EFFICIENCY OF VERTEBRATE LOCOMOTORY MUSCLES

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SUMMARY

We have examined the efficiency of vertebrate striated muscle at two
different organizational levels: whole animals and isolated muscles.
Terrestrial locomotion is used as a model of 'normal' muscular contraction;
animal size and running speed are used as independent variables in order to
change either the metabolic requirements of the muscles or the mechanical
power production by the muscles over a wide range of values. The weight-
specific metabolic power input to an animal increases nearly linearly with
speed and increases with decreasing body size, while the weight-specific
mechanical power output increases curvilinearly with speed and is
independent of size. Consequently, the efficiency of the muscles in producing
positive work increases with speed and the peak efficiency increases with
increasing body size, attaining values of over 70 % in large animals, but only
7 % in small ones. The isolated muscle experiments were performed on frog
muscle, and rat 'fast' and 'slow' muscles. We measured the work done, the
oxygen consumed during recovery from the stimulation, and calculated the
efficiency and the 'economy' (the cost of maintaining tension). The muscles
were made to: (i) emulate the contractions seen during locomotion, i.e.
shorten after a pre-stretch; or (ii) shorten at the same velocity and from the
same muscle length as in (i), but without the pre-stretch. It was found that in
mammalian muscles the peak efficiency with a pre-stretch attained high
values, approaching the peak efficiencies in large animals. The maximum
efficiency (attained at 1 length s^{-1} in fast muscle and at 0·5 lengths s^{-1} in slow
muscle) did not differ much in the two muscles, whereas economy was greater
in the slow muscle than in the fast muscle.

INTRODUCTION

In this paper we will examine the efficiency of vertebrate striated muscle during
terrestrial locomotion. First we will examine whole animal locomotion, then we will
review some recent experiments on isolated frog and rat muscle, and finally we will
conclude by looking at isolated muscles in the context of the whole animal in order to
speculate on how the muscles are used during a 'natural' activity such as locomotion.

But first a few words of caution: 'efficiency' is a word that can be found in
cookbooks, economic theories and treatise on thermodynamics; in order to have any

meaning, the word must be carefully defined in each context. In this paper we will use as our operational definition of efficiency:

$$\text{positive work efficiency} = \frac{\text{mechanical power output}}{\text{metabolic power input}}, \qquad (1)$$

where metabolic power input includes recovery (i.e. the initial heat plus the recovery heat, or their metabolic equivalent). This definition is correct when the muscle performs positive work only. In a more general definition of efficiency the denominator would be defined as the total power input (we will return to this point later in the paper). Also, we will define 'muscle' to include the tendons, i.e. the muscle, as used it in this paper, extends from origin to insertion.

WHOLE ANIMAL LOCOMOTION

In order to calculate the efficiency of locomotion in whole animals it is only necessary to measure the metabolic power input and the mechanical power output. We will use body size and speed of locomotion as independent variables in order to manipulate both the power input and the power output over a wide range of values.

Metabolic power input

Oxygen consumption is an accurate measure of the metabolic energy input to an animal provided the measurements are made during a metabolic 'steady state'. Measurements of steady state oxygen consumption have been made by a number of investigators: to date more than 62 avian and mammalian species over a size range of 7 g to 250 kg have been measured as they stood, walked, ran, hopped or galloped at a constant speed on a treadmill (Taylor, Heglund & Maloiy, 1982). With very few exceptions, it was found that the oxygen consumption rate increased linearly with increasing speed, and the mass-specific oxygen consumption rate (i.e. the metabolism per gram of animal) increased with decreasing body size. All of the data can be combined into one equation that can be used accurately to predict the metabolism of an animal just from the body size and the running speed. If we use an energetic equivalent of $20 \cdot 1 \text{ J ml}^{-1}$ of oxygen consumed (this is a good assumption because the net energy contribution of anaerobic glycolysis is nil during steady state) the equation becomes:

$$\dot{E}_{metab}/M_b = 10 \cdot 7 M_b^{-0 \cdot 316} V + 6 \cdot 03 M_b^{-0 \cdot 303}, \qquad (2)$$

where $\dot{E}_{metab}/M_b$ is in W kg^{-1}, V is in m s^{-1}, and M_b is in kg.

Mechanical power output

It may at first be difficult to understand what work is done by the muscles during steady speed locomotion on level ground. No work is being done to increase the

average kinetic energy of the body since the average speed is constant; and no work is done to increase the average potential energy of the body since the average height of the centre of mass is also constant. Work is done to overcome the resistance of friction; there is wind friction, friction against the ground, and friction within the body itself. The work required to overcome wind resistance has been calculated for humans, who present a relatively large frontal area to the air during running. Wind resistance accounts for less than 2 % of the total mechanical power output at $2 \cdot 8 \, \text{m s}^{-1}$, and less than 8 % at $8 \cdot 3 \, \text{m s}^{-1}$ (Heglund, 1979). No work is done against the ground unless the subject deflects the ground (such as running in sand) or slips. Frictional losses within the body mainly occur within the muscles. Antagonist muscles can do work on each other, but this appears to be relatively minor. (Alexander & Vernon, 1975, have calculated that this accounts for only about 15 % of the total positive work performed by a kangaroo hopping at $5 \cdot 5 \, \text{m s}^{-1}$.)

Most of the positive work of terrestrial locomotion involves: (i) maintaining the oscillations of the kinetic and potential energy of the centre of mass of the body as it goes up and down and accelerates and decelerates within each step; and (ii) maintaining the oscillations in kinetic energy of the limbs and other parts of the body relative to the centre of mass as they alternately move back and forth each step. Within each step the work done by the muscles to increase the instantaneous kinetic or potential energy of the body during a positive work phase is subsequently reabsorbed by the muscles during a negative work phase and either dissipated as frictional heat within the muscle or stored elastically for use during the positive work phase of the next cycle. We cannot determine what fraction of the energy absorbed during the negative work phase is dissipated as heat or is stored elastically.

The energy required to lift and reaccelerate the centre of mass for each step can be measured easily and accurately with a force platform (Cavagna, 1975). These measurements have been made on a variety of large (Cavagna, Heglund & Taylor, 1977) and small (Heglund, Cavagna & Taylor, 1982) birds and mammals walking, running, hopping and galloping at a wide range of speeds. The mass-specific positive muscular work, calculated as the sum of the increments in the total (kinetic plus potential) energy of the centre of mass, increases linearly with speed and appears to be independent of size. All of the data can be expressed by one equation which relates the rate at which this work must be performed to speed:

$$\dot{E}_{cm}/ \, M_b = 0 \cdot 685V + 0 \cdot 072, \qquad (3)$$

where $\dot{E}_{cm}/M_b$ is in W kg^{-1} and V is in m s^{-1}.

The energy required to maintain the oscillations in kinetic energy of the limbs and body segments relative to the centre of mass is measured by analysis of films taken of the animals as they run on a treadmill, along with information about the mass, location of the centre of mass, and the moment of inertia about the centre of mass for each of the limb and body segments (Fedak, Heglund & Taylor, 1982). The mass-specific positive muscular work, calculated as the sum of the increments in the total kinetic energy relative to the centre of mass, appears to increase curvilinearly with speed and

is independent of size. The equation which relates the rate at which this work is performed to speed is:

$$\dot{E}_{kc}/M_b = 0.478V^{1.53},\tag{4}$$

where $\dot{E}_{kc}/M_b$ is in $W\,kg^{-1}$ and V is in $m\,s^{-1}$.

The total positive mechanical power output can be calculated as the sum of the two components described above (Heglund, Fedak, Taylor & Cavagna, 1982):

$$\dot{E}_{tot}/M_b = 0.478V^{1.53} + 0.685V + 0.072,\tag{5}$$

where $\dot{E}_{tot}/M_b$ is in $W\,kg^{-1}$ and V is in $m\,s^{-1}$. Thus the total positive work of locomotion, expressed in mass-specific terms, is independent of size and increases curvilinearly with speed. The above analysis of the total power output has been somewhat simplified: for details concerning the assumptions about work reducing transfers of energy between E_{cm} and E_{kc}, and between the segments involved in the E_{kc} calculations see Heglund et al. 1982.

The efficiency of animal locomotion

The weight-specific metabolic power input to an animal increases linearly with speed and is much higher in smaller animals. In contrast, the positive mechanical power required during locomotion increases curvilinearly with speed and is independent of size of the animal. For example, if we compare a 30 g quail to a 100 kg ostrich moving at $3\,m\,s^{-1}$, we find that the quail is consuming oxygen per gram of tissue at a rate 15 times higher than the ostrich, but the two animals are doing work at about the same rate per gram of tissue. The ratio of the power output to the metabolism may be considered the positive work efficiency as defined by equation 1; we find that this efficiency increases with speed in all of the animals, and increases with increasing body size. The peak value measured in quail was 7 %, while that measured in humans and kangaroos was over 70 %.

This result is intriguing because it is not what any of the current models of animal locomotion would predict. Several questions need to be answered. (i) Why is the efficiency of the large animals so high? 70 % is unreasonably high in the light of the muscle experiments previously done by A. V. Hill and others, as discussed in the next section of this paper. (ii) Why is the efficiency of the small animals so low? Again, classical thought on this would predict a peak efficiency approaching 25 % for all animals. (iii) Why does the efficiency increase continuously with increasing running speed? Simply on the basis of the force-velocity curve the efficiency should be zero at zero shortening velocity (the work done is zero because the displacement is zero), attain a maximum at an intermediate shortening velocity, and then go back down to zero at the maximum shortening velocity (the work done is zero because the force is zero). The isolated muscle experiments will answer some of these questions, and raise new ones as well.

ISOLATED MUSCLE EXPERIMENTS

While it is conceptually easy to measure the metabolic power input and mechanical power output of animals over a relatively wide size range, we have little control over, and sometimes are not even able to measure, many other important variables concerning muscular efficiency. Isolated muscle experiments, on the other hand, allow us directly to control many of the parameters of interest (e.g. stimulation patterns, shortening velocity, etc.), often at the expense of other parameters (e.g. recruitment patterns of different fibres within a muscle, maintenance of the blood supply, etc.).

Relatively few measurements of efficiency have been made in isolated muscles; the energy input has always been calculated as the heat evolved by the muscle: efficiency = work/(work + heat) (Hill, 1939; Woledge, 1968; Gibbs & Gibson, 1972; Wendt & Gibbs, 1973). The peak efficiency determined in every case, excluding tortoise muscle, was less than 25 %.

In recent experiments we measured the mechanical efficiency in isolated frog sartorii, rat extensor digitorum longus (EDL, a primarily fast fibre muscle) and rat soleus (a primarily slow fibre muscle) by measuring the mechanical work done and the subsequent recovery oxygen consumption. The muscles, about the size of a paper match (so that oxygen diffusion is not a problem) were placed in a sealed glass chamber full of oxygenated saline. The muscles were connected to a force transducer at one end, and to an electronically controlled lever system at the other end. An oxygen electrode measured the decrease in the chamber P_{O_2}, from which the oxygen consumption could be calculated. A computer controlled the stimulation and length changes of the muscle; the work done could be calculated from the developed force and length changes of the muscle. In an effort to simulate the way muscles are used during locomotion, shortening was immediately preceded by stretching of the contracting muscle. In this situation part of the positive work done during shortening can be derived from mechanical energy stored in the muscle during the negative work phase (i.e. during stretching). For comparison, the efficiency was also measured during shortening under identical conditions, except that shortening occurred from a state of isometric contraction. This is a situation where only chemical energy can be the origin of the work done.

Shortening from a state of isometric contraction

The net weight-specific oxygen consumed per stimulus, the weight-specific work done per stimulus during shortening from an isometric contraction, and the efficiency of work production are shown as a function of contraction velocity in Fig. 1. In the sartorius both the oxygen consumption and the positive work appear to increase linearly with contraction velocity up to a speed of about $1 \cdot 0$ muscle length s^{-1}. The EDL oxygen consumption and work initially increase, then decrease with increasing speed. In the soleus the data are too few to describe a function, however oxygen consumption appears to be nearly independent of speed and the work appears to reach a maximum at intermediate speeds.

The oxygen consumption and work per stimulus decrease markedly from the sartorius to the EDL and from the EDL to the soleus, yet the efficiency differs much less. The efficiency increases to 25 % in the sartorius; it was not possible to obtain reliable data at speeds of contraction greater than $1 \cdot 5$ lengths s^{-1} because there was a redevelopment of tension at the end of the shortening. The peak efficiency in the EDL is about 19 %, occurring at a speed of shortening of $1 \cdot 0$ length s^{-1}. In the soleus the peak efficiency is about 15 % at $0 \cdot 5$ lengths s^{-1}.

Shortening after forcible stretching of the active muscle

The oxygen consumption of a muscle does not seem to be drastically affected by a pre-stretch, as shown in Fig. 2 (the dotted lines in Fig. 2 are redrawn from Fig. 1 for comparison). On the contrary, the pre-stretch had a marked effect on the work
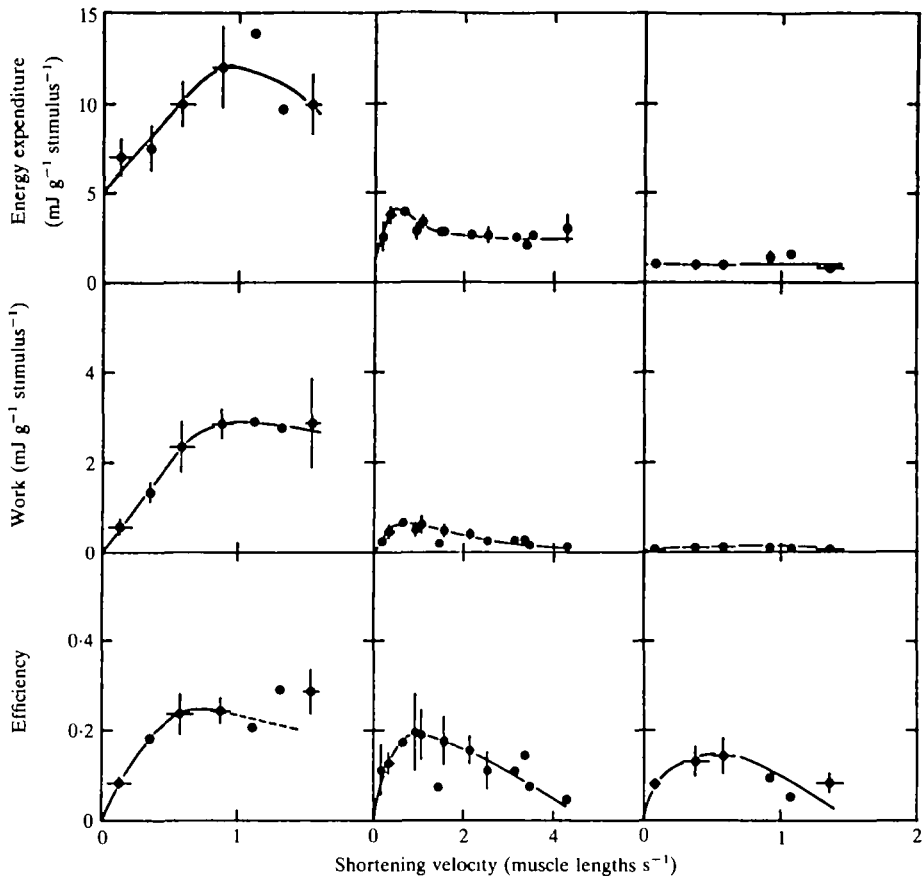

Fig. 1. Results of all the experiments done, with muscle shortening from a state of isometric contraction, in frog sartorius (left column), rat extensor digitorum longus (EDL) (middle column) and rat soleus (right column). The top row shows the energetic equivalent of the net oxygen consumed by the muscles, the second row shows the corresponding positive work done by the muscles and the bottom row shows the calculated efficiency, all as a function of shortening speed. The vertical and horizontal bars indicate the standard deviations of the points averaged. The lines were drawn by hand.

performed during the subsequent shortening in all three muscles. The average ratio of work performed after a pre-stretch to the work performed at the same contraction velocity but without a pre-stretch was 1·3 in the sartorius, 3·4 in the EDL and 3·2 in the soleus.

The positive work efficiency after a pre-stretch is much greater than that measured without a pre-stretch, attaining peak values of about 38 % in the sartorius, 50 % in the EDL and 40 % in the soleus. The peak efficiencies measured with and without a pre-stretch seem to occur at similar speeds of contraction. In the mammalian muscles, the positive work efficiency after a pre-stretch tends to remain relatively high at the high speeds of contraction; at the highest speeds measured, the ratio of the efficiency after pre-stretch to the efficiency without pre-stretch was about 6 in the EDL and 2 in the soleus.
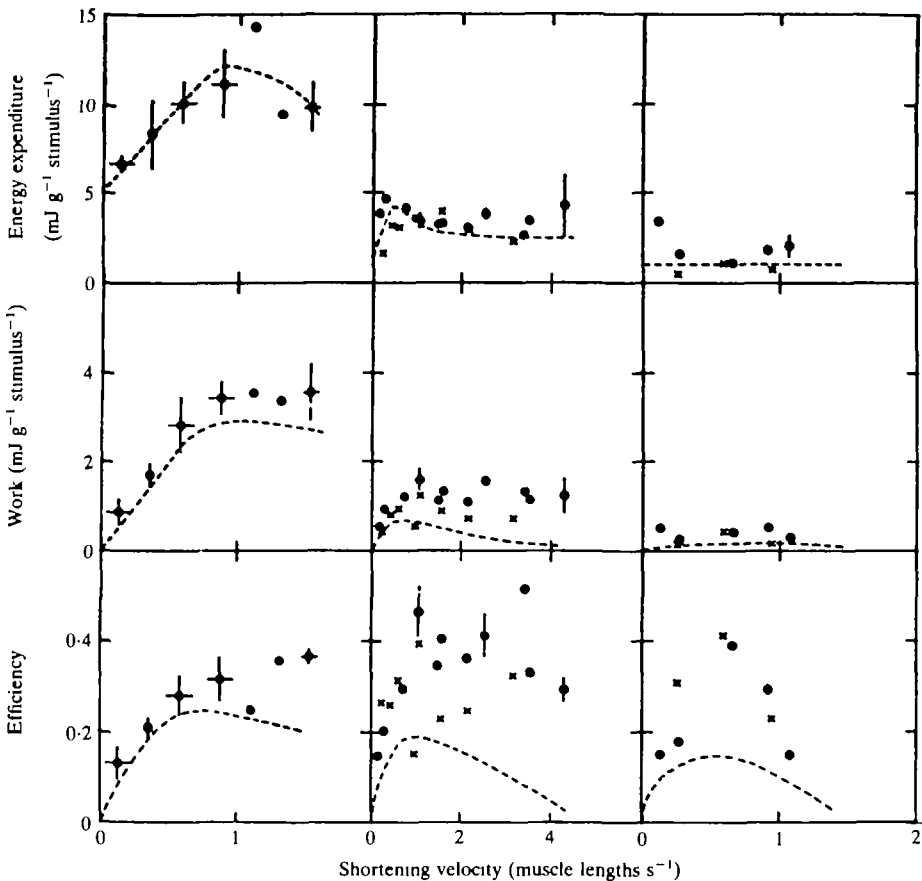

Fig. 2. Results of all the experiments done, with the muscle shortening immediately after a pre-stretch, in frog sartorius (left column), rat extensor digitorum longus (EDL) (middle column) and rat soleus (right column). The interrupted lines are copied from Fig. 1 and show the hand-drawn average values from the corresponding experiments with the muscle shortening from a state of isometric contraction. The crosses indicate experiments in which some isometric force was allowed to develop before the pre-stretch, and the dots indicate experiments in which the muscle was stretched after stimulation but before the development of any isometric force. Other indications as in Fig. 1.

Economy

The 'economy' of the EDL and soleus was measured in the experiments without a pre-stretch as the tension-time integral divided by the energetic equivalent of the net oxygen consumed. The soleus is about twice as economical as the EDL over the entire range of shortening speeds. These data allow us to make a distinction between muscles that are able to maintain tension economically (e.g. soleus), and muscles that are able to produce positive work (e.g. EDL). Slow muscle will be particularly suitable for postural needs, whereas fast muscle will be more efficient in maintaining tension over a greater displacement during shortening at a given speed.

Agreement with previous studies

The intercept of energy expenditure *vs* speed relationship in sartorius represents the energy expenditure during an isometric contraction; this value ($5 \cdot 73$ mJ g^{-1} stimulus^{-1}) is in good agreement with previous findings on the same muscle (Kushmerick & Paul, 1976; Chapman, Gibbs & Loiselle, 1982; Hill, 1972; Baskin, 1965).

The additional energy, above the isometric value, spent during shortening (Fenn effect) should be about twice the work done plus twice the shortening heat in the sartorius (assuming the recovery heat equals the initial energy output). The work done has been measured for each sartorius, and the shortening heat was calculated from the normalized *a* coefficient of 455 g cm^{-2} given by Abbott (1951) and the shortening distance for each muscle. The calculated values of additional energy are, on average, 20 % greater than the values actually measured.

Wendt & Gibbs (1973) and Gibbs & Gibson (1972) measured the efficiency of rat EDL and soleus at 27 °C with a myothermic technique. They found peak efficiency values of 9·5 % with 1-s tetani and 16 % with 0·5-s tetani in the EDL, and 18·5 % in the soleus. They conclude that the fast-twitch EDL muscle sacrifices energetic economy in return for speed of response. This conclusion is not supported by the present efficiency measurements, but is in agreement with our measurements of economy.

The increase in the efficiency due to a pre-stretch is greater in the mammalian muscles than in the sartorii. This may be due to: (a) a relatively greater compliance of the tendons of mammalian muscles (particularly of EDL), since a greater compliance will allow more mechanical energy to be stored during the stretch for a given increase of the force; and (b) the greater speeds of shortening attained in the experiments on mammalian muscle. In fact, contrary to the work done by the contractile component, the release of the mechanical energy stored during stretching is unaffected by the high speeds of shortening.

HOW ARE MUSCLES USED DURING LOCOMOTION?

The first of the three questions about whole animal locomotion that we wanted to answer in the isolated muscle experiments concerned the high peak efficiency in large

animals. Positive work efficiencies of > 0.7 were observed in man and kangaroo at high speeds of running and hopping, exercises in which the muscles shorten immediately after being forcibly stretched. The efficiencies measured in the isolated mammalian muscles approach these high values due to an increase in the positive work done after a pre-stretch. Clearly the mechanical energy stored within the muscle (tendons and cross-bridges) during the negative work phase can be recovered and used in the positive work phase.

The positive work efficiency, calculated using equation 1, ignores the contribution to the energy input of the muscle made by the absorption of mechanical energy during the negative work phase; as noted earlier, a proper definition of the overall efficiency of the animal would have the total energy input (metabolic plus mechanical) in the denominator of equation 1. In terrestrial locomotion the work done on the external environment (e.g. work done to overcome wind resistance, to deflect the ground, etc.) is small; if we assume it is zero, then the total negative muscular work done must be equal the total positive muscular work done. We have measured the total positive work done, so by rearrangement and substitution we can calculate the overall efficiency as:

$$\text{overall efficiency} = \frac{E'}{1 + E'},\qquad(6)$$

where E' is the efficiency as measured using equation 1. The overall efficiency measures the efficiency of the contractile engine and the efficiency of the energy storage and recovery; this results in a 'proper' peak efficiency of 6.5% in small animals and 41% in large animals.

We do not have a clear answer to the second question, concerning the low efficiency in small animals. However, our data on the economy of muscles comprised of slow contracting fibres (soleus) relative to muscles comprised of fast contracting fibres (EDL) may be at least part of the answer, since small animals have muscles of higher contraction velocity than the homonymous muscles of large animals. It could be that the cost of maintaining tension dominates the cost of locomotion in small animals. Efficiency, which is concerned with work production rather than force generation, may therefore not be a productive way of analysing the cost of locomotion. In this regard it is interesting to note that, over a wide range of speed, the metabolic energy consumption of mammalian muscle, as shown in Figs 1 and 2, is nearly independent of the speed of contraction, the presence or absence of a pre-stretch, or even the amount of work done; although it is very dependent upon the intrinsic velocity of the muscle (i.e. 'fast' *vs* 'slow' as discussed in many other papers in this volume). The paper by Taylor in this volume gives several predictions based on this 'cost of maintaining tension' to the cost of terrestrial locomotion.

The final question asked on the basis of the whole animal experiments concerned the means by which the efficiency was maintained at high levels even at the highest speeds of locomotion; in fact in all animals studied, the peak efficiency occurred at the highest running speeds. The present experiments show that previous stretching of the contracting muscle is the only way to maintain a high efficiency during high speeds of

shortening. In the EDL, for example, at shortening speeds sufficient for the efficiency measured without a pre-stretch to drop nearly to zero (5 lengths s^{-1}), the efficiency measured after a pre-stretch remains higher than even the peak efficiency measured with no pre-stretch (Fig. 2).

REFERENCES

ABBOTT, B. C. (1951). The heat production associated with the maintenance of a prolonged contraction and the extra heat produced during large shortening. *J. Physiol., Lond.* 112, 438–445.

ALEXANDER, R. McN. & VERNON, A (1975). The mechanics of hopping by kangaroos (*Macropodidae*). *J. Zool., Lond.* 177, 265–303.

BASKIN, R. J. (1965). The variation of muscle oxygen consumption with load. *J. Physiol., Lond.* 181, 270–281.

CAVAGNA, G. A. (1975). Force platforms as ergometers. *J. appl. Physiol.* 39, 174–179.

CAVAGNA, G. A., HEGLUND, N. C. & TAYLOR, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* 233, R243–R261.

CHAPMAN, J. B., GIBBS, C. L. & LOISELLE, D. S. (1982). Myothermic, polarographic, and fluorometric data from mammalian muscles. *Fedn Proc. Fedn Am. Socs exp. Biol.* 41, 176–184.

FEDAK, M. A., HEGLUND, N. C. & TAYLOR, C. R. (1982). Energetics and mechanics of terrestrial locomotion. II. Kinetic energy changes of the limbs and body as a function of speed and body size in birds and mammals. *J. exp. Biol.* 97, 57–66.

GIBBS, C. L. & GIBSON, W. R. (1972). Energy production of rat soleus muscle. *Am. J. Physiol.* 223, 864–871.

HEGLUND, N. C. (1979). Size scaling, speed and the mechanics of locomotion. Ph.D. thesis, Harvard University, Cambridge, MA.

HEGLUND, N. C., CAVAGNA, G. A. & TAYLOR, C. R. (1982). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. exp. Biol.* 97, 41–56.

HEGLUND, N. C., FEDAK, M. A., TAYLOR, C. R. & CAVAGNA, G. A. (1982). Energetics and mechanics of terrestrial locomotion. IV. Total mechanical energy changes as a function of speed and body size in birds and mammals. *J. exp. Biol.* 97, 57–66.

HILL, A. V. (1939). The mechanical efficiency of frog's muscle. *Proc. R. Soc. B* 127, 434–451.

HILL, D. K. (1972). Resting tension and the form of the twitch of rat skeletal muscle at low temperature. *J. Physiol., Lond.* 221, 161–171.

KUSHMERICK, M. J. & PAUL, R. J. (1976). Aerobic recovery metabolism following a simple isometric tetanus in frog sartorius muscle at 0°C. *J. Physiol., Lond.* 254, 693–709.

TAYLOR, C. R., HEGLUND, N. C. & MALOIY, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. exp. Biol.* 97, 1–21.

WENDT, I. R. & GIBBS, C. L. (1973). Energy production of rat extensor digitorum longus muscle. *Am. J. Physiol.* 224, 1081–1086.

WOLEDGE, R. C. (1968). The energetics of tortoise muscle. *J. Physiol., Lond.* 197, 685–707.