SCALING OF MUSCLE FIBRES AND LOCOMOTION

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Summary

To reconcile the scaling of the mechanics and energetics of locomotion to recent data on the scaling of the mechanics of muscle fibres, I have extended the theory of Taylor and colleagues that the energetic cost of locomotion is determined by the cost of generating force by the fibres. By assuming (1) that the cost of generating force in a fibre is proportional to V_{max} (maximum velocity of shortening) and (2) that, at physiologically equivalent speeds, animals of different body sizes recruit the same fibre types, this extension quantitatively predicts the scaling of the energetics of locomotion, as well as other observations, from the scaling of V_{max} of the muscle fibres. First, the energetic cost of locomotion at physiologically equivalent speeds scales with $M_b^{-0.16}$, where M_b is body mass, as does V_{max} of a given fibre type. However, the energetic cost at absolute speeds (cost of transport) scales with $M_b^{-0.30}$, because small animals must compress their recruitment order into a narrower speed range and, hence, recruit faster muscle fibre types at a given running speed. Thus, it costs more for small animals to move 1 kg of their body mass 1 km not only because a given muscle fibre type from a small animal costs more to generate force than from a large one, but also because small animals recruit faster fibre types at a given absolute running speed.

In addition, this analysis provides evidence that V_{max} scales similarly to $1/t_c$ (where t_c is foot contact time) and muscle shortening velocity (V), in agreement with recent models. Finally, this extension predicts that, at physiologically equivalent speeds, the weight-specific energetic cost per step is independent of body size, as has been found empirically.

Introduction

Over the past 20 years, Taylor and colleagues have examined how the energetics and mechanics of locomotion scale with body size in mammals. They found that although the weight-specific mechanical power used for running is independent of body size (Heglund *et al.* 1982), the energetic cost to move a gram of tissue a given distance scales with $M_b^{-0.30}$ (Taylor *et al.* 1982). Load-carrying experiments led Taylor *et al.* (1980) to postulate that the energetics of locomotion depended on force generation by the muscles. They further proposed that the increased energetic cost of locomotion in small animals is due to the increased cost of

generating force in their fibres, which in turn is associated with their higher maximum velocity of shortening (V_{max}).

If this theory is correct, then we should be able to predict the scaling of whole-animal energetics from that of isolated muscle fibres. The paucity of data on the scaling of muscle properties with body size prevented quantitative testing of this theory in the past. With recent information on the scaling of muscle properties with body size (Rome *et al.* 1990; Altringham and Young, 1991), we can begin to test this hypothesis.

Theory

The hypothesis of Taylor *et al.* (1980) (Taylor's hypothesis) is formally stated in equation 1.

$$\dot{E} = \bar{F}_{muscle} \times \text{cost of generating force} \times \text{average fibre length}, \tag{1}$$

where $\dot{E}$ is metabolic rate during running (watts), $\bar{F}$ is average muscle force (newtons), cost of generating force is given per unit length (watts per newton metre) and average fibre length is given in metres. According to Biewener (1989*a*), because small animals have a more crouched posture (and thus lower effective mechanical advantage) than large ones, they must generate greater weight-specific forces to support their body weight. Hence,

$$\bar{F}_{muscle} = M_b^{-0.26} \times \bar{F}_{ground} \times \text{constant}. \tag{2}$$

However, Alexander *et al.* (1981) found that the fibres in small animals tend to be shorter than in large ones. Fibre length in proximal muscles scaled with $M_b^{0.30}$, whereas fibre length in distal muscles scaled with $M_b^{0.17}$. Thus, weighting the two exponents by relative muscle mass gives:

$$\text{average fibre length} = M_b^{0.27} \times \text{constant}. \tag{3}$$

When equation 1 is rewritten in terms of ground forces (equation 4), the scaling exponents in equation 2 and equation 3 reduce to $M_b^{\approx 0}$, thereby cancelling the size-dependent effects associated with differences in posture.

$$\dot{E} \propto \bar{F}_{ground} \times \text{cost of generating force} \times \text{constant}. \tag{4}$$

Because the average ground force equals body weight (W_b), this can be rewritten as:

$$\frac{\dot{E}}{W_b} \propto \text{cost of generating force} \times \text{constant}. \tag{5}$$

Taylor *et al.* (1982) have shown that:

$$\frac{\dot{E}}{W_b \times S} \propto M_b^{-0.30} \times \text{constant}, \tag{6}$$

where S is running speed. Substituting equation 5 into equation 6 gives:

$$\text{Cost of generating force} \propto M_b^{-0.30} \times S. \tag{7}$$

Thus, although the cost of generating force increases with running speed, at a given absolute running speed, the cost of generating force simply scales with $M_b^{-0.30}$.

Formally, the cost of generating force is a function of where on the force–velocity curve the muscles are operating (i.e. V/V_{max}; where V is shortening velocity during locomotion). As V increases, force decreases but the rate of ATP splitting increases, so that when V equals V_{max}, the cost of generating force is infinite. For this treatment, however, we assume that the cost of generating force is that during isometric contractions ($V=0$). This assumption is made for a number of reasons. First, it is probably a good approximation. During locomotion, muscle performs both shortening contractions (in which the cost of generating force is higher than during isometric contractions) and lengthening contractions (in which the cost of generating force is lower than during isometric contractions). Second, with the information available we cannot calculate the energetics of muscles during locomotion any more accurately. There is no information on V/V_{max} in mammals during lengthening and shortening (as there is in fish, Rome *et al.* 1988) and, even if there were, there is very little information on the energetics of lengthening muscle. Third, Alexander's (1991) analysis (based on a number of assumptions) concludes that the energetic cost of the muscle performing the contractions during locomotion is likely to be a constant multiple of the cost of generating force during isometric contractions. Hence, if energetic cost during *isometric* contractions underestimates the cost during locomotory contractions, it would do so by a constant which is *scale-independent*. Finally, the cost of generating *isometric* force can be approximated by using the Huxley (1957) model (see below) and can be measured in skinned fibres over a wide range of animal size (as suggested in Rome *et al.* 1990).

Although, there is no information on how the cost of generating force in isolated fibres scales with M_b, Rome *et al.* (1990) have recently found that V_{max} of the slow oxidative (SO, type I) fibres scales with $M_b^{-0.18}$ and that of fast glycolytic fibres (FG, type IIb) scales with an even smaller exponent ($M_b^{-0.07}$) (N.B. a given fibre type is qualitatively similar in small and large animals in *relative* V_{max}, order of recruitment and aerobic capacity, but differs quantitatively in such parameters as V_{max}). Thus, V_{max} of a single fibre type scales with a smaller exponent than does the cost of generating force during locomotion (Rome *et al.* 1990). This quantitative discrepancy in the scaling exponents seems puzzling because from a theoretical viewpoint (see below) one might anticipate that the cost of generating force in isolated fibres is proportional to V_{max}. Explaining this discrepancy thus presents a further challenge for Taylor's hypothesis (equation 1).

Do V_{max} and the cost of generating force in isolated fibres scale differently?

The simplest explanation of the apparent discrepancy noted above is that the cost of generating force simply increases more rapidly than V_{max} in isolated fibres. The empirical evidence is equivocal on this point. There is some empirical evidence supporting the disproportionate increase in the cost of generating force

compared to V_{max} (frog vs tortoise muscle, Woledge, 1968; Q_{10} values of V_{max} and the cost of generating force in frog fibres, Rome and Kushmerick, 1983), but there is also empirical evidence suggesting that the cost of generating force and V_{max} scale similarly (mouse soleus vs EDL, Crow and Kushmerick, 1982, 1983).

From a theoretical analysis based on the Huxley (1957) model of crossbridge dynamics, it is likely that the cost of generating force scales similarly to V_{max}. In this analysis, the rate of crossbridge attachment is $f(1-n)$ and the rate of crossbridge detachment is gn, where f is the attachment rate constant, g is the detachment rate constant, and n is the proportion of attached crossbridges.

Huxley's model shows that:

$$V_{max} \propto g. \tag{8}$$

If we assume that the force per crossbridge during isometric contractions is independent of fibre V_{max}, then force is proportional to the number of attached crossbridges (n). In a steady state, the rate of crossbridge attachment equals the rate of crossbridge detachment [i.e. $f(1-n)=gn$]. Thus, solving for n, gives:

$$\text{Force} \propto \frac{f}{(f+g)}. \tag{9}$$

If we assume that one ATP is split for each crossbridge undergoing an attachment–detachment cycle, then the rate of ATP splitting at steady state will be equal to the rate at which crossbridges are detaching (gn). Substituting equation 9 for n, gives:

$$\text{ATP} \propto \frac{fg}{f+g}. \tag{10}$$

It is not known whether f changes in proportion to g as fibre V_{max} increases. This would be a necessary condition to keep the force constant (which it appears to be, Rome $et\ al.$ 1990) and for the ATP turnover rate to increase in proportion to V_{max}. However, because the cost of generating force is the ratio of equation 10 to equation 9, this will reduce mathematically to:

$$\frac{\text{ATP}}{\text{force}} \propto g. \tag{11}$$

Hence, irrespective of how f changes with g, the cost of generating force is proportional to g (and thus to V_{max}). Although the above analysis is fairly convincing, this treatment of the Huxley (1957) model is oversimplified. Detachment rate, g, is a function of crossbridge position and average crossbridge position depends on shortening velocity (Huxley, 1957). The g while shortening at V_{max} (equation 8) will be faster than the g at isometric conditions (equation 11). It is reasonable to suppose that $g_{isometric}/g_{V_{max}}$ will be the same in fibres with different values of V_{max}, but this is unproved. Hence, further empirical evidence is necessary to support the similarity of the scaling exponents and exclude the possibility that the cost of generating force in isolated fibres scales differently from V_{max}.

How can the cost of generating force during locomotion scale differently from
V$_{max}$ of a single fibre type if they scale similarly in isolated fibres?

The difference between the exponents for V_{max} of a single fibre type and the cost of generating force *during locomotion* seems paradoxical *only* because of the implicit assumption that *the same muscle fibre types are recruited at a given absolute speed in both small and large animals*. Only in this case would there be the expectation that the scaling exponent from a particular muscle fibre type should agree with the scaling exponent for the cost of generating force (or cost of transport) in locomoting animals. This assumption, however, seems unlikely. Fibres are recruited in a fixed order (Henneman *et al.* 1965) and, as speed increases, animals recruit faster fibre types (Rome *et al.* 1984). Because large animals can run faster than small ones (at least over much of the size range), it seems inevitable that the small animals will go through their recruitment order at a slower running speed.

Although muscle recruitment in mammals has not been measured as a function of running speed, it is reasonable to expect that animals cannot sustain exercise intensities where there is a significant recruitment of anaerobic fibres. Maximum sustainable galloping speed (where presumably all aerobic fibres are recruited) scales with $M_b^{0.17}$ (e.g. $3.1\,\mathrm{m\,s^{-1}}$ in rats and $11\,\mathrm{m\,s^{-1}}$ in horses as in Fig. 1A; calculated from Heglund and Taylor, 1988). Thus, small animals must recruit their aerobic fibre types (SO and fast oxidative glycolytic, FOG) over a smaller running speed range and, thus, their recruitment order will be effectively 'compressed' into a narrower range of locomotion speeds (as has been previously reported in cold fish *vs* warm ones, Rome *et al.* 1984). Hence, at a given running speed, the small animal will have to recruit faster fibre types than the large animal, as illustrated in Fig. 1A. This means that, when measuring $\dot{E}$ at a given *absolute* running speed (e.g. $3.1\,\mathrm{m\,s^{-1}}$), we might be comparing the cost of generating force (and V_{max}) of FOG fibres in the small animal (rat) with the cost of generating force (and V_{max}) of SO fibres in the large animal (horse). This would result in a larger difference in the cost of generating force (and V_{max}) between the large and small animal than would be given by the scaling exponent for a single fibre type (Fig. 1B), and hence potentially explain the discrepancy in scaling exponents between the cost of generating force during locomotion and V_{max} of a single fibre type.

If this explanation is correct, then if we extend Taylor's hypothesis to assume (1) that at physiologically equivalent speeds, the same muscle fibre types will be used in small and large animals, and (2) that the cost of generating force is proportional to V_{max}, then at a physiologically equivalent speed, the following equation should hold:

$$\frac{\dot{E}}{W_b} \propto M_b^{\approx -0.18}, \tag{12}$$

where -0.18 is the approximate scaling exponent for V_{max} of a single aerobic fibre type. This prediction is supported by measurements of energetics at physiologically equivalent speeds. Although $\dot{E}$ has not been reported specifically at
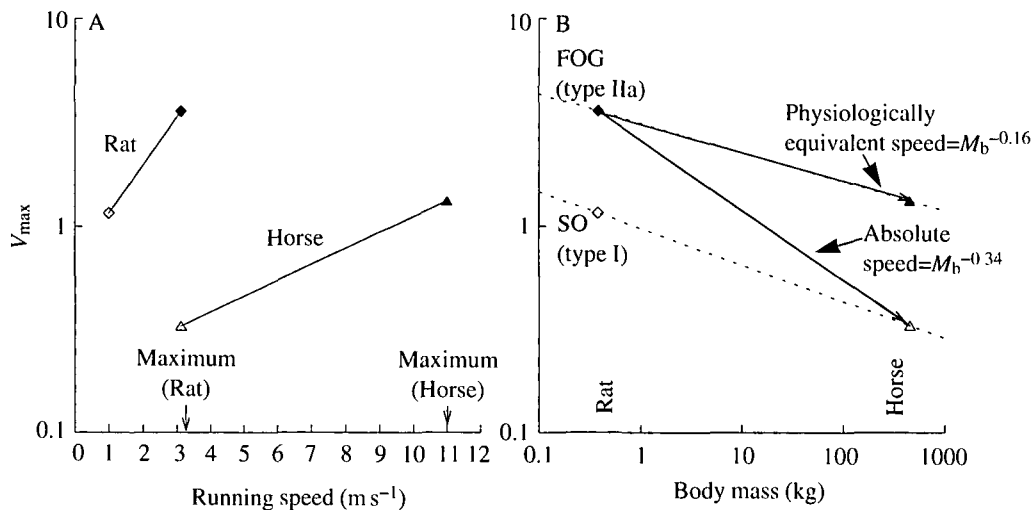
Fig. 1. How compression of recruitment order in small animals influences scaling of the energetics of locomotion. (A) A schematic representation of recruitment of different fibre types (open symbols=SO, closed symbols=FOG) as a function of running speed in the rat (diamonds) and the horse (triangles). The V_{max} values for each fibre type (data from Eddinger *et al.* 1986; Rome *et al.* 1990) have been measured from skinned fibres at 15 °C except for the rat FOG, which is calculated from the V_{max} of rat FG data. This figure demonstrates five points. First, at physiologically equivalent speeds, the animals use the same fibre types. Thus, at the maximum sustainable galloping speed (3.1 m s^{-1} in rats, 11 m s^{-1} in horses), all aerobic (SO and FOG) fibres are recruited. Second, the physiologically equivalent speed occurs at a much higher running speed in large animals than in small ones (e.g. maximum sustainable galloping speeds are 11 m s^{-1} and 3.1 m s^{-1} for the horse and rat, respectively; calculated from Heglund and Taylor, 1988). Third, the recruitment order is therefore compressed into a slower range of running speeds in the small animal. Fourth, at an absolute running speed, the small animal will be recruiting faster fibre types. For instance at 3.1 m s^{-1}, the horse is probably using only slow fibres (SO) as this is close to its minimal trotting speed (Heglund and Taylor, 1988). Fifth, V_{max} increases more rapidly with running speed in the small animal than in the large one, in a similar fashion to the way $1/t_c$ does. B shows how V_{max} of SO and FOG fibres scale with M_b. If one measures $\dot{E}$ at physiologically equivalent speeds (i.e. maximum sustainable galloping speed), then the animals would be using the same fibre types. Hence the V_{max} and the cost of generating force in the fibres being *utilized* would scale the same as V_{max} of the FOG fibres ($M_b^{\approx -0.16}$). This agrees with how $\dot{E}$ of animals running at physiologically equivalent speeds scale. If $\dot{E}$ is measured at an absolute speed, such as 3.1 m s^{-1}, then the rat would be using both its FOG and SO fibres, but the horse at this speed will be using only its SO fibres. Thus, we would be comparing the mechanics and energetics of the FOG fibres in the rat to that of SO fibres in the large animals. This would give an equivalent scaling exponent of $M_b^{\approx -0.34}$ for the cost of generating force and V_{max} of the *recruited* fibres, which is close to the scaling exponent for $\dot{E}$ at absolute running speeds.

physiologically equivalent speeds, it can be back-calculated from the reported findings that the cost per step is independent of body size at physiologically equivalent speeds (such as the trot–gallop transition and maximum sustainable

galloping) and that stride frequency at a physiological speed scales with $M_b^{-0.16}$ (Heglund and Taylor, 1988). Thus, as found by Biewener (1989*b*):

$$\frac{\dot{E}}{W_b} \propto \text{stride frequency} \times \text{cost per step} = M_b^{-0.16} \times \text{constant}. \tag{13}$$

The fact that the scaling exponent for $\dot{E}$ is nearly the same as that for V_{max} of SO fibres supports this extension of Taylor's hypothesis. It is worth noting that one obtains similar results no matter which 'physiologically equivalent speed' is considered, but that different physiologically equivalent speeds may reflect different design constraints (R. McN. Alexander, personal communication). For instance, Alexander and Jayes (1983) have shown a mechanical basis for the trot–gallop transition, whereas maximum sustainable performance is, at least in part, a reflection of an animal's metabolic capacity. We use maximum sustainable galloping speed throughout this discussion because it gives a better estimation of the cost of transport and provides a more obvious endpoint of muscle fibre recruitment.

This extension, however, must also explain why the cost of transport scales with $M_b^{-0.30}$. It should be noted that the $\dot{E}$ at maximum sustainable galloping speed described in equation 12 and equation 13 occurs at a much faster *absolute* running speed in large animals than in small ones ($M_b^{0.17}$; Heglund and Taylor, 1988; e.g. $11\,\text{m}\,\text{s}^{-1}$ in horse *vs* $3.1\,\text{m}\,\text{s}^{-1}$ in rat; Fig. 1A). Hence, dividing the $\dot{E}$ at maximum sustainable galloping speed (equation 13) by the absolute running speed at which this occurs, approximates the cost of transport:

$$\frac{\dot{E}}{W_b \times S} \propto \frac{M_b^{-0.18}}{M_b^{0.17}} \times \text{constant} = M_b^{-0.35} \times \text{constant}. \tag{14}$$

This scaling exponent is similar to that measured for the cost of transport ($M_b^{-0.30}$, equation 6). It should be noted that the scaling exponent may be somewhat smaller for FOG fibres than for SO fibres (-0.18; Rome *et al.* 1990; Altringham and Young, 1991). If so, than this would result in better agreement between V_{max} and both the $\dot{E}$ at a physiologically equivalent speed and the cost of transport.

Finally, this extension of Taylor's hypothesis is consistent with Kram and Taylor's (1990) recent finding that:

$$\frac{\dot{E}}{W_b} \propto \frac{1}{t_c} \times \text{constant}, \tag{15}$$

where t_c is foot contact time (t_c decreases with increasing running speed because stride frequency increases but duty factor remains constant). Equation 15 not only empirically defines the scaling of $\dot{E}/W_b$ of animals of different sizes, but empirically defines how $\dot{E}/W_b$ increases with increasing running speed in a given animal. Although the relationship between tension rise during locomotion and V_{max} is too complex to approach by the Huxley (1957) model, there is some

empirical evidence to suggest that V_{max} would be proportional to $1/t_c$ (Stevens and Renaud, 1985). If so, then $1/t_c$ can be viewed as a mechanical correlate of V_{max} of the fibres that are active. Hence, at physiologically equivalent speeds, $1/t_c$ should scale as V_{max} (i.e. as $M_b^{-0.18}$). Back-calculating from $1/t_c = S/l_c$, where l_c is stride length (Kram and Taylor, 1990), gives good agreement ($M_b^{-0.14}$), thus supporting this notion. A similar approach to that used in equation 14 shows that V_{max} and $1/t_c$ also increase similarly with increasing running speed in animals of different body size. Thus, the fact that $1/t_c$ increases much more rapidly with running speed in small animals than in large ones supports the hypothesis that small animals go through their range of V_{max} values over a smaller speed range (compress recruitment order), thus producing a steeper slope of V_{max} of recruited fibres vs running speed (as in Fig. 1A).

Alexander (1991) suggests that it might be more important for V_{max} to scale as V rather than to scale as $1/t_c$, to maintain a constant V/V_{max} for maximum efficiency as Rome et al. (1988) have shown to occur in fish. However, it seems possible that both V and $1/t_c$ scale similarly, and that V_{max} scales appropriately for both. Lindstedt et al. (1985), by a combination of anatomical and physiological analyses, showed that the absolute length (Δl) by which knee extensors shorten scales with $M_b^{0.26}$. Because the muscle fibres in small animals are shorter than in large animals (equation 3), the strain ($\Delta l/$fibre length) should be approximately scale-independent (depending on exact fibre architecture), and hence V, at both physiologically equivalent and absolute running speeds, should scale as stride frequency (as does $1/t_c$ and V_{max}).

Discussion

This extension of Taylor's hypothesis explains from first principles why the cost of transport has a larger scaling exponent than for V_{max} in a single fibre type, while $\dot{E}$ at physiologically equivalent speeds and V_{max} in a single fibre type have similar scaling exponents. Thus, it provides strong support for Taylor et al.'s (1980) original hypothesis that the energetic cost of locomotion is determined by the cost of generating force in the fibres. Further, this treatment recognizes that the recruitment order in small animals is probably compressed into a narrower speed range than in large ones. Thus, it costs more for small animals to move 1 kg of their body mass 1 km not only because a given muscle fibre type from a small animal costs more to generate force than from a large one, but also because small animals recruit faster fibre types at a given absolute running speed (Fig. 1).

Finally, this extension of Taylor's hypothesis, unlike previous papers (Heglund and Taylor, 1988), affords no special significance to the constancy of the cost per step at physiologically equivalent speeds, because it can explain the scaling of the energetics of locomotion without invoking it. It has been suggested that the constant cost per step is a basic property of locomotion and it costs small animals more to run at a given speed because they must take more steps and incur more cost associated with turning their muscles on and off (Heglund and Taylor, 1988).

Although, mathematically, the cost per step is constant, it is simply explained by this extension of Taylor's hypothesis:

$$\frac{E}{W_b \times step} \propto \frac{\int F dt}{W_b \times step} \times cost\ of\ generating\ force$$

$$\propto \frac{1}{M_b^{-0.16}} \times M_b^{-0.18} = M_b^{\approx 0}. \quad (16)$$

The weight-specific tension–time integral per step $[\int F dt/(W_b \times step)]$ is simply proportional to $1/(stride\ frequency)$, because $\int F dt/step = W_b/(stride\ frequency)$ (N.B. stride frequency scales with $M_b^{-0.16}$; Heglund and Taylor, 1988). However, the cost of generating force increases in proportion to stride frequency (equation 12), and hence the product of the two terms is a constant.

To test this extension of Taylor's hypothesis further, it is necessary to test the new assumptions on which it is based. One must determine scaling of the cost of generating force and V_{max} with body size and determine the running speed of recruitment of different fibre types in mammals. As suggested by Alexander (1991), it would also be useful to compare the energetics of muscle undergoing lengthening and shortening contractions to the isometric case.

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