THE DYNAMICS OF QUADRUPEDAL WALKING

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(With Twelve Text-figures)

INTRODUCTION

Locomotion involves the harmonious activity of the entire animal depending especially on the co-ordinated action of the muscles, bones, nervous system and sense organs. A study of animal motion therefore deals with mechanical aspects of the integrated action of physiological systems which are more frequently studied separately. In the present investigation a preliminary analysis is made of the mechanics of walking as performed by the cat, one of the less specialized mammalian quadrupeds.

Graphic records of the position of the body of an animal taken at a series of brief intervals furnish a basis for a quantitative description of the motion of walking. From such records the relationship of distance and time can be obtained, and velocities and accelerations may be computed. If in addition the distribution of mass in the body is known, kinetic energy and external forces may also be calculated. This is the general procedure of Braune & Fischer (1895–1904) in their important investigations of human locomotion. Since the early work of Marey (1884) and of Muybridge (1899) the development of the motion-picture camera has provided improved means of recording motion. Bernstein (1927), dealing with human locomotion, and Fenn (1929), studying energy expenditure in human running, have used cinematic recording effectively. In order to obtain accelerations by this method, however, measurements taken from the photographs must be plotted against time and differentiated twice, since acceleration is the second derivative of displacement with respect to time. This procedure is attendant with several possible errors which may appear in exaggerated form in the results. An alternative approach is possible through measurement of the external forces which act on the animal during the walk. The acceleration of the mass centre can then be obtained directly from the equation:

$$F = Ma,$$

where F = external force, M = mass, and a = acceleration.

This method of analysis involves fewer approximations, and errors are confined to the one measurement. Its direct approach to the forces involved in locomotion is advantageous. Furthermore, it allows the measurement of forces acting through a single limb, an essential requirement for an analysis of the disposition of forces in the body.[1]

METHODS AND DATA

Measurement of external forces

Disregarding air resistance, the external forces acting on the cat as it walks are the reactions at the surfaces of contact of the feet with the ground and gravity, a known constant. In order to measure the reactions at the feet these forces may be employed to activate some recording mechanism. Vertical reactions in locomotion were measured by Basler (1935) with an apparatus recording the vibration frequencies of strings under varying tension. Elftman (1934) and Elftman & Manter (1934), measuring human foot pressure, employed the principle of the deformation of rubber pyramids when subjected to pressure. The apparatus which finally

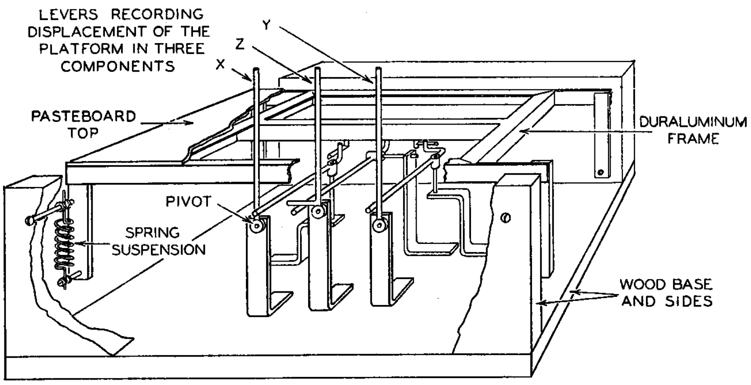

Fig. 1. Diagram of one of the three adjacent platforms by means of which the external forces acting on the animal were recorded.

proved most successful for the measurement of the quantities desired in the present investigation consists essentially of light platforms supported at the corners by springs (Fig. 1). The springs offer greatest resistance to forces which tend to move the platform downward, but they also resist displacement of the platform horizontally. The frames of the platforms were made of duralumin and the covering layer consisted of corrugated paper with a rough top surface.

Periods in which three of the cat's feet make contact occupy about half the time during the walk. Consequently three separate platforms are required to measure the reactions on each foot individually. By making each platform $7\frac{1}{2}$ in. long and arranging them end to end there is a favourable chance for each foot to rest on a separate platform without interference, providing the first step lands squarely on the first platform.

[1] Grateful acknowledgement is made to Prof. Herbert Elftman for his continued interest in this work; also to Mr J. M. Garrelts of the Physics Department of Columbia University for his criticism of the procedure and methods which are used.

The small displacements of the platforms (never exceeding 1·3 mm. and considerably less than that during most of a record) are magnified greatly with a double lever system in order that they may be read from photographs. The first lever, of thin tubular aluminium, activates a straw-recording lever which moves in the photographic plane. Three recording levers attached to each platform register displacements in three rectangularly directed components. Each platform was calibrated by applying known forces in the three component directions and measuring the resulting displacements of the recording levers along a fixed line.

Measurement of velocities and accelerations

Cinematic records were taken with a 16 mm. camera as the cat walked slowly across the platforms. A grid of white threads arranged just in front of the narrow pathway for the animal gave reference squares allowing measurements of the position of the body. Orthogonal axes were defined following the notation of Fischer (1895):

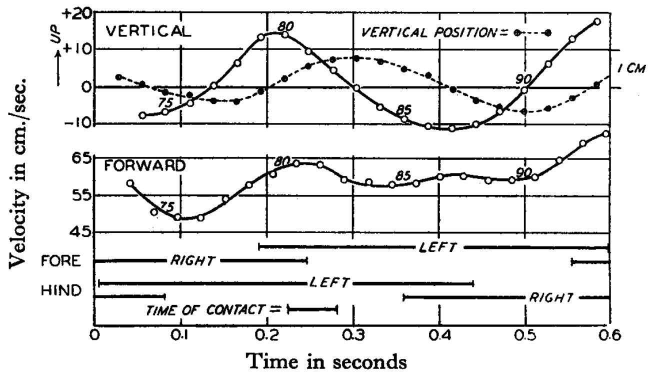

Fig. 2. Velocity of the centre of gravity of the body in vertical and forward components obtained from the cinematic record. Periods during which each foot makes contact with the ground are shown below. Dotted curve gives the vertical position of the centre of gravity. Small numbers show frames of the photographic record.

x axis: parallel to the earth in the direction of progression; *z* axis: vertical; *y* axis: perpendicular to the other two axes (lateral). The *x*-*z* plane, which coincides with the photographic plane, may be considered to contain all the motion of the body for the purpose of an approximate analysis. Records of forces exerted on the platforms indicate the minor importance of lateral motion (Fig. 3).

Velocity and acceleration of the centre of gravity. Life-sized outlines of the cat were traced from the projected negatives at $\frac{1}{38}$ sec. intervals and the position of a point on the trunk near the centre of gravity was marked. The path of this point closely approximates the path of the actual centre of gravity and is used as such in this analysis.[1] The vertical position of this point was measured in each of the eighteen stages which constitute a series representing all phases of the walk.

[1] (A comparison of the paths of this point and that of the true centre of gravity as obtained by the "Hauptpunkt" method of Fischer (1899) reveals synchronous maxima and minima and coincident points of inflexion.)

Fig. 2 includes a curve of the vertical position of the centre of gravity with time as abscissa. Since velocity is defined as rate of change of position with respect to time, $v = ds/dt$, the slope of the position-time curve represents velocity at any chosen moment. The vertical component of velocity of the centre of gravity was calculated by measuring tangents to this curve at the regular succession of intervals in the record. The method of measuring tangents was essentially that described by Richards & Roope (1930) involving the use of an isoceles prism. Arbitrary units in which velocities were measured as angular functions were converted into cm./sec. by a conversion factor dependent on the scales used in plotting the data.

The forward component of velocity was computed in a different manner. The average velocity for each interval between measured positions of the centre of

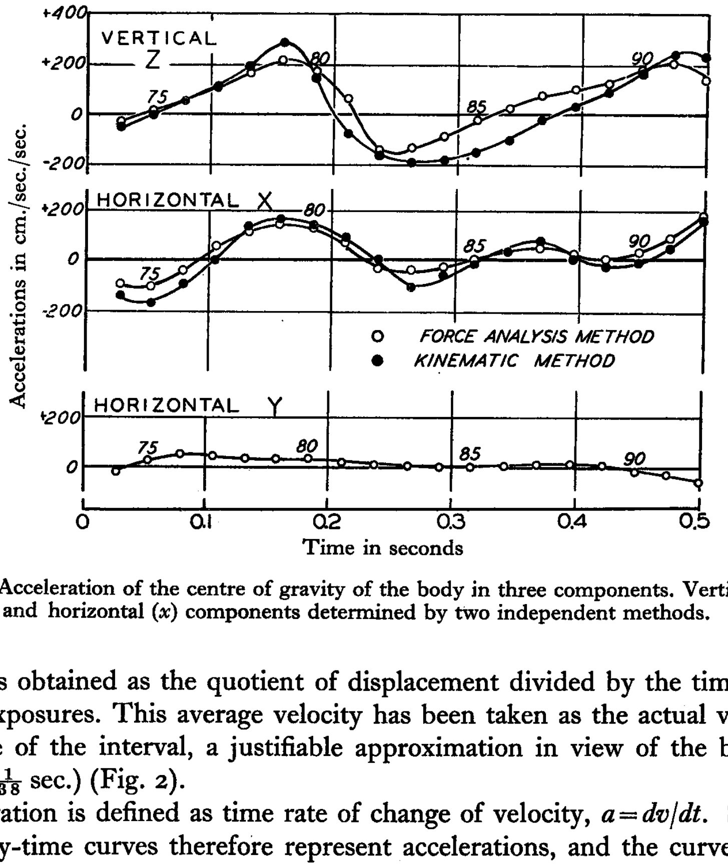

Fig. 3. Acceleration of the centre of gravity of the body in three components. Vertical (z) and horizontal (x) components determined by two independent methods.

gravity was obtained as the quotient of displacement divided by the time elapsed between exposures. This average velocity has been taken as the actual velocity at the middle of the interval, a justifiable approximation in view of the brief time occupied ($\frac{1}{38}$ sec.) (Fig. 2).

Acceleration is defined as time rate of change of velocity, $a = dv/dt$. Slopes of the velocity-time curves therefore represent accelerations, and the curves for the acceleration of the centre of gravity in the vertical and in the horizontal directions can be calculated by following the same procedure of graphic differentiation a second time. The results of these determinations are shown in Fig. 3 superimposed on corresponding curves which were obtained directly from measurements of external forces acting on the cat. The general agreement of these data verifies the characteristics of the acceleration curves.

Velocity and acceleration of limb segments. In a consideration of the cat's body as a mechanical system it is necessary to treat it as if it were made up of a number of rigid segments. An attempt was made to place the divisions between these units at joints where the major movements take place as the animal walks. The following twelve segments were used: trunk, head, upper arm (2), forearm and paw (2), thigh (2), shank (2), hind foot (2). In each frame of the cinematic record outline

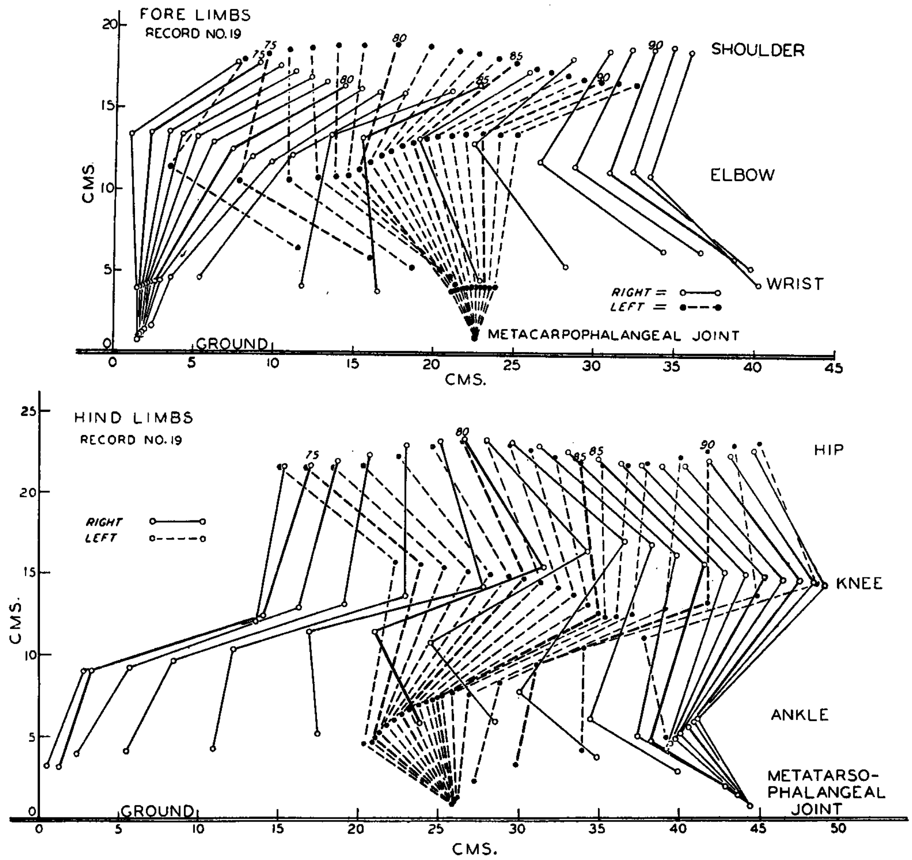

Fig. 4. Positions of the limbs during walking as determined at intervals of $\frac{1}{38}$ sec. Lines connect joint axes of the limb segments. Numbers indicate frames of the photographic record.

models of the bones were carefully adjusted in conformity with the traced outlines of the cat. The positions of the joint axes of separate limb segments were marked and lines drawn to represent each segment in the successive positions that it occupied during walking (Fig. 4). From these recorded positions of the limb segments calculations were made of the velocity and acceleration of the centre of gravity of each segment following the procedure used in calculating these quantities for the centre of gravity of the whole body. Angular velocities and accelerations

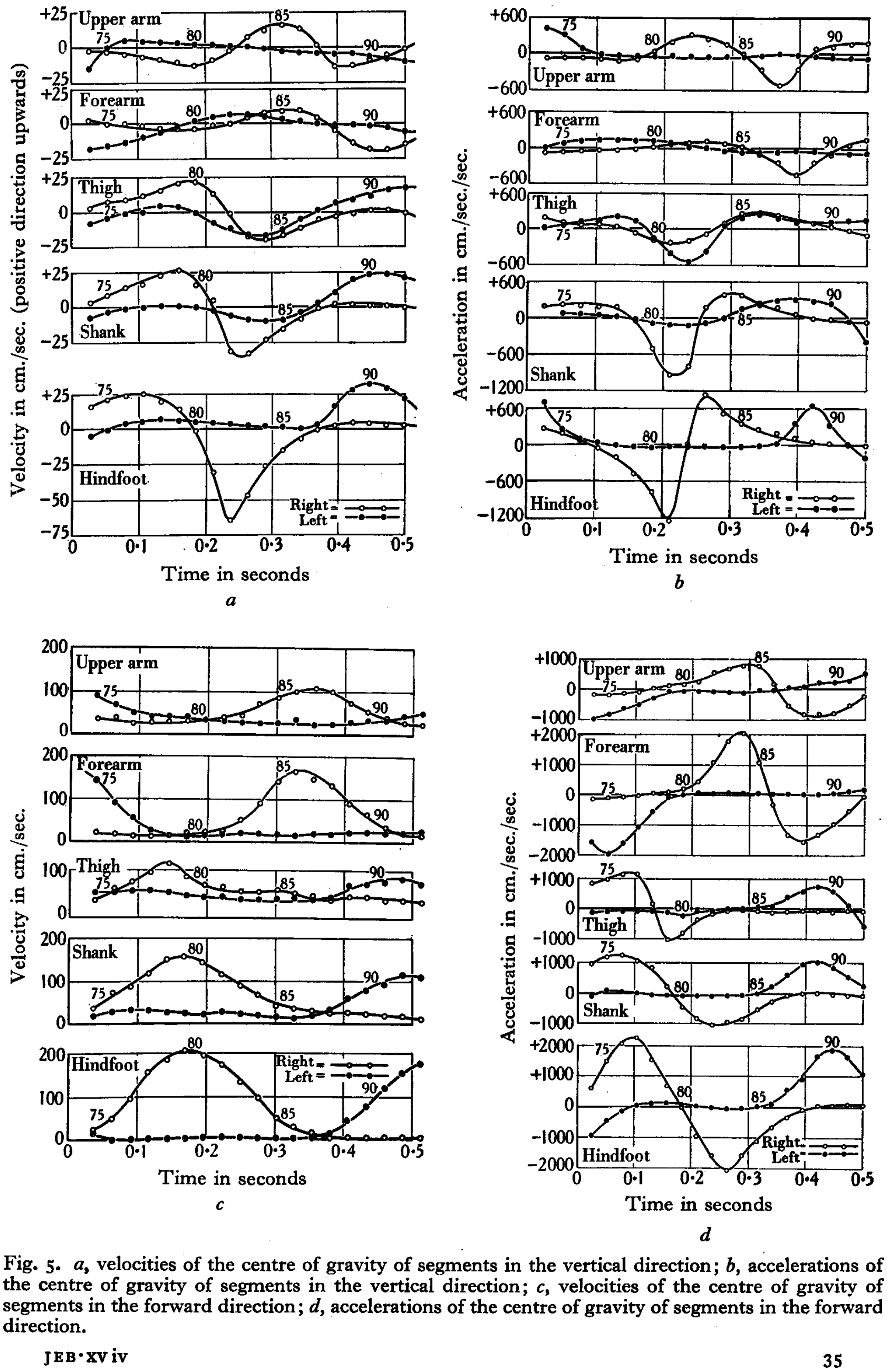

Fig. 5. *a*, velocities of the centre of gravity of segments in the vertical direction; *b*, accelerations of the centre of gravity of segments in the vertical direction; *c*, velocities of the centre of gravity of segments in the forward direction; *d*, accelerations of the centre of gravity of segments in the forward direction.

were calculated by graphic differentiation of measurements of angular position. The results of these computations are shown in Figs. 5 and 6.

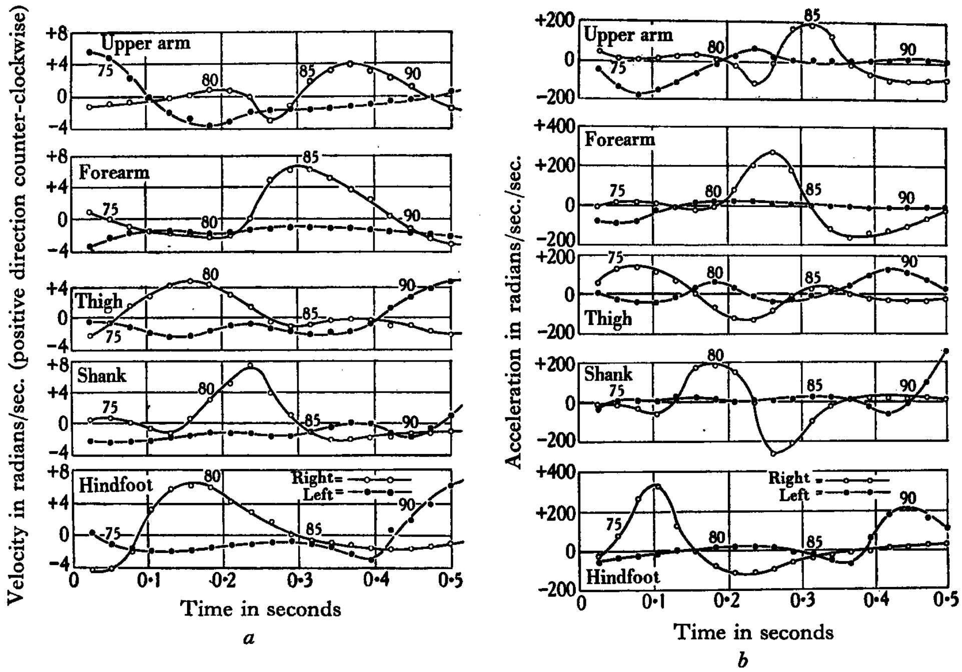

Fig. 6. *a*, angular velocities of the limb segments; *b*, angular accelerations of the limb segments.

Measurements of centres of gravity and moments of inertia

The weight and centre of gravity of each body segment were determined individually. Before separating the parts the body was frozen with the skin left in place. Each cut was designed to pass through the joint axis and to separate adjacent parts equally. The following values were found for the weights of the segments of the body of the cat used in these experiments:

Segment	Weight g.	% of total
Trunk and tail	2109	63·0
Head	250	7·5
Upper arm (left)	94·5	2·7
Forearm and paw (left)	78·5	2·3
Total for left forelimb	173	5·1
Total for right forelimb	179	5·3
Thigh (left)	192·5	5·8
Shank (left)	85·8	2·6
Hindfoot (left)	33·8	1·1
Total for left hindlimb	312	9·5
Total for right hindlimb	319	9·6
Total body weight	3342	

Centres of gravity were determined by placing each segment on a small board and balancing it on a taut wire. Two intersecting planes of balance determine the combined centre of gravity of board and segment and, since the centre of gravity of the board is measurable, the centre of gravity of the segment alone can be obtained by a simple calculation. These determinations are summarized in the following table:

Segment	Actual length of bone mm.	Distance between proximal and distal joint axes mm.	Distance of the centre of gravity from the proximal joint axis mm.
Upper arm	94·5	82·0	39·0
Forearm and paw	147·5	128·0	54·0
Thigh	109·5	95·0	48·5
Shank	111·0	113·0	46·0
Hindfoot	88·0	62·5	41·5

The centre of gravity of the trunk lies about half-way between the dorsal and ventral surfaces at a distance of 54% of the length of a line from the atlanto-occipital joint to the acetabulum. The whole body has its centre of gravity approximately 2 cm. lower and 1 cm. anterior to that of the trunk alone.

Values for the moments of inertia were obtained experimentally from the frozen segments. A small stiff wire, fastened through the segment perpendicular to the orientation of the plane of motion during walking, served as a supporting axis for suspension between two smooth, parallel and level bars. By timing the oscillations while the segment swings as a pendulum through small angles the moment of inertia may be calculated according to the equation:

$$I=\frac{T^2cMg}{4\pi^2}=\text{moment of inertia about an axis of suspension,}$$

where T = time for one period of oscillation, c = distance from the axis of suspension to the centre of gravity, M = mass, g = gravitational constant.

By application of the parallel axis theorem the moment of inertia about the centre of gravity, (I_0), becomes

$$I_0=I-Mc^2.$$

The improvized pendulum was set swinging, first about an axis near one end, then about an axis near the other, giving two separate determinations for comparison. The number of complete oscillations was counted for 20 sec. intervals, an average of several determinations being taken. The moments of inertia of the segments of the body of the cat as measured by this method are:

Segment	Moment of inertia about the centre of gravity		
	Proximal suspension g. cm.^{2}	Distal suspension g. cm.^{2}	Average g. cm.^{2}
Hindfoot	526	504	510
Shank	943	907	925
Thigh	2460	2360	2410
Upper arm	726	743	735
Forearm and paw	2249	2117	2183

Forces involved in walking

Each leg repeats its motion in each successive step, a part of its cycle being occupied in sweeping forward to a new contact and the remainder consisting of its action as a mechanism for the dynamic support and the propulsion of the body. These cycles of the four legs are not randomly spaced but take a well regulated order, left fore, right hind, right fore, left hind, left fore, etc. (Fig. 2). Three limbs contribute to the support of the body about half the time; during the remainder, the weight of the body is borne by two limbs alone. The timing arrangement is such that there are short periods of overlapping when both right and left members are on the ground occurring alternately in the fore and hind quarters. One consequence of this sequence is that the time during which the body is supported by only two limbs is broken up into very short intervals.

The vertical component of external forces applied in walking. The vertical components of external reactions on individual feet as well as the effect of the sum of these actions on the body are shown in Fig. 7. Except for whatever accelerations of the mass centre these forces produce, they represent reactions to gravitational force. A comparison of the measured amounts of vertical force acting on individual feet indicates that approximately three-fifths of the total reaction is distributed on the forelimbs during walking. This is to be attributed chiefly to the fact that the centre of gravity of the cat lies nearer to the forelimbs than to the hind, and that more weight is normally borne by the forelimbs in standing. The changes in vertical reaction producing the distinctive shape of the curve are dynamic characteristics of locomotion. The greatest upward thrust on the forefoot occurs when the step is about three-fourths completed. The forelimb is also pushing the body forward at this time and the muscles of the shoulder are tense. In co-operation with the hindlimb of the opposite side which is also producing its maximum vertical reaction at about this time, an upward thrust of 4000 g. is produced. Since this force exceeds the weight of the animal by 600 g., it produces an upward acceleration of the body's mass centre. Each period of upward acceleration is followed by an interval in which the mass centre accelerates negatively, or downward. During this period the total reaction on the feet falls 600 g. short of the body weight. It is significant that the maximum upward acceleration of the body occurs while three feet are on the ground, negative acceleration, while only two feet support the body. Similarly, in human walking and also in the walk of the alligator, the body's support is strongest at the time of upward acceleration.

The horizontal component of external force applied in walking. The horizontal force produced by the frictional resistance between the foot and the ground is negative, in a direction opposing the progression of the animal, during the first part of a step. Later on, a forwarding impetus is produced as the limb exerts a backward push against the ground, causing a positive horizontal reaction. Fig. 8 shows the x component of horizontal force acting on individual fore- and hindfeet from three separate records. Impulse given to the body is equivalent to the product of external force and the time during which it acts. Since horizontal external force acting on a single limb is negative during a part of the step and positive during another, horizontal impulse may be considered to consist of negative (retarding) and positive (forwarding) portions. Areas above and below the base line in Fig. 8 represent positive and negative impulses.

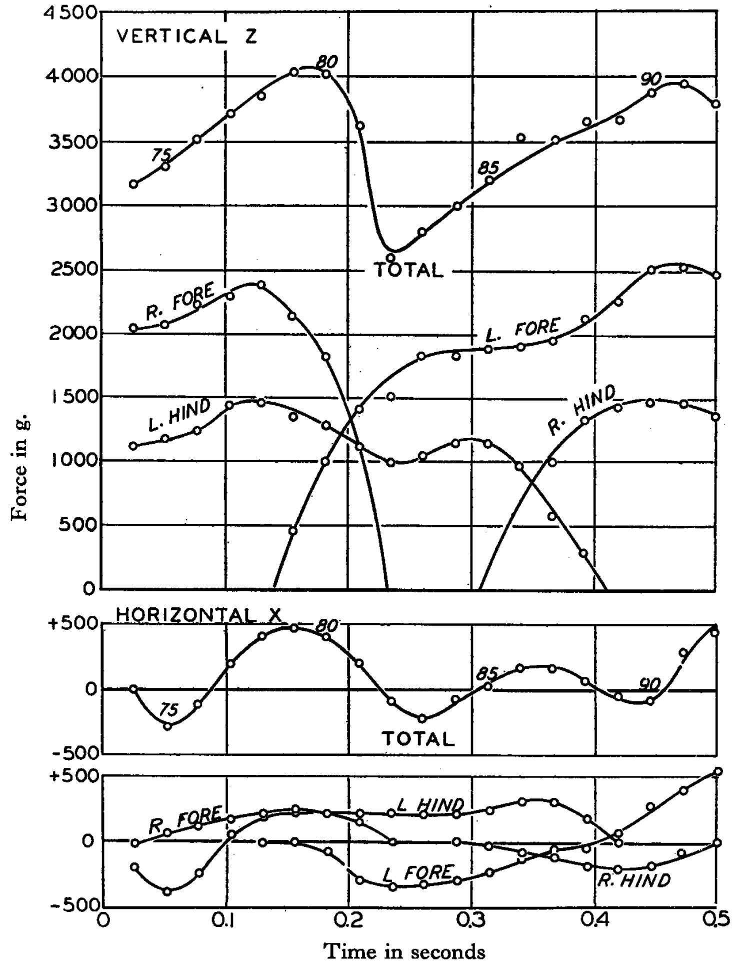

Fig. 7. Forces acting on individual feet registered by the platforms on which the animal walked. Record covers the period in which the animal made no contact except with the platforms. Positive x forces are directed forward.

A comparison of the force curves of fore- and hindlimbs shows characteristic differences in their action during walking. Forces of backward and forward propulsion are larger in forelimbs than in hind and their action is consequently more vigorous. The period of negative action is prolonged in the forelimb and, as a result, impulse delivered over the whole step has a small negative (retarding) value. The hindlimb, producing a smaller positive force for a longer period, contributes a small forwarding impulse to the body.

In the cat the order of the steps is such that fore- and hindlimbs have opposing actions most of the time and the total effect on the locomotion of the animal represents a balance of antagonistic forces applied horizontally. This effect is essentially a damping of fluctuations in horizontal force. The cyclical changes in horizontal acceleration of the body which are produced by these forces are consequently less marked than they might be without this stabilizing action. By restricting acceleration changes the velocity of the body is also maintained at a more nearly steady level and less energy is expended in momentary periods of increasing and decreasing velocity.

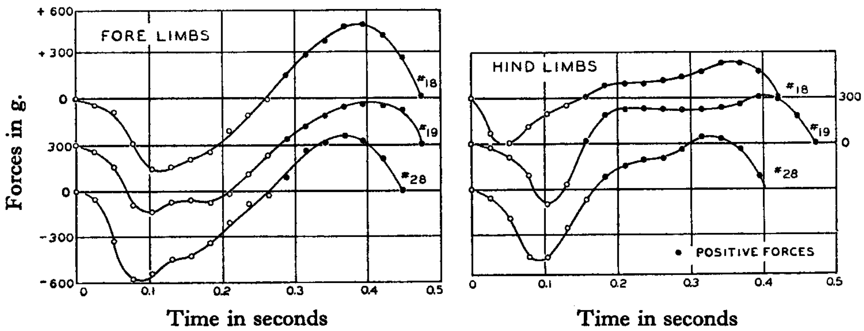

Fig. 8. x component of horizontal force acting on fore- and hindlimbs during single steps. Areas between the curves and the zero base line represent negative and positive impulse. Records Nos. 18, 19 and 28.

Energy expenditure in walking

A body moving with constant velocity on a level frictionless surface maintains its mechanical energy without change. No transference of potential energy to kinetic occurs and no work is done on the body. An animal walking on a level surface at a stabilized average speed is by no means functioning under the same conditions. As a mechanical system it differs from the theoretical one in these respects:

(1) *Some energy is required to overcome frictional resistance.* Only a small amount of energy is dissipated by friction, however. Joint surfaces are remarkably smooth and, in addition, they are provided with excellent lubrication. Air resistance is also small at the relatively slow speed used in walking.

(2) *Movement of parts of the body relative to each other involves energy.* A considerable amount of energy is expended in this manner, due chiefly to the movements of the limbs as they perform successive steps.

(3) *Fluctuations in the velocity of the mass centre requires energy expenditure.* Although the animal may maintain a constant average velocity, its instantaneous velocity is always changing under the influence of the propulsive strokes of the limbs with corresponding periodic changes in kinetic energy.

The kinetic energy of the body of the cat was obtained by summing the kinetic energies of separate parts in each phase of the record of the walk. Each segment considered as a rigid body moving in the plane formed by the x-z axes has kinetic energy of:

$$\text{kinetic energy (in ergs)} = \tfrac{1}{2}mv^2 + \tfrac{1}{2}I\omega^2,$$

where m = mass of the segment (grams), v = velocity of its centre of gravity (cm./sec.), I = moment of inertia about an axis through the mass centre perpendicular to the plane of motion (g. cm.^{2}), ω = angular velocity (radians/sec.).

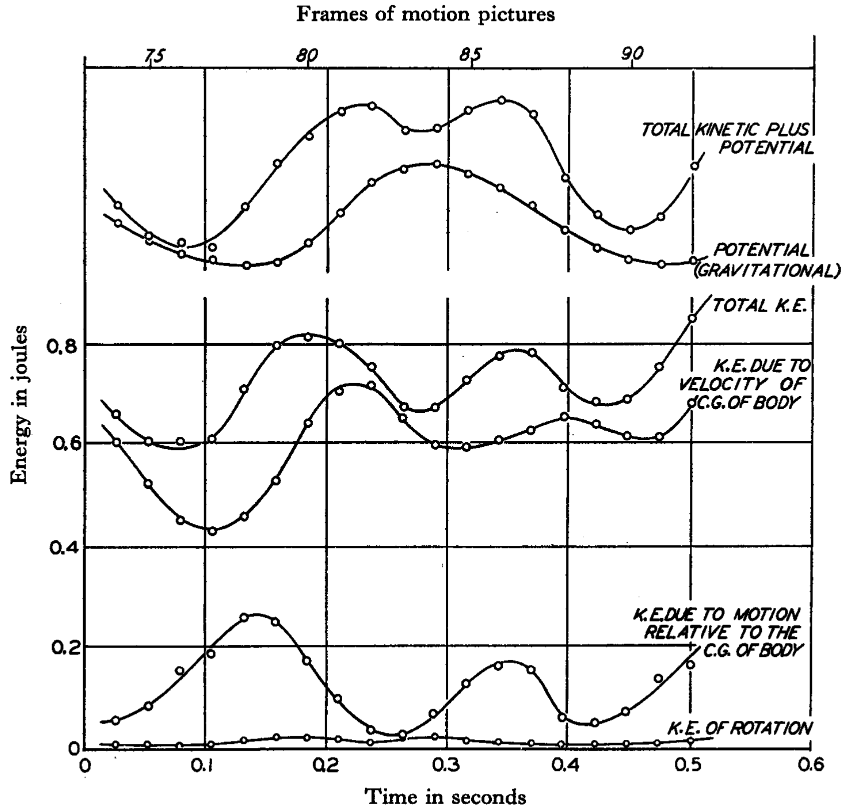

Fig. 9. Energy of the body during walking. Record No. 19. Potential energy plotted to the same scale but with different base line. Ergs have been converted to joules to avoid large numbers.

The first of these terms represents a component due to translation of the mass centre of the segment. The second term, which is due to rotation about the centre of gravity, contributes but little to the total since the moments of inertia of limb segments are relatively small and the angular velocities of the segments are also small. Values for the kinetic energy of the body during the walk are shown in Fig. 9.

The kinetic energy of the body can be divided into portions, one equivalent to that which the body would have if its mass were concentrated at the centre of gravity, and a second which results from motion of segments of the body relative to the centre of gravity. The first portion was calculated as $\frac{1}{2}MV^2$, M = mass of the whole body and V = velocity of its centre of gravity (Fig. 9). On subtracting this amount from the total kinetic energy a quantity is obtained which represents the kinetic energy contributed by the motion of parts relative to the mass centre. This kinetic energy of relative motion fluctuates from near zero to more than one-fourth the total kinetic energy of the body. It is associated with the motion of the limbs, an action which involves a period of high velocity as the foot is brought forward, followed by a period of low velocity while the foot carries out a propulsive stroke. As the kinetic energy of the limbs increases, mechanical work is done on them, presumably by the action of muscles. This factor of energy expenditure cannot be eliminated in animal locomotion and, as higher speeds are employed, an increasingly greater demand of muscular work will follow, since kinetic energy increases with the square of velocity.

The total kinetic energy of the body fluctuates about an average value in a regular fashion during the course of locomotion. At a time when total kinetic energy is increasing a transfer of energy from some other source is being effected. Similarly, while the kinetic energy of the body is decreasing, some of this energy is being converted into energy of a different sort. The body possesses potential energy due to its position above the ground equal to Mgh (ergs) (M = mass in grams, g = gravitational constant, h = height of the centre of gravity in cm.). If kinetic energy were transferred into gravitational potential energy, it could be stored momentarily and allowed to reappear at a later point in the locomotor cycle. The curve obtained by adding total kinetic energy and gravitational potential energy fluctuates almost as much as the curve for kinetic energy alone (Fig. 9). This demonstrates that the changes which occur in kinetic energy cannot be fully accounted for as transference to potential energy but must involve other energy sources such as muscles.

The action of muscle tensions

An analysis of locomotion requires interpretation not merely in terms of external force, but in terms of internal forces of muscle tension which are applied through the agency of the locomotor apparatus to produce these external forces. The internal forces which muscles can produce are capable of moving parts of the body, but unless external resistance is encountered they cannot move the centre of gravity of the body from rest. Muscles perform the work of locomotion but in order to initiate and to regulate motion they must act against an external resistance which, in the case of land living animals, is the earth's surface.

If imaginary sections are passed through the joint axes connecting one rigid segment of the cat with other parts of the body, that segment may be treated as a separate, free body. In accordance with D'Alembert's principle the external forces which act on it, and the reversed effective forces satisfy equilibrium conditions from which unknown forces of reaction at the joint and of tension about it may be solved. Following this procedure a tentative analysis of muscle forces in action about the joints of the limbs of the cat in walking has been made.

In the construction of a free-body diagram of a segment all the external forces which act on it must be represented. Such a diagram of the hind foot during one phase of its contact with the ground is given in Fig. 10. The external forces acting on this segment are the following:

The reaction at the surface of contact with the ground. These forces were measured separately for each foot at discrete instants during the step and are represented in the free-body diagram by appropriate vectors.

The reactions at the proximal end in contact with the adjacent segment. This force consists of a compression stress as long as the foot remains on the ground. It is represented in the free-body diagram in two components, one in the vertical direction and one in the horizontal which remain to be solved.

The actions of muscles, tendons and ligaments. These structures are transected by the section and whatever tensions they may possess now become external forces.

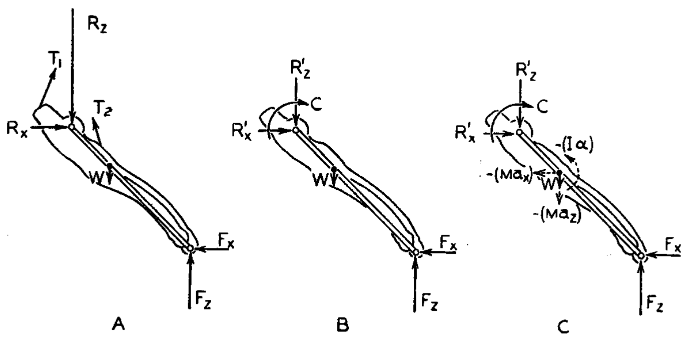

Fig. 10. Free-body diagrams of the hind foot. A, external forces shown; B, external forces with muscle action shown as a resultant couple; C, reversed effective forces (dotted) included. F_z, F_x = reactions through contact with the ground; R_z, R_x = forces of reaction at the joint; R_z', R_x' = forces of reaction without the portion contributed by muscle action; T_1, T_2 = muscle tensions; C = resultant couple produced by muscle action; W = gravity acting at the mass centre; m = mass; a_z, a_x = linear components of acceleration; α = angular acceleration.

No distinction can be made between tensions originating in muscles and that which might exist in ligaments. However, R. Fick (1910) has shown that ligaments do not play an important part in restricting normal movements of the limbs. The limbs of the cat do not reach the limit of their range of movement in walking and the tensions produced about the joints are probably due to muscle action rather than to the stretching of ligaments. Borelli (1679) recognized that tension is applied equally at each end of a muscle and this fact has received appropriate emphasis from Fischer (1906). Each muscle passing over a joint has a dual action, the production of parallel forces of tension exerted on the adjacent segments and a compression stress of equal magnitude acting at the contact of the joint surfaces of the segments. The total effect of the action of a one-joint muscle can be most simply represented by two equal and opposite couples, one on each of the adjacent members on which the muscle acts. The action of a two-joint muscle can also be resolved into a number of couples as is shown in Fig. 11. Since the resultant of any number of couples is also a couple, the resultant action of all muscles which produce tensions about a joint axis is a single couple. This resultant represents the difference between moments of muscle tensions which tend to rotate the member in opposite directions. It is indicated in the free-body diagram by a curved arrow.

The effective force system is equivalent to the resultant of all the external forces acting on the body which cause it to possess its momentary acceleration characteristics. The addition of this force system, reversed in direction, in the free-body diagram, is exactly sufficient to place the system in static balance. The following components comprise the effective force system:

ma_z, a force acting at the centre of gravity in the z direction,
ma_x, a force acting at the centre of gravity in the x direction.
$I\alpha$, a torque acting on the segment,

where m = mass of the segment, a_z, a_x = linear components of acceleration, α = angular acceleration, I = moment of inertia about the centre of gravity.

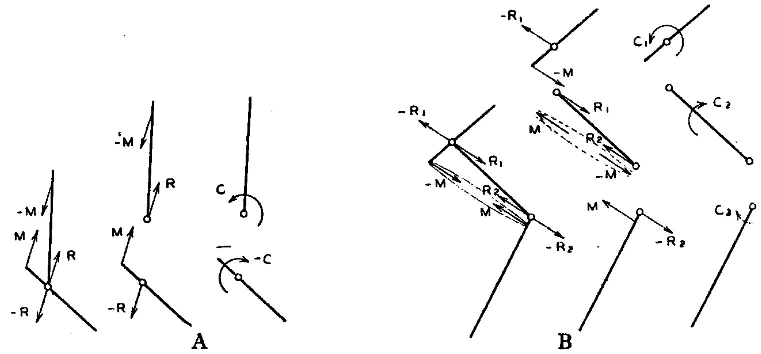

Fig. 11. A, action of a one-joint muscle in producing couples; B, action of a two-joint muscle in producing couples; M = tension in the muscle; R = reaction at the joint; C = couple produced by muscle tension and the reaction to it at the joint.

Masses, moments of inertia, linear and angular accelerations have been obtained by methods previously described. Since forces are expressed in grams, masses and moments of inertia were converted to gravitational units in calculating effective forces. When these effective forces (reversed in direction) have been included in the free-body diagrams (Fig. 10), the appropriate equations of equilibrium are applicable:

The algebraic sum of vertical forces ... ... $(\Sigma F_z) = 0$.
The algebraic sum of horizontal forces ... ... $(\Sigma F_x) = 0$.
The algebraic sum of moments about the centre of gravity $(\Sigma M_{c.g.}) = 0$.

From these three independent equations the forces of reaction and the muscle torque about the joint may be calculated.

In constructing the free-body diagrams of the foot one factor requires special consideration. Although the magnitude and direction of the external reactions on the sole of the foot were measured, it was not feasible to determine the precise point of application of the resultant of this reaction. An estimated position, inferred from the nature of the step, was used for the period toward the end of the step when the pressure under the foot shifts forward in the region of the toes. The correction which has resulted by taking this into account is indicated in Fig. 12. General features of the final results are not greatly changed.

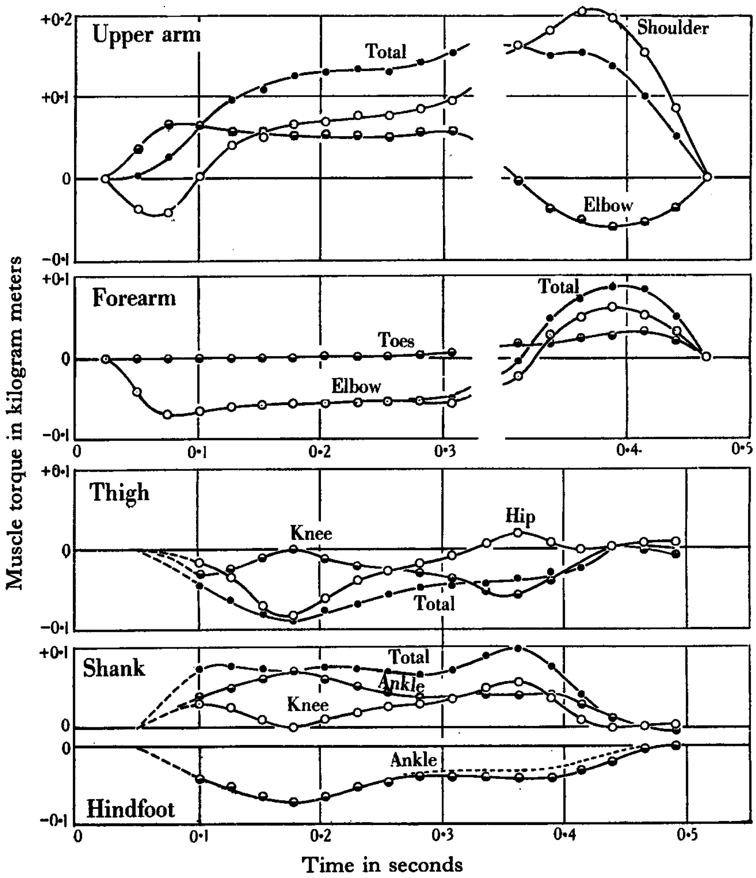

Fig. 12. Muscle torques acting about the joints of the limbs during walking, calculated for the portion of the step in which the foot is on the ground. The first portions of the forelimb curves are based on data for the left leg, the last portions are from the right leg. The dotted curve of torque on the hindfoot is the torque obtained if no correction is made for tension about the joint between the metatarsals and the toes. Record No. 19.

After the solution of the free-body diagrams for the foot, it is possible to proceed to the adjacent segment (shank) using the values which have been determined for the forces at and about the ankle joint. In this manner muscle torques about each of the joints of the fore- and hindlimbs were calculated for each phase of the period during which they make contact with the ground. Results of these calculations are given in Fig. 12.

If all the principal muscles which pass over a joint are considered with careful regard to the action of the torques which they are capable of producing, the action of different muscles at different times during the step can be specified. To avoid possible ambiguity rotations and torques are considered positive if their direction is counter-clockwise in the animal when viewed from the right side. Although actual torques cannot be assigned to antagonistic muscle groups from the calculated value of their resultant action, these data do specify which of the two has the predominant effect and its measured amount at any moment during the step.

Muscle action in the forelimb

The main action about the shoulder joint is a very large torque developing gradually and reaching its maximum late in the step. The large scapular muscles (supraspinatus, infraspinatus and subscapularis) are of major importance in this action with the possible assistance of the biceps brachii and clavo-brachialis. Tension in these muscles is necessary to support a large proportion of the body weight which is transmitted to the forelimb through the serratus anterior and the scapular blade. In addition to this function of static support the maximum torque in these muscles coincides with the production of an upward and forward thrust by the forelimb which contributes to the acceleration of the mass centre of the body.

Muscles develop greater tensions when they contract isometrically and it is noteworthy that the large scapular muscles act normally under circumstances approaching this condition since they do not shorten more than 2 mm. during walking. With leverage of less than 1 cm. they develop a torque of approximately 0·20 kg. metres, or a tension of about 20 kg. This indicates that extremely large tensions occur in muscles as they perform normal functions in the animal as well as in maximal contractions of isolated muscles in the laboratory.

For the first three-fourths of the step the torque at the elbow-joint is in the proper direction to be produced by the triceps brachii alone. Its action is fairly strong until the latter part of the step when the predominating torque is in the opposite direction. This could be assigned to any or all of the following muscles: biceps brachii, brachialis, clavo-brachialis or the extensors of the hand.

Muscle action in the hindlimb

The most significant feature of the muscle torques produced on the thigh are the maxima occurring about the hip-joint in the first half of the step and about the knee-joint near the end of the step. The hamstring group of muscles is the most powerful of the muscles capable of acting in the proper direction to produce the first maximum and it is likely that the most important action of the hamstrings occurs at this time. The torque which is developed about the knee could be produced only by the quadriceps femoris and the sartorius. This torque develops early in the step, dips toward zero, then rises gradually to reach its maximum near the end of the step. The drop which occurs could be due to a decrease in tension in these muscles, or it might be caused by an increase in the tension of muscles having opposing action, namely the hamstring group or the gastrocnemius. The fact that the hamstrings are probably in action at this time suggests that they are involved in this effect.

The foot is subjected to negative torque about the ankle during the entire step, a maximum being produced toward the end of the first third and another at the conclusion of the step. The first maximum should probably be attributed to the action of the triceps surae, the largest of those muscles which are in a position to produce negative torque. The flexors of the toes are active in maintaining a torque on the toes toward the end of the step and it is likely that they are responsible, at least in part, for the second maximum occurring at the ankle.

SUMMARY

The cat was used as a representative quadruped for a study of the action of the locomotor apparatus in walking. In the analysis the body was considered as being made up of eleven parts behaving in such a fashion that they could be considered as rigid bodies. The weight of each part was determined, the position of its centre of gravity and also its moment of inertia. Moving pictures were taken of the cat walking over a specially constructed platform which recorded the pressure exerted by each foot during the stride. The photographs recorded the position of the various parts of the body at successive instants. These records were analysed in terms of displacement, velocity and acceleration of the centre of gravity of the body as a whole, and also of its parts.

A comparison of vertical forces acting on single limbs of the cat during the walk shows that the reactions are greater on the forelimbs. This is not only due to the location of the centre of gravity nearer the forelimbs, but also is the result of a thrust produced at the forelimb which is largely responsible for an upward acceleration of the centre of mass of the body. Horizontal forces produced at the forefeet also tend to be greater than those at the hind. When horizontal impulse over the whole step is considered, it is shown that the forelimbs produce more retarding action, while the hindlimbs contribute more forwarding impulse to the body. The arrangement of steps is such that horizontal reactions on fore- and hindlimbs are antagonistic, thus damping fluctuations in horizontal acceleration and velocity of the centre of gravity with a probable saving in energy expenditure.

The kinetic energy of the body, derived from the data of the mass and velocity of separate parts, maintains an average level but undergoes cyclical changes during the stride. A possible transfer into gravitational potential energy can account for only a part of these kinetic energy changes which are thought to involve muscle action.

An analysis of the relationship between muscle forces about the joints and forces of reaction which co-operate to produce the recorded movement of an individual segment of the limbs allows the calculation of the resultant muscle torque acting on that segment. This provided actual measurements for the total muscle torque about each of the joints of the limbs at any instant. Correlation of these torques with the action of definite muscle groups indicates roughly the manner in which these muscles function in quadrupedal walking.

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