Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure

GIOVANNI A. CAVAGNA, NORMAN C. HEGLUND, AND C. RICHARD TAYLOR
Istituto di Fisiologia Umana dell’Università di Milano, Centro di Studio per la Fisiologia del Lavoro Muscolare del CNR, 20133 Milano, Italy, and Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138

CAVAGNA, Giovanni A., Norman C. Heglund, and C. Richard Taylor. Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. Am. J. Physiol. 233(5): R243-R261, 1977 or Am. J. Physiol.: Regulatory Integrative Comp. Physiol. 2(3): R243-R261, 1977. – The work done during each step to lift and to reaccelerate (in the forward direction) and center of mass has been measured during locomotion in bipeds (rhea and turkey), quadrupeds (dogs, stump-tailed macaques, and ram), and hoppers (kangaroo and springhare). Walking, in all animals (as in man), involves an alternate transfer between gravitational-potential energy and kinetic energy within each stride (as takes place in a pendulum). This transfer is greatest at intermediate walking speeds and can account for up to 70% of the total energy changes taking place within a stride, leaving only 30% to be supplied by muscles. No kinetic-gravitational energy transfer takes place during running, hopping, and trotting, but energy is conserved by another mechanism: an elastic "bounce" of the body. Galloping animals utilize a combination of these two energy-conserving mechanisms. During running, trotting, hopping, and galloping, 1) the power per unit weight required to maintain the forward speed of the center of mass is almost the same in all the species studied; 2) the power per unit weight required to lift the center of mass is almost independent of speed; and 3) the sum of these two powers is almost a linear function of speed.

ON FIRST CONSIDERATION, the methods which vertebrates have utilized to move along the earth's surface seem both diverse and complex. Some use two legs while others use four. They walk, amble, trot, pace, canter, gallop, and hop (19). Biologists have concentrated on describing differences between locomotory types, and detailed descriptions exist for the foot-fall patterns and the anatomic features associated with the different modes of locomotion (16, 17, 19).

In this paper we have tried to find mechanisms which are common to these different modes of terrestrial locomotion. We selected animals to represent what appear to be three very different types of locomotion: bipedal birds which walk and run (turkey and rhea); quadrupedal mammals which walk, trot, and gallop (dog, monkey, and ram); and bipedal mammals which hop (kangaroo and springhare).

We measured the forces applied by the animals to the ground as they moved at different speeds and used different gaits. These force measurements were used to calculate the mechanical energy which must be provided by the locomotory system to move the animal's center of mass forward relative to the ground. We considered only the situation after an animal had accelerated and reached a constant average speed. Locomotion at a constant average speed consists of a series of cycles (steps or strides), during which both the gravitational potential energy and the kinetic energy of the center of mass oscillate between maximum and minimum values as the center of mass rises, falls, accelerates, and decelerates. Forces must be applied to the ground to raise and reaccelerate the center of mass (12, 15), and mechanical work is performed (work = force × displacement). This has been called the external work output $W_{ext}$ of locomotion (7), and the rate at which this work is performed is then external power output ($P_{ext}$). $W_{ext}$ is only part of the total work done by the animal during locomotion. The muscles also perform work to change the kinetic energy of the limbs relative to the center of mass. This has been called the internal work output $W_{int}$ of locomotion; we did not measure $W_{int}$ in this study, but it has been measured for man (5), quail (10), and kangaroos (2) by other investigators.

Contracting muscles use chemical energy to supply some, but not necessarily all, or even most, of $W_{ext}$. Almost no additional energy would be required to maintain a constant forward speed of the center of mass, if the decrements of the gravitational potential energy (as the center of mass decreases in height during each stride) and the decrements of kinetic energy (as the animal slows during each stride) could be stored and/or used to reaccelerate and raise the center of mass during another part of the stride.

There are two mechanisms for alternately storing and recovering energy within each stride: 1) an exchange between gravitational potential energy and kinetic energy, as occurs in a swinging pendulum; and 2) an exchange between mechanical energy stored in muscle's elastic elements and recovered as both kinetic and gravitational energy, as in a bouncing ball. Both of these storage-recovery mechanisms have been found to be important for minimizing the chemical energy input required for $W_{ext}$ in human locomotion: the pendulum in the walk and elastic storage in the run (6–8, 13, 20). We wanted to know if these mechanisms are utilized in...
some regular way by all terrestrial vertebrates, and if so, how.

**MATERIALS AND METHODS**

**Animals**

We tried to achieve as great a diversity of locomotory modes as possible in our selection of animals. We chose a large bird, the rhea (*Rhea americana*, one animal weighing 22.5 kg) and a smaller bird, the wild turkey (*Meleagris gallopavo*, two animals each weighing 7 kg). Locomotion in these two bipeds could be compared with that of man, who had already been carefully studied with the same apparatus (9). Bipedal locomotion in birds looks quite different from that of humans, since the ankle of the bird occupies a similar position relative to the ground as the knee of humans. Thus the leg of a bird appears to bend in the opposite direction from a leg of a human.

For our quadrupedal animals we selected one which was a highly specialized and efficient runner and appeared to move gracefully and effortlessly at all speeds: the dog (*Canis familiaris*, a small terrier weighing 5 kg and a large mongrel weighing 17.5 kg). We compared the dog with another quadruped which was highly specialized to use its legs for nonlocomotory tasks, and which appeared to move awkwardly and inefficiently at all speeds (i.e., with its legs flailing and swinging in all directions): a monkey, the stump-tailed macaque (*Macaca speciosa*, two males, each weighing 3.6 kg). We selected the ram (*Ovis musimon*, two animals weighing 60 and 85 kg) because it was the largest quadruped we could conveniently find that was still within the capacity of our force plates.

We selected two hoppers which were very far apart phylogenetically: the kangaroo (*Megaalea rufa*, one female weighing 20 kg and one male weighing 21 kg), which is a marsupial, and the springhare (*Pedetes cafer*, one animal weighing 2.5 kg), which is a rodent. This suggests that their saltatory modes of locomotion have evolved independently.

**Procedures**

The horizontal and vertical components of the resultant force applied by the animal to the ground were measured by means of a force platform. The lateral movements were disregarded. The animals were not restrained in any way when they ran across the force platform. We called, coaxed, or chased them (more or less vehemently) to achieve a range of speeds. The animals were not restrained in any way when they ran across our force plates (Fig. 1). In fact it was often not possible to identify which record came from which animal without knowing the absolute values of the forces involved. A great deal of information (e.g., the patterns of thrust from individual feet) can be obtained from these records, but we have omitted this detailed information in this paper. Instead, we have concentrated on trying to understand general mechanisms which animals utilize to keep their center of mass moving forward at a constant average speed.

Walking in all of our experimental animals involved an alternate exchange between the kinetic energy and the gravitational potential energy of the center of mass within each stride. In this respect, walking is similar to a swinging pendulum or an egg rolling end-over-end (7). The mechanical energy which the muscles have to provide to keep the center of mass moving forward is decreased by the amount of this exchange which depends on three factors: 1) the phase relationship between the changes in kinetic energy and gravitational potential energy within the stride; 2) the relative magnitude of the two; and 3) the degree of symmetry between the two (i.e., how closely they approximate mirror images of each other).

If the kinetic and gravitational potential energy changes are 180° out of phase, if their magnitudes are equal, and if the changes are symmetrical, then the muscles will not need to provide any additional energy to keep the center of mass moving, provided of course friction and wind resistance are neglected. The amount of muscular work required to keep the center of mass of a walking animal moving at a constant speed will depend on the deviation of the measured kinetic and potential energy changes from this optimal condition.

**Phase relationship between kinetic and gravitational potential energy**. The phase relationship between the

...
<table>
<thead>
<tr>
<th>Symbol</th>
<th>Meaning</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\tilde{\alpha}_f$</td>
<td>average deceleration forward of the center of mass taking place at each step as a consequence of the impact with the ground, $-\tilde{\alpha}<em>f = -\Delta V_f/t</em>{dec}$, where $-\Delta V_f$ is a decrement of $V_f$ and $t_{dec}$ is the time during which this decrement takes place</td>
</tr>
<tr>
<td>$E_e$</td>
<td>elastic energy stored during the negative work phase of each step and delivered during the positive work phase</td>
</tr>
<tr>
<td>$E_{kf}$</td>
<td>kinetic energy of forward motion of the center of mass</td>
</tr>
<tr>
<td>$E_{kv}$</td>
<td>kinetic energy of vertical motion of the center of mass</td>
</tr>
<tr>
<td>$E_p$</td>
<td>gravitational potential energy of the center of mass</td>
</tr>
<tr>
<td>$E_{tot}$</td>
<td>total mechanical energy of the center of mass, $E_{tot} = E_{kf} + E_p + E_{kv}$</td>
</tr>
<tr>
<td>$f$</td>
<td>step or stride frequency</td>
</tr>
<tr>
<td>$F_r$</td>
<td>horizontal component of the resultant force exerted by the feet against the ground</td>
</tr>
<tr>
<td>$g$</td>
<td>acceleration of gravity</td>
</tr>
<tr>
<td>$K$</td>
<td>slope of a linear relationship, starting from the origin, calculated for the function $-\tilde{\alpha}_f = f(V_f)$; i.e., $K = -\tilde{\alpha}_f V_f$</td>
</tr>
<tr>
<td>$K'$</td>
<td>$K' = K \cdot (t_{dec}/t_f)$</td>
</tr>
<tr>
<td>$L$</td>
<td>length of the step or stride, $I = \bar{V}_f \tau$</td>
</tr>
<tr>
<td>$L_c$</td>
<td>forward displacement of the center of mass taking place during each step or stride while the body is in contact with the ground, $L_c = \bar{V}_f t_c$</td>
</tr>
<tr>
<td>$L_{dc}$</td>
<td>forward displacement of the center of mass taking place at each step of walking when both feet contact the ground, $L_{dc} = \bar{V}<em>f t</em>{dc}$</td>
</tr>
<tr>
<td>$L_{wc}$</td>
<td>forward displacement of the center of mass taking place at each step of walking when one foot only is in contact with the ground, $L_{wc} = \bar{V}<em>f t</em>{wc}$</td>
</tr>
<tr>
<td>$m$</td>
<td>body mass</td>
</tr>
<tr>
<td>$P$</td>
<td>body weight</td>
</tr>
<tr>
<td>$S_f$</td>
<td>sum of the upward displacements of the center of mass taking place during a cycle of movement $\tau$; $S_f = W_{ext}/P$</td>
</tr>
<tr>
<td>$t_{act}$</td>
<td>fraction of the period $\tau$ during which the forward speed $V_f$ increases</td>
</tr>
<tr>
<td>$t_c$</td>
<td>fraction of the period $\tau$ during which the feet contact the ground</td>
</tr>
<tr>
<td>$t_{dec}$</td>
<td>fraction of the period $\tau$ during which the forward speed $V_f$ decreases</td>
</tr>
<tr>
<td>$t_e$</td>
<td>fraction of the period $\tau$ during which the body is off the ground</td>
</tr>
<tr>
<td>$\bar{V}_O_2$</td>
<td>rate of oxygen consumption, above the rest rate, which we have converted to metabolic power input using the energetic equivalent of 4.8 cal/ml O$_2$</td>
</tr>
</tbody>
</table>

Changes in kinetic and gravitational potential energy can be easily seen from the records of instantaneous kinetic and potential energy of the center of mass over a series of strides in Fig. 2 (computed from the force and velocity data presented in Fig. 1). The top line of each experiment in Fig. 2 represents the kinetic energy due to the velocity of the center of mass in the horizontal direction ($E_{hf}$), the two middle lines (which almost completely overlap) are the gravitational potential energy ($E_p$) and the sum of the gravitational potential energy plus the kinetic energy due to the velocity of the center of mass in the vertical direction ($E_{kv}$). The kinetic energy in the vertical direction ($E_{kv}$) is so small compared to $E_p$ that two separate lines representing $E_p$ and $E_p + E_{hv}$ can only be distinguished in a few of the records (e.g., the rhea walking at 3.7 km h$^{-1}$). The records of the turkey and the rhea clearly show that at slow walking speeds $E_{hf}$ is at its maximum when $E_p$ is at its minimum, i.e., they are almost completely out of phase; as the animals walk faster, $E_p$ and $E_{hv}$ become more and more in phase with one another (compare the experiments where the turkey walks at 3.4 km h$^{-1}$ vs. 4.6 km h$^{-1}$ or where the rhea walks at 2.2 km h$^{-1}$ vs. 5.1 km h$^{-1}$). The bottom line in Fig. 2 ($E_{tot}$) is the instantaneous sum of $E_{hf}$ and ($E_p + E_{hv}$). When the two curves are 180° out of phase, the oscillations of $E_{tot}$ are less than those of $E_{hf}$ or ($E_p + E_{hv}$) individually by the amount of the exchange between the two (see Fig. 2, man walking at 3.9 km h$^{-1}$). When the $E_{hf}$ and the ($E_p + E_{hv}$) curves are almost completely in phase, little exchange is possible, and the increments of $E_{tot}$ approach the sum of the increments of the two curves (see Fig. 2, ram walking at 4.6 km h$^{-1}$). Other experiments in Fig. 2 show a range of phase relationships between these two extremes. **Magnitude of kinetic and gravitational potential energy changes.** In a simple pendulum the change in gravitational potential energy ($\Delta E_p$) will equal the changes in kinetic energy in the forward ($\Delta E_{hf}$) and vertical directions ($\Delta E_{hv}$) at each instant in time.

$$\Delta E_p = \Delta E_{hf} + \Delta E_{hv}$$  \hspace{1cm} (1)
FIG. 1. Experimental records obtained during walking. Each set of records indicates from bottom to top: vertical force exerted by the feet against the ground \((F_y)\), oscillations of vertical component of velocity of the center of gravity \((V_y)\), forward component of force exerted on the ground \((F_x)\) and oscillations of forward component of velocity of the center of gravity \((V_x)\). Positive values of \(F_y\) indicate a backward push of the foot against the ground; during this push the forward velocity \(V_x\) increases; the opposite occurs when \(F_y\) is negative. Velocity tracings begin and end when the animal crossed two photocells over the platform. Meaning of integration constant is described by Cavagna (3). For turkey and rhea, records are given for different speeds of walking to show modifications of the tracings with speed. Note similarity of records between different animals and man.

3), and the transfer of kinetic energy into gravitational potential energy could only take place between \(E_{kf}\) and \(E_{kg}\). Alexander has concluded that most of the energy used during this stiff-legged walking would go into replacing the \(\Delta E_{kg}\) lost during each step. It would therefore be advantageous to keep \(\Delta E_{kg}\) small. One way to do this is to keep the amplitude of the swing small. For example, in Fig. 3 (top) \(\Delta E_{kg} = \Delta E_{dr}\) when \(\varphi\) is 45° and \(\Delta E_{kg} > \Delta E_{dr}\) when \(\varphi < 45°\). It can be seen clearly in Fig. 2 that walking animals keep \(\Delta E_{kg}\) small, in fact it never exceeds 6% of \(\Delta E_{dr}\).

Not only is \(\Delta E_{kg}\) small during walking, but it appears also to be converted directly into \(\Delta E_{kg}\) by the application of a force normal to the direction of the velocity of the center of mass as it falls forward. The extension of the back foot which occurs during walking (9) may apply
just such a normal force (Fig. 3, bottom). Also the center of mass continues to fall after the front foot hits the ground during part of the period of double support. If the two feet act to apply a resultant force normal to the direction of the velocity of the center of mass during this time, then there could also be a transfer of $E_{kr}$ into $E_{kr}$. Our records of the potential energy changes of the center of mass before and during the period of double contact show that $E_p$ decreases gradually as the center of mass approaches its lowest point (as in Fig. 3, bottom); this is consistent with a transfer of $E_{kr}$ into $E_{kr}$.

How do the relative magnitudes of $\Delta E_p$ and $\Delta E_{kr}$ compare during walking in bipedal birds and quadrupedal mammals? Summing the increments of $(E_p + E_{kr})$ over a stride gives the positive work done against gravity ($W_v$) and dividing by the stride period gives the average power ($W_v$). Forward work ($W_f$) and dividing by the stride period gives the average forward power ($W_f$). Mass specific power, $W_{fr/m}$ and $W_{fr/m}$, is plotted as a function of walking speed in Fig. 4. Using these graphs it is easy to compare the relative magnitudes of the positive energy changes in $E_p$ and $E_{kr}$ and to see how they vary as a function of walking speed. In both birds (rhea and turkey) $W_v \approx W_f$ at the slowest walking speeds, and $W_f \approx W_v$ at the highest walking speeds as has been found in man (9). There is a similar trend in the ram, but at its highest walking speeds $W_f \approx W_v$. In the dogs $W_f \approx W_v$ over the entire range of walking speeds and in the monkey $W_v > W_f$ over the entire range of speeds. The point which emerges from the measurements of $W_f$ and $W_v$ is that their relative magnitudes are often similar during walking. Therefore, from the viewpoint of relative magnitude alone, it is possible to have a significant transfer of energy between kinetic and gravitational potential

FIG. 2. Experimental records of mechanical energy changes of center of mass of body during walking. Curves were calculated from records of Fig. 1; they were drawn directly using the plotter output of a computer. In each set of tracings, the upper curve refers to kinetic energy of forward motion $E_{kf} = \frac{1}{2} m V_f^2$; the middle curve to the sum of gravitational potential energy $E_p$ and kinetic energy of vertical motion $E_{kr} = \frac{1}{2} m V_r^2$; the bottom curve to total energy $E_{tot} = E_{kf} + E_p + E_{kr}$. Curves $E_p$ and $(E_p + E_{kr})$ are also given (thin line), but often they cannot be distinguished from $(E_p + E_{kr})$ and $E_{tot}$ curves, since $E_{kr}$ is very small in walking. Note that at low and average speeds $E_p$ and $E_{kr}$ change in opposition of phase as in a pendulum.
energy within the stride in all of the animals. How important is the exchange between kinetic and gravitational potential energy within each stride? As mentioned at the beginning of this discussion, phase angle and the relative amplitude of kinetic and potential energy changes are only two of the factors which determine the completeness of the exchange between kinetic and gravitational potential energy; symmetry is also important. The two changes plotted as a function of time must be mirror images of one another if the exchange is to be complete. If there is an increase in potential energy without a simultaneous and equal decrease in kinetic energy, then contracting muscles (or stored elastic energy) must provide the missing energy. Likewise, if there is a decrease in potential energy without a corresponding increase in kinetic energy, the energy must either be lost as heat, or stored in elastic elements.

Perhaps the simplest way to quantify the net effect of all three parameters is to compare the magnitude of the power output required to maintain a constant walking speed if there were no exchange ($|W_d| + |W_e|$) with the amount of power actually expended ($W_{ext}$). $W_{ext}$ can be calculated from $E_{tot}$ (Fig. 2) by summing all the increments in $E_{tot}$ over a stride and dividing by stride period, just as $W_d$ and $W_e$ were calculated from $E_{kf}$ and $(E_p + E_{el})$. This was done and $W_{ext}$ is plotted as a function of walking speed in the second (from the top) set of graphs in Fig. 4. The magnitude of the exchange between gravitational potential energy and kinetic energy is then equal to the total power, which would be required if there were no exchange ($|W_d| + |W_e|$) minus $W_{ext}$. This difference can be expressed as a percentage of the total power required with no exchange

$$\% \text{ recovery} = \frac{|W_d| + |W_e| - W_{ext}}{|W_d| + |W_e|} \times 100 \quad (2)$$

If the exchange were complete, then $W_{ext}$ would be zero, and the recovery would be 100%.

Percentage recovery is plotted as a function of walking speed in the third (from the top) set of graphs in Fig. 4. The figure shows clearly that there was a large exchange between gravitational potential energy and kinetic energy during walking in all of our animals. This exchange reached a maximum at intermediate walking speeds in bipeds: 70% in the rhea at 3-4 km·h⁻¹, and 70% in turkeys at 3-4 km·h⁻¹. The exchange declined at slower and faster walking speeds. This is identical to the situation which Cavagna et al. (9) found in man, and their curve has been plotted as a dotted line in the graph of percent recovery for the turkey for comparison. Percent recovery in the quadrupedal ram also reached a maximum (35%) at intermediate walking speeds (3-4 km·h⁻¹) and decreased at slower and faster speeds. In dogs and monkeys, percent recovery reached values of 50%, but it did not change in a regular way with speed.

The external work required to move one kilometer has been calculated by dividing $W_{ext}$ by speed and is plotted in the bottom set of graphs in Fig. 4. It appears that there is an optimal walking speed for both birds and the ram, where $W_{ext}$ to move a given distance is minimal and the exchange between gravitational potential energy and kinetic energy is maximal. This is also the case for man (9) as can be seen from the dotted line in the turkey graph.

Running, Trotting, and Hopping

Just as we had found a remarkable similarity in the force and velocity records obtained during walking (Fig. 1), we also found a striking similarity in the force and velocity records of humans, birds, dogs, monkeys, rams, kangaroos, and springhares as they ran, trotted, or hopped across the force plates (Fig. 5). Running, trotting, and hopping animals all used their muscles to push upward and forward simultaneously during one part of the stride and to break their fall and slow their forward speed simultaneously in another part of the stride. There was usually, but not necessarily, an aerial phase. The relative proportion of the time spent in the air was largest in the hoppers (up to 75% of the step period), intermediate in runners (up to 30% of the step period), and smallest in the trotters (0-15% of the step period). It is easy to identify this aerial phase on the
MECHANISMS OF TERRESTRIAL LOCOMOTION

BIPEDS

QUADRUPEDS

FIG. 4. Top set of graphs gives power required to lift center of mass \( W_c \) and to reaccelerate center of mass in the forward direction \( W_f \) during each step of walking at different speeds. Second (from the top) set of graphs gives total external power \( W_{ext} \) as a function of walking speed. Third set of graphs gives percent recovery of mechanical energy (Eq. 2) resulting from an exchange between gravitational potential energy \( E_g \) and kinetic energy of forward motion \( E_{kv} \). Bottom set of graphs gives external work per unit distance \( W_{ext}/(\text{kg-km}) \).

force and velocity records of Fig. 5, since both \( F_f \) and \( F_v \) are zero when the animal is not touching the plate. Also \( V_f \) remains constant and \( V_v \) changes at a rate of 9.8 m/s^2 due to the acceleration of gravity.

Phase relationship and exchange between kinetic and gravitational potential energy within each stride. Energy changes due to the motion in the vertical \( E_g + E_{kv} \) and forward \( E_{kv} \) directions were always almost completely in phase during running, trotting, and hopping (Fig. 6); therefore there was little possibility for an exchange between the two. \( W_{ext} \sim |W_f| + |W_c| \) and percent recovery calculated using Eq. 2 was nearly zero (Fig. 7).

\( E_{kv} \) becomes quite large in parts of the stride during running (much greater than during walking). It reaches maximum values twice: at the instant the animal leaves the ground (easily seen in Fig. 6 as the point where \( E_p + E_{kv} \) becomes constant) and at the instant the animal lands (seen in Fig. 6 as the point where \( E_p + E_{kv} \) starts to decrease again). After the animal leaves the ground, \( E_{ext} \) decreases as the center of mass rises, until it is completely converted into \( E_p \) when the center of mass reaches its maximum height. At this instant the vertical velocity is zero and the \( E_p \) and \( E_{kv} \) curves in Fig. 6 coincide. Then the animal begins to fall as \( E_p \) is converted into \( E_{pv} \); this then decreases as
RUN = HOP = TROT

**Magnitude of kinetic and gravitational potential energy changes.** Perhaps the most unexpected and intriguing finding of this study was that the mass specific power output for reaccelerating the center of mass (in the forward direction) was nearly the same for bipedal running, quadrupedal trotting, and hopping when plotted as a function of speed ($W/m$ in Fig. 8). In all of the animals $W/m$ seemed to approach zero at zero running speed and increased more and more steeply with increasing speed. The functions relating $W/m$ and speed for birds, springhares, kangaroos, dogs, monkeys, and rams are almost completely superimposable. Even the data which Cavagna et al. (9) obtained from humans in running (dotted line in kangaroo graph in Fig. 8) are hardly distinguishable from the data from our diverse assortment of animals.

The mass specific power output for raising the center
of mass within each stride ($\dot{W}_m/m$ in the top set of graphs in Fig. 8) was almost independent of running speed in all of the animals. Since the vertical displacement of the center of mass $S_v$ generally decreased with increasing speed (Fig. 9) and

$$\dot{W}_m/m = S_v \cdot g \cdot f \approx \text{const}$$

(where $g$ is the acceleration of gravity) an increase in stride frequency $f$ must compensate for the decrease of $S_v$. $\dot{W}_m/m$ was greater in hopping than in running or trotting as a result of the greater vertical displacement of their center of mass. $S_v$ does not seem to depend on body mass alone, nor on the overall dimensions of the body; e.g., in the springhare (2.5 kg), $S_v$ is greater than in the ram (85 kg). It seems more likely that $S_v$ depends on the peculiar characteristics of the elastic system on which the body bounces at each step. For example when the kangaroo decelerates downward and forward, its feet are flexed so that the Achilles tendons are stretched storing elastic energy. In order to release this elastic energy an extension of the feet is necessary, but this implies an appreciable upward displacement of the body of the order of magnitude of the dimensions of the foot of the kangaroo (Fig. 9). In other words, to
Utilize the elastic energy stored by his elastic system, the kangaroo must "jump over his feet."

In running, trotting, and hopping the mass specific power for external work \( (W_{ext}/m) \) is

\[
W_{ext}/m = |W_p/m| + |W_g/m|
\]

since there is no exchange between \( E_p \) and \( E_{kp} \). \( W_{ext}/m \) increased linearly in all the animals with increasing speed as in man (Fig. 8). The equations for these lines, calculated using the method of least squares, are given in Table 2. The high correlation coefficients for a linear relationship indicate that the curvilinear relationship for \( W_p/m \) must be compensated for by a curvilinear relationship for \( W_g/m \) as has been described for man (9). Thus \( W_p/m \) is probably not independent of speed but our data are too scattered to define this relationship precisely.

Is there storage and recovery of mechanical energy in elastic elements? Measuring the magnitude of the exchange between kinetic energy and gravitational potential energy is easily done and its importance can be quantified as percent recovery using Eq. 2. Determining the magnitude of an exchange between kinetic and/or gravitational potential energy and elastic potential energy \( (E_e) \) is much more difficult. There is a way, however, to approach the question of elastic storage using our force plate measurements (8). We can compare the mechanical power output of the animal with its chemical power input and define the efficiency (\( \gamma \)) with which an animal converts stored chemical energy into positive mechanical work as

\[
\gamma = \frac{W_{ext} + W_{int}}{W_{metab}}
\]

where \( W_{ext} \) is external power output, \( W_{int} \) is internal power output, and \( W_{metab} \) is the chemical power input into the muscles for locomotion \( (W_{metab} \) during locomotion, \( -W_{metab} \) at rest).

The maximum efficiency with which muscles can convert chemical energy into positive mechanical work is about 0.25. If the efficiency of locomotion at steady state exceeds 0.25, then the explanation has to be storage and recovery of energy using muscle's elastic elements. Neglecting the cost of negative work, the efficiency with which the contractile machinery of muscle transforms chemical energy into positive work becomes

\[
\gamma_m = \frac{(W_{ext} + W_{int}) - W_e}{W_{metab}}
\]

where \( W_e \) is the power output delivered free of cost during the recoil of stretched elastic elements (i.e., the energy stored during the deceleration, when the muscle performs negative work, and released during the sub-
Fig. 8. Above: mass specific power for raising center of mass against gravity within each stride, $W_{c/m}$ (top set of graphs); mass specific power for reaccelerating center of mass in the forward direction after the deceleration due to impact with the ground, $W_{r/m}$ (middle set of graphs); and mass specific power for total external work, $W_{ext/m}$, are plotted as a function of running speed. Curves through $W_{r/m}$ data were calculated using Eq. 18. Straight lines through $W_{ext/m}$ data were calculated using least-squares method (equations are given in Table 2). Dotted lines are data from man (9). Some values of $W_{c/m}$ for rhea and spring hare (open circles) have been calculated from the equation $W_{c/m} = \Delta V_f V_f f$, using data such as those in Fig. 5. All other values (closed and half closed symbols) were calculated as described in (3). Below: mass specific power data, given above, were divided by the average speed $V_f$ to obtain work done per unit distance, $W/(m \cdot L)$. 

**Table 2**

<table>
<thead>
<tr>
<th>Species</th>
<th>$W_{c/m}$ (cal/Mg.m)</th>
<th>$W_{r/m}$ (cal/Mg.m)</th>
<th>$W_{ext/m}$ (cal/Mg.m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring hare</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dogs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monkeys</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rams</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Fig. 8.** Above: mass specific power for raising center of mass against gravity within each stride $W_{c/m}$ (top set of graphs); mass specific power for reaccelerating center of mass in the forward direction after the deceleration due to impact with the ground $W_{r/m}$ (middle set of graphs); and mass specific power for total external work, $W_{ext/m}$, are plotted as a function of running speed. Curves through $W_{r/m}$ data were calculated using Eq. 18. Straight lines through $W_{ext/m}$ data were calculated using least-squares method (equations are given in Table 2). Dotted lines are data from man (9). Some values of $W_{c/m}$ for rhea and spring hare (open circles) have been calculated from the equation $W_{c/m} = \Delta V_f V_f f$, using data such as those in Fig. 5. All other values (closed and half closed symbols) were calculated as described in (3). Below: mass specific power data, given above, were divided by the average speed $V_f$ to obtain work done per unit distance, $W/(m \cdot L)$. 

**Table 2**

<table>
<thead>
<tr>
<th>Species</th>
<th>$W_{c/m}$ (cal/Mg.m)</th>
<th>$W_{r/m}$ (cal/Mg.m)</th>
<th>$W_{ext/m}$ (cal/Mg.m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhea</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring hare</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dogs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Monkeys</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rams</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
We have measurements of \( \dot{W}_{ext} \) and \( \dot{W}_{metab} \) for our animals, but not of \( \dot{W}_{int} \). However, if we calculate the efficiency of doing external work (\( \gamma' \)) from our data

\[
\gamma' = \frac{\dot{W}_{ext}}{\dot{W}_{metab}}
\]

and if \( \gamma' > 0.25 \) this clearly indicates a large amount of storage of energy in elastic elements, since \( \dot{W}_{r} \) must then account for both \( (\dot{W}_{ext} - 0.25 \dot{W}_{metab}) \) and all of the \( \dot{W}_{int} \) according to Eq. 7.

\( \gamma' \) has been calculated as a function of speed for all of the animals and is plotted in Fig. 10. It increases from about 0.10 to 0.15 as turkeys increase running speed from 5 to 20 km·h\(^{-1}\); from 0.25 to 0.27 as dogs increase trotting speed from 5 to 15 km·h\(^{-1}\); from about zero to 0.23–0.25 as monkeys increase trotting or galloping speed from 5 to 25 km·h\(^{-1}\); from 0.16 to 0.25 as springhares increase their hopping speed from 10 to 25 km·h\(^{-1}\); and from 0.24 to 0.76 as kangaroos increase their hopping speed from 10 to 30 km·h\(^{-1}\).
MECHANISMS OF TERRESTRIAL LOCOMOTION

TABLE 2. External power per unit of body mass ($W_{ext}/m$) relative to average forward speed ($V_f$)

<table>
<thead>
<tr>
<th>Quadrupeds</th>
<th>$W_{ext}/m$</th>
<th>$r$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dog, 5 kg, trot</td>
<td>9.84 + 1.98 $V_f$</td>
<td>0.945</td>
</tr>
<tr>
<td>Dog, 17.5 kg, trot</td>
<td>12.30 + 2.65 $V_f$</td>
<td>0.968</td>
</tr>
<tr>
<td>Dog, gallop</td>
<td>23.03 + 4.24 $V_f$</td>
<td>0.966</td>
</tr>
<tr>
<td>Monkey, trot</td>
<td>18.65 + 6.68 $V_f$</td>
<td>0.987</td>
</tr>
<tr>
<td>Monkey, gallop</td>
<td>39.57 + 8.05 $V_f$</td>
<td>0.936</td>
</tr>
<tr>
<td>Rama, trot</td>
<td>15.96 + 1.95 $V_f$</td>
<td>0.622</td>
</tr>
</tbody>
</table>

$W_{ext}/m$ is measured in cal/kg-min and $V_f$ is measured in km/h.

FIG. 10. External power output, $W_{ext}$, total energy expenditure calculated from the oxygen consumption, $W_{mee}$; data for birds from Fedak et al. (14), data for kangaroos from Dawson and Taylor (11), and data for springhares and dogs from unpublished measurements by Taylor; and efficiency of doing external work ($\gamma' = W_{ext}/W_{mech}$) are given as a function of speed. Dotted horizontal line indicates upper limit of 0.25 for efficiency of transformation of chemical energy into mechanical work by the contractile machinery of muscle. High $\gamma'$ values attained by some animals suggest a substantial recovery of mechanical energy through muscle elasticity.

We can reasonably conclude from the values of $\gamma'$ that dogs, monkeys, kangaroos, and springhares rely on power recovered from elastic elements. This can be very large; for example, when a kangaroo hops at 30 km-h$^{-1}$, $W_e$ amounts to a minimum of two-thirds of the measured $W_{ext}$ plus all the $W_{int}$.

It is interesting to note that $\gamma'$ often increases with increasing speed, suggesting that elastic storage and recovery become relatively more important at higher speeds. This is in agreement with the findings on man (5, 6) and on isolated muscle (4).

How does the external power absorbed and delivered when the animal is in contact with the ground change with speed? The muscles and tendons can absorb and deliver external power (thanks to external forces) only when an animal is in contact with the ground. During each step (or stride) there is a time when the animal is in contact with the ground ($t_c$) and a time when it is in the air ($t_a$).

$$\tau = t_c + t_a$$

where $\tau$ is the period of a repeating change in forward velocity and height of the center of mass. In both running and trotting there was a symmetrical change in forward velocity and height at each step: in this case $\tau$ is the period of a step. When the animal changed from a trot to a gallop there were no longer two symmetrical steps in each stride and $\tau$ became the period of a stride. Values of $t_c$ and $t_a$ were measured from the force records and are plotted in Fig. 11. The value of $t_a$ decreased markedly with increasing speed in all of our animals while $t_c$ either increased or remained constant. The increase in $t_a$ in Fig. 11 when animals changed from a trot to a gallop is the result of $\tau$ changing from the period of a step to the period of a stride.

The distance an animal moves forward while it is in contact with the ground can be measured fairly accurately from $t_c$ and $V_f$:

$$L_c = t_c V_f$$

because the oscillations in the speed around $V_f$ are small. Two curves are plotted in Fig. 11 using Eq. 10 for two values of $L_c$ which just bracket the observed values for $t_c$. These two values for $L_c$ approximate minimum and maximum values and show how $L_c$ changes with speed.

As speed increases, either $t_c$ must decrease and/or $L_c$ must increase. For a given $W_{ext}$/step, the power must increase as $t_c$ decreases. However, the power could be kept constant with increasing speed, if $L_c$ increases proportionately to $V_f$. Some animals increase $L_c$ appreciably as they move faster; however $t_c$ decreases in all animals, approaching a minimum value of about 0.1 s (also observed in man by Cavagna et al. (9)).

The animal decelerates and falls (i.e., performs negative work) during the first part of the time of contact ($t_{dec}$), and it accelerates and lifts its center of mass during the second part ($t_{acc}$).

$$t_c = t_{dec} + t_{acc}$$

Since $t_c$ decreases and $W_{ext}$ increases with increasing speed, the external power which must be absorbed and delivered by the muscles and tendons must increase. Both the external power which has to be dissipated and/or stored while the animal decelerates ($W_{ext}/t_{dec}$) and the external power which has to be recovered and/or supplied by the muscles while it reaccelerates ($W_{ext}/t_{acc}$) have been calculated (Table 3). In the turkeys $W_{ext}/t_{dec}$ is more than 60% greater than $W_{ext}/t_{acc}$. This would be expected from the force-velocity relationship of muscle: larger forces are developed when the muscles are stretched (during deceleration) than when they shorten (during acceleration). Thus muscles will require less time to decelerate the body than to reaccel-
Fig. 11. Time in which the feet contact the ground (t<sub>c</sub>, closed symbols) and in which the body is off the ground (t<sub>v</sub>, open symbols) during each step of running (circles and squares) and each stride of galloping (triangles) are given as a function of speed. Interrupted lines were constructed assuming that forward displacement when the body is in contact with the ground (L<sub>c</sub> = t<sub>c</sub> · V<sub>f</sub>) is independent of speed and equal to the indicated value.

Why do animals use nearly the same mass specific power to reaccelerate in the forward direction at a given speed? Cavagna et al. (9) derived an equation for the mass specific power output due to the forward speed changes in man

\[ W_m = K' \frac{V_f^2}{1 + \frac{t_c}{L_c} \cdot V_f} \]  

where \( K' = K \cdot t_{dec}/t_{acc} \), and \( K \) is the slope of a linear relationship found between the average deceleration forward of the center of mass during each step (\(-\ddot{a}_f\)) and the average speed of locomotion (\(V_f\)).
To see whether Eq. 12 applies generally to running, trotting, and hopping, we calculated values for the constant $K'$ and $t_{oL}$, for all our animals. $K'$ was calculated as follows: $-\alpha_f$ (measured from the force and velocity records) was plotted as a function of $V_f$, and a line for the best fit of a linear relationship between $-\alpha_f$ and $V_f$ (with its origin at zero) was calculated using the method of least squares. The slope of this line ($K$) was multiplied by an average value for $t_{oL}/L_c$ (taken directly from the force records and included in Table 4) to give $K'$. In all the animals except the kangaroo, $t_{oL}/L_c$ was independent of speed, and we were able to calculate average values for this constant (Table 4). In the kangaroo $t_{oL}/L_c$ increased linearly with $V_f$, and we used the equation for this linear relationship

$$t_{oL} (s \cdot m^{-1}) = 0.656 - 0.043 V_f (m \cdot s^{-1})$$

(13)

instead of a constant.

The relationships between $W/m$ and $V_f$, calculated using Eq. 12, are plotted as solid lines in the second from the top set of graphs on Fig. 8. The calculated lines are in good agreement with the experimental data, in spite of the many simplifications which we made when calculating the constants.

Both $K$ and $t_{oL}/L_c$ vary a great deal from animal to animal (Table 4), but they change in such a way that the relationship between $W/m$ and $V_f$ remains nearly the same in all our animals. Animals which have the largest $K$ (like the hoppers) also have the largest $t_{oL}/L_c$; thus the effect of a large $K$ on increasing $W/m$ is nearly exactly compensated for by a larger $t_{oL}/L_c$. This suggests that the animals which suffer a big forward deceleration when they land at a given speed (i.e., have a large $K$) increase the time which they spend in the air in order to minimize $W/m$ (Fig. 12). However, they have to pay a price for their large $t_{oL}/L_c$ in a greater $W/m$.

### Galloping

Like the two other modes of locomotion, galloping also involved a similar mechanism in all animals, although this might not be obvious when one first looks at the complex force and velocity tracings of galloping animals (Fig. 13). The force tracings are particularly difficult to interpret because of the "ringing" of the force plate. The artifacts due to these vibrations were excluded in our computations of energy changes (3).

### Table 4. Constants for equation relating $W/m$ and $V_f$ (Eq. 12 in text)

<table>
<thead>
<tr>
<th>Animal</th>
<th>$K$</th>
<th>$t_{oL}/L_c$</th>
<th>$t_{oL}/L_c$</th>
<th>$t_{oL}/L_c$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turkey</td>
<td>0.971</td>
<td>0.375 ± 0.043</td>
<td>0.329</td>
<td>0.133 ± 0.033</td>
</tr>
<tr>
<td>Rhea</td>
<td>0.514</td>
<td>0.412 ± 0.030</td>
<td>0.340</td>
<td>0.119 ± 0.035</td>
</tr>
<tr>
<td>Springhare</td>
<td>0.536</td>
<td>0.469 ± 0.030</td>
<td>0.251</td>
<td>0.116 ± 0.031</td>
</tr>
<tr>
<td>Kangaroo</td>
<td>1.120</td>
<td>0.451 ± 0.022</td>
<td>0.539</td>
<td>0.474 ± 0.057</td>
</tr>
<tr>
<td>Dog, trot</td>
<td>0.458</td>
<td>0.450 ± 0.040</td>
<td>0.656</td>
<td>0.576 ± 0.084</td>
</tr>
<tr>
<td>Dog, gallop</td>
<td>0.331</td>
<td>0.458 ± 0.045</td>
<td>0.141</td>
<td>0.054 ± 0.018</td>
</tr>
<tr>
<td>Ram, trot</td>
<td>0.442</td>
<td>0.508 ± 0.024</td>
<td>0.225</td>
<td>0.091 ± 0.004</td>
</tr>
</tbody>
</table>

$t_{oL}/L_c$ and $t_{oL}/L_c$ values are means ± SD. *In kangaroo $t_{oL}/L_c$ increases with $V_f$ as shown in Fig. 13. In table and in Fig. 12 an average value was used.

FIG. 12. Animals that suffer a large forward deceleration when they land at a given running speed (large $K$ on abscissa) increase the time they spend in air (large $t_{oL}/L_c$ on ordinate) to minimize $W/m$ (Eq. 12). See text.
It is much easier to refer to the energy records (Fig. 14) than to the force and velocity records in order to understand galloping. Motion pictures were taken simultaneously with the force and velocity measurements to determine the sequence of foot-fall patterns and to correlate these with the energy records. In this paper we will discuss the energy records from dogs to explain the mechanism of galloping, since essentially the same mechanism was found in the monkey and ram.

At slow speeds, galloping combines the two separate mechanisms utilized in walking and running. Within a stride there are times when $E_p$ is converted into $E_{kg}$, $E_{kg}$ is converted into $E_p$, and $E_p$ increases simultaneously with $E_{kg}$. As the animals gallop faster and faster, the exchange between gravitational potential energy and kinetic energy becomes smaller and approaches zero. At the highest galloping speeds the animal bounces first on its hind legs and then on its front legs.

**Phase relationship and exchange between kinetic and gravitational potential energy during each stride.** At slow galloping speeds, $E_p$ decreases while the average $E_{kg}$ increases after the two back feet contact the ground (the numbers 1, 2, 3, and 4 above the $E_{kg}$ line in Fig. 14 indicate the sequence of foot-falls beginning with the first rear foot). The decrease of $E_p$, simultaneous with the increase of $E_{kg}$ indicates a shift of gravitational potential energy into kinetic energy while the animal is falling forward. When $|\Delta E_{kg}| > |\Delta E_p|$, an additional
forward thrust must be provided by the muscles of the rear legs. After this, an aerial phase may take place (it takes place in the 17.5-kg dog galloping at 21.3 km·h⁻¹ whereas it does not in the 5-kg dog). The forward fall is stopped by the contact of the first front leg (no. 3 in Fig. 14). The dog then “pole vaults” over the second front leg (no. 4 in Fig. 14): this is indicated by an increase of \( E_p \) simultaneous with a decrease of \( E_{kf} \), i.e., \( E_{kf} \) is converted into \( E_p \). Since \( |\Delta E_{kf}| > |\Delta E_p| \) some of \( E_{kf} \) either goes into stored elastic energy or is lost as heat. After pole vaulting, the dog pushes upward and forward simultaneously off this second front foot; both \( E_p \) and \( E_{kf} \) increase, and the center of mass returns to its original height. An aerial phase usually takes place after this push-off until the first rear foot strikes the ground again and the cycle repeats itself. Thus there is little symmetry between the changes in \( E_p \) and \( E_{kf} \); sometimes during the stride they change in opposite directions, and other times they change in the same direction.

The percent recovery calculated using Eq. 2 jumps from about zero at the highest trotting speeds to about 30% at the slowest galloping speeds in dogs, monkeys, and rams (Fig. 7). As a result of this exchange \( W_{ext} \) dropped in all the animals as they changed from a trot to a gallop, even though the speed stayed the same or increased (Fig. 8). The value of \( \gamma' \) (calculated according to Eq. 8) decreased (Fig. 10), indicating less storage in elastic elements in a slow gallop than in a fast trot. Thus changing from a trot to a gallop involves changing...
from a mode of locomotion which relies heavily on elastic recovery to one which combines both the spring and the pendulum mechanisms.

As galloping animals increase their speed, the changes in $E_p$ and $E_{kf}$ become more and more in phase until at the highest speeds almost no exchange is possible. At these high speeds there are two bounces per stride, first off the back feet followed by an aerial phase, then off the front feet followed by a second aerial phase. At the highest speeds, the two front feet hit the ground almost simultaneously as do the two rear feet. The center of mass regains its initial height after each bounce, and there are two nearly identical changes in $E_p$, and $E_{kf}$ per stride which are in phase, just as in the trot. Therefore at the highest speeds $t_c$ and $t_v$ in Fig 11 and $S_r$ in Fig 9 (which is measured as $W_r P$) must be divided into half to calculate the period and displacement during each bounce. At intermediate speeds, when a decrease in height of the center of mass may occur within the stride, $S_r = \frac{W_r}{P}$ may indicate a vertical lift greater than the actual one.

**Magnitude of kinetic and gravitational potential energy changes.** $W_{ext}$ increases with speed during galloping in nearly the same manner as during running. The curves calculated using Eq. 12 ($t_c$ and $t_v$ are taken as the sum of the times of flight and of contact within the stride and $\alpha_f$ as the average of the forward decelerations taking place during the stride) fit the experimental data. There is little difference between $W_{ext}$ at a given speed whether a bird runs, a kangaroo hops, or a quadrupedal gallops. In addition, one monkey galloped at all speeds while the other monkey trotted at all speeds, yet there was no difference between the two functions relating $W_{ext}$ to $V_f$.

$W_{ext}$ remains nearly constant with increasing speed and has the same value both in the trot and a gallop (Fig. 8).

Despite the fact that $W_{ext} = f(V_f)$ and $W_{ext} = f(V_f)$ are the same in trotting and galloping, $W_{ext}$ is smaller at low speeds of the gallop as the result of the exchange between $E_p$ and $E_{kf}$ which we have already discussed. This leads to a discontinuity in the function $W_{ext} = f(V_f)$ when the dogs shift from a trot to a gallop.

**DISCUSSION**

Evolution seems to have been very conservative in designing vertebrate locomotory systems for moving along the ground. What at first seemed a bewildering array of modes of locomotion—bipedal walking in humans and in birds, quadrupedal walking in mammals, trotting, galloping and hopping—can all be reduced to two general mechanisms, a pendulum and a spring, which have been utilized either singly or in combination, to minimize the expenditure of chemical energy by the muscles for lifting and reaccelerating the center of mass within each stride. During walking, there is an alternate exchange between kinetic and gravitational potential energy. This exchange can be as large as 70% of the energy changes taking place as the center of mass rises and falls and accelerates and decelerates within each stride. Walking involves essentially the same mechanism in humans and in birds despite the fact that legs appear to bend in opposite directions. Quadrupeds walk as if they were simply two bipeds walking nearly synchronously, one behind the other. During running, trotting, and hopping, animals store energy in elastic elements as the center of mass decelerates simultaneously in the vertical and forward directions, and they recover some of this stored energy as it reaccelerates. Galloping involves a combination of the two mechanisms.

**Walking**

There is an optimal speed for walking in man at which the exchange between $E_p$ and $E_{kf}$ is maximal and both $W_{ext}$ and $W_{metab}$ (per kilometer) are minimal. The pendulum model is a good approximation of the mechanism of walking at this optimal speed (9). The mechanics of walking deviates from the pendulum model both at lower and higher speeds because of 1) the difference in the relative magnitude of $W_p$ and $W_f$, i.e., $W_p > W_f$ at the optimal speed, $W_p > W_f$ at lower speeds and $W_f > W_p$ at higher speeds; and 2) the phase relationship between $E_p$ and $E_{kf}$, which become more and more in phase as the walking speed increases. Man pushes off from the foot just before it leaves the ground and this tends to lift the center of mass. This push becomes larger at higher speeds, and $E_p$ and $E_{kf}$ become more and more in phase until there is almost no exchange between $E_p$ and $E_{kf}$ when walking speeds exceed 13 km·h⁻¹. However, man can still walk at speeds exceeding 18 km·h⁻¹.

We find that walking in our animals is essentially the same as that described for man. This similarity is most clearly seen in the birds. Using measurements of $V_0$, as a function of speed during walking in the rhea, we found a minimum $W_{metab}$ per kilometer where $W_{ext}$ per kilometer is also minimal (unpublished observations of C. R. Taylor). The push from the rear foot can be seen at high speeds as a second peak in the $F_r$ and $V_r$ records of the rhea and turkey (Fig. 1); this is almost identical to a secondary peak in the $F_f$ and $V_f$ records observed in man at high speeds of walking.

In conclusion, a pendulum model applies only at intermediate walking speeds; $E_{kv}$ is always small and can be converted into $E_{kf}$ therefore the simplest pendulum models—such as the stiff-legged walk of Alexander (1), which assumes that $W_{ext}$ is used to replace the $E_{kv}$ lost at each step—do not seem to explain walking in our animals or in man. $W_{ext}$ is done at each step of walking (see increments of $E_{total}$ in Fig. 2) to increase $E_p$ and/or $E_{kf}$ above the values attained by means of the described shift of kinetic into potential energy and vice versa. In other words $W_{ext}$ is used to complete the vertical lift and to give an additional push forward, thus keeping the "egg rolling."

**Running and Galloping**

$W_{metab}$ increases linearly with running and galloping speed in most animals from a positive $y$ intercept which is about 1.5-2.0 times $W_{metab}$ predicted for rest (21). $W_{metab}$ is used by muscles to provide mechanical power for locomotion. This power consists mainly of $W_{ext}$.
Mechanisms of terrestrial locomotion

\[ \approx |W_r| + |W_f| + W_{\text{int}} \] to accelerate the limbs relative to the center of mass. Both \( W_r = f(V_r) \), (Eq. 12), and \( W_{\text{int}} = f(V_r) \), (5), originate from zero and increase more and more steeply with increasing speed; they therefore cannot explain the positive \( y \) intercept of \( W_{\text{metab}} = f(V_r) \). \( W_{\text{int}} \) however, is about constant and does not go to zero at zero running speed; work against gravity has to be performed at about the same rate at low as well as high speeds (Fig. 8). This rate of working, required to start the mechanism of running, may help to explain the \( y \) intercept of the relationship between \( W_{\text{metab}} \) and \( V_r \).

The same argument can be seen in terms of the work done per unit distance, \( W_{\text{int}}/(L \cdot m) \) and \( W_f/(L \cdot m) \) increase while \( W_r/(L \cdot m) \) decreases with increasing speed (Fig. 8). Within the speed range of our experimental data the increase in \( W_r/(L \cdot m) \) and the decrease in \( W_r/(L \cdot m) \) approximately compensate for each other and \( W_{\text{ext}}/(L \cdot m) \) is approximately independent of speed in most of the animals. However, if we extrapolate these functions to lower speeds, \( W_{\text{ext}}/L - (W_r/V_r) \) would increase and tend to infinity when \( V_r \) approaches zero, because \( W_r \) is high also at the lowest speeds. This may help to explain the similar increase for \( W_{\text{metab}}/(L \cdot m) \) which has been observed in most animals at low speeds (21). The increase in \( y' \), which we find in most of our animals with increasing speed (Fig. 10), will also increase the \( y \) intercept in the relationship \( W_{\text{metab}} = f(V_r) \), i.e., it may also be important in explaining the increase in \( W_{\text{metab}}/(L \cdot m) \) at low speeds.

Values of \( y \) (Eq. 5), increasing linearly with \( V_r \), are also important in explaining the increase in \( W_{\text{metab}} \) and hence in \( V_f \).

On the other hand, the evidence of elastic recovery reached in the present paper could be invalidated by errors of measurement of 1) metabolic power minus resting metabolism: the metabolic measurements were made at different time and on a treadmill, whereas the mechanical power was measured during running on the floor; 2) mechanical power output: these can derive from both the methods used (3) and from irregularities of the run of the animals. In addition, the assumption that the maximal efficiency of the contractile component is 0.25 may be incorrect; and mechanical energy could be stored not in elastic elements but in some other unrecognized sites.

A preliminary account of part of this work was presented at the Symposium on Biodynamics of Animal Locomotion, Cambridge, England, September 1975.

Received for publication 28 October 1976

REFERENCES