the parade gait. Plots for a slow trot done with animation fall on an area of the graph where the geometric pattern of support sequences is complex: Sequences 5 through 7, 9 through 15, and 21 others could theoretically be identified.

When led just too fast for a comfortable walk, some horses assume a gait between the walk and jog (horse 15) for which there is no common name.

The running trot is used by virtually all carnivores, ungulates, and perissodactyls. The walking trot, by contrast, is used by animals with short or laterally placed legs: many amphibians and lizards, crocodilians, and the hippopotamus. At the very slow walk most of these animals shift to the lateral-sequence, diagonal-couplets gait which has shorter bipedal, and longer tripedal support patterns. Walking diagonal-sequence gaits are used by most primates, the aardvark, giant armadillo, and kinkajou. Running diagonal-sequence gaits are, so far, known to be used by the opossum and some lemurs (each at the slow run only), and duiker, and muntjac.

Summary and Comment

All gaits of horses except the canter and gallop have been described, distinguished, and related to each other and to the similar gaits of 157 other genera of quadrupeds. A scheme for naming gaits has been devised. Any particular series of strides can be expressed in terms of two percentage figures. These figures can be plotted on a graph from which it is possible (with the use of overlays) to read out, for any per-

formance represented, the sequence of footfalls and the sequence and relative durations of all combinations of support by the several feet. The method makes it possible to compare hundreds of records simultaneously and to ask (and answer) new kinds of questions about quadrupedal gaits: What is the nature and magnitude of variability? How many gaits are theoretically possible? Why are some of these not used? How, and why, do the various gaits correlate with body size, structure, and performance? What has been the phylogeny of gaits?

The horse, as a species, is more versatile in the selection of gaits than is any other quadruped. It uses several gaits unique to itself. The various named gaits of horses are not distinct and independent but instead form a continuum within which boundaries are somewhat arbitrary and often based on factors of breed and style rather than on differences in the general manner of moving the legs. Limited data show no significant differences between the gaits of colts and adults. Variation in the performance of a given gait is roughly twice as great for the species as for individuals, and greater for artificial than for natural gaits.

If the analyses herein presented were sufficiently refined, extended, and correlated with blue-ribbon performances, they would probably be useful to breeders and trainers. It is now desirable to relate the various gaits to force vectors at the ground and within the body and to apply the findings to mechanical analysis of the bone-muscle system.

References and Notes

1. E. Muybridge, *Animals in Motion* (Chapman and Hall, London, 1899); republished with minor changes, L. S. Brown, Ed. (Dover, New York, 1957).
2. Such a group of diagrams has been called a “footfall formula.” The thing shown by a footfall formula is a support sequence. I did not make this distinction in (8).
3. For example, by A. B. Howell, *Speed in Animals* (Univ. of Chicago Press, Chicago, 1944); see chap. 10.
4. Paul Magna de la Croix wrote 17 papers on locomotion between 1927 and 1936. These were imaginative and new in approach but suffered from errors, generalizations, and conceptual limitations.
5. S. M. Manton, *J. Linnean Soc. London Zool.* **41**, 529 (1950); **42**, 93 (1952); **42**, 118 (1952); **42**, 299 (1954).
6. M. Hildebrand, *Res. Film* **5**, 1 (1964).
7. ———, *J. Mammalogy* **42**, 84 (1961).
8. ———, *Arch. Néerl. Zool.*, in press.